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# Assessment of risk to native *Frankenia* shrubs from an Asian leaf beetle, *Diorhabda elongata deserticola* (Coleoptera: Chrysomelidae), introduced for biological control of saltcedars (*Tamarix* spp.) in the western United States

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**Abstract**

Exotic saltcedars, *Tamarix* spp. (Tamaricaceae: Tamaricales) from Central Asia and the Mediterranean area, have invaded much of the western United States, where they degrade natural riparian areas, reduce water supplies, and interfere with agriculture and recreation. The major taxa are *Tamarix ramosissima* Ledeb., *Tamarix chinensis* Lour., and hybrids with these and *Tamarix canariensis* Willd. throughout much of the West, and *Tamarix parviflora* DC. in parts of California. The biology and host range of the leaf beetle, *Diorhabda elongata* Brullé subspecies *deserticola* Chen from Central Asia, indicate that it is a safe and potentially effective biological control agent. Here we report that species of the somewhat related native North American shrubs, *Frankenia* spp. (Frankeniaceae: Tamaricales), appear to be at little risk from the introduction of *Diorhabda elongata deserticola*. In laboratory, greenhouse, and outdoor cages at Temple, Texas and Albany, California, 0–27% of larvae were able to complete their development on four North American species of *Frankenia* compared to 53–56% on *Tamarix* host species, depending on the species tested and the growing conditions of the plants. However, adults were not attracted to, did not feed upon, and rarely laid eggs on *Frankenia* spp. Forced closer contact with *Frankenia* in smaller cages and even removing all *Tamarix* host plants did not increase adult selection of *Frankenia* plants nor oviposition on them. Adults from larvae reared on *Frankenia* did not show adaptation to nor increased utilization of the plant, compared to those reared on *Tamarix*. *D. e. deserticola*, therefore, appears sufficiently host-specific for field release in North America. Published by Elsevier Science (USA).

*Keywords:* *Diorhabda elongata deserticola*; Saltcedar; *Frankenia*; *Tamarix*; Weeds; Classical biocontrol; Insect host range; Biocontrol nontarget impacts; Riparian ecosystems

## 1. Introduction

Exotic, invading saltcedars, *Tamarix* spp. (family Tamaricaceae: order Tamaricales), are deciduous shrubs or small trees from the Old World that are causing great damage to western riparian areas. They displace native plant communities, degrade wildlife habitat including that of many endangered species, use great quantities of water which reduces stream flow and groundwater levels, increase wildfires and soil salinity, and reduce agricultural production, and recreational usage of infested areas (reviewed by DeLoach et al., 2000, 2003). Although some 10 species of *Tamarix* have been introduced into the United States, the most damaging species are *Tamarix ramosissima* Ledebour, *Tamarix chinensis*

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Loureiro, and hybrids between them and with *Tamarix canariensis* Willdenow throughout much of the west, and *Tamarix parviflora* de Candolle and its hybrids in parts of California. The other six introduced species occur mostly in the southeastern states as minimally naturalized, escaped ornamentals (Baum, 1978; Crins, 1989; Gaskin and Schaal, 2002).

Most taxonomists place the Tamaricaceae with the Frankeniaceae as a two-family group that constitutes the order Tamaricales (Rusanov, 1949; Spichiger and Savolainen, 1997). The Frankeniaceae is a small family of four genera and ca. 90 species of small halophytic shrubs or herbs of mostly temperate distribution (Whalen, 1980, 1987). The largest group of *Frankenia* species occurs in Australia and several species occur in the Mediterranean area; one species is found more or less continuously from Europe to Central Asia and through Africa to the Cape of Good Hope (Good, 1974). Eight species occur in southern South America (Chile, Argentina, southwestern Bolivia, and the southernmost tip of Peru), one of which, *Frankenia salina* (Molina) I.M. Johnson, has conspecific populations in Central and North America (Whalen, 1980). *Frankenia* is the largest genus and the only genus of the family that is native in the Western Hemisphere. The six species that are native to North America are the only plants here that are somewhat closely related to *Tamarix*.

Whalen (1980, 1987) recognized six North American species of *Frankenia* that occur mostly in desert areas of the southwestern United States and northern Mexico. In the *chilensis* group are two species, *F. salina* from California and Baja California, one location in Sonora and two in Coahuila, and in Chile; and *Frankenia johnstonii* Correll from southern Texas and Nuevo Leon. In the *jamesii* group are *Frankenia jamesii* Torrey ex. A. Gray from the Trans-Pecos region of Texas, and from New Mexico and Colorado; *Frankenia palmeri* S. Watson from Baja California and coastal Sonora; *Frankenia gypsophila* I.M. Johnston from Nuevo Leon and adjacent areas of Zacatecas and San Louis Potosi; and the closely related *Frankenia margaritae* F. Gonzales Medrano known only from the type locality in Nuevo Leon. One species, *F. johnstonii*, grows on arid rocky hillsides and was known only from four locations in south Texas when it was listed as a Federal endangered species in 1984; however, it is now known from over 50 locations in that area and it could be proposed for delisting.

*Frankenia salina* is a common floral component in alkali sinks in the desert and also in salt marshes along coastal areas and in riparian areas inland in southwestern North America. The inland populations formerly were designated as *Frankenia grandifolia* Cham. and Schlecht. var. *campestris* and the coastal populations as *F.g.* var. *grandifolia*, which differ slightly in morphology (Whalen, 1980). None of the North American *Frankenia* species are of economic or of exceptional ecological importance, i.e., they are not dominant species in any plant communities and no species of vertebrates are known to depend on them for livelihood. A portion of the ranges of *F. salina*, *F. jamesii*, and *F. johnstonii* extend into areas where saltcedar has invaded.

Kovalev (1995), Baum (1978), and Whalen (1987) note that *Tamarix* and *Frankenia*, the major genera of the two families Tamaricaceae and Frankeniaceae (order Tamaricales), have different centers of origin and different centers of evolutionary radiation and species diversity. The presumed center of origin of *Tamarix* is central Asia, where 23 of the 54 species recognized by Baum (1978) occur. However, in this area, only three species of *Frankenia* subgenus *afra* occur, and no members of the other subgenus *oceania* (Afro-Australian and South American species) occur there. Kovalev (1995) also found that the phytophagous insect fauna of *Tamarix* and *Frankenia* are almost completely distinct; he found records of only two *Tamarix* -restricted insects that also have *Frankenia* spp. as hosts, both belonging to groups of unstable oligophages. He found more diverse relationships between *Tamarix*-restricted insect genera and unrelated plant genera of Salicales and Plumbaginales than with *Frankenia*. This analysis of coevolution led Kovalev (1995) to state that, "...introduction of tamarisk phytophages into the USA is a priori safe for American species of the genus *Frankenia*." However, we still believe that we should test *Frankenia* very carefully, and continue to monitor field populations for potential adverse effects.

Biological control is a proven and appropriate method for controlling exotic, invasive weeds in infested natural areas. Careful host-range testing ensures that important native and agricultural plants are not damaged. Of the many insect species in Asia that apparently attack only *Tamarix*, we have selected a leaf beetle, *Diorhabda elongata* Brullé subspecies *deserticola* Chen, as the first biological control agent to consider for introduction. DeLoach et al. (2003) described the known distribution and host range of *D. e. deserticola* based on literature and field observations in Asia and on tests of a wide range of plants in a quarantine laboratory in the United States. Lewis et al. (2003) report the insect's biology, ecology, and behavior in Asia and under quarantine in the United States.

Previous laboratory assays of larvae of *D. e. deserticola* in 1992–1993 and 1999–2000 suggested little potential (0–2% survival) to damage *Frankenia* spp. (DeLoach et al., 2003). A subsequent study reported here (Test L8) revealed that a substantial percentage of larvae can mature to the adult stage when forced to feed on the intact foliage of certain species of growing, potted *Frankenia* plants. Because of this, we conducted intensive testing of adult attraction to and of the ability of *D. e. deserticola* larvae to develop on *Frankenia* spp. These results are reported here, with larval and adult tests numbered consecutively with those previously reported in DeLoach et al. (2003).

## 2. Materials and methods

### 2.1. Test plants

All four species of *Frankenia* that occur in the United States were included in tests at the USDA-ARS laboratories in Temple, Texas and Albany, California. The additional two species that occur in Mexico were not readily obtainable and were not included in our tests. We considered *Frankenia* spp. as "critical" test plants, i.e., those that might be within or near the normally acceptable host range of *D. e. deserticola* but on which no damage or only a low level of damage would be acceptable.

Whole plants of *F. jamesii* were dug from the soil near Salt Flat in western Texas and near Pueblo, Colorado. Plants of *F. salina* were collected as rooted stolons from salt marshes near Point Isabel in San Francisco Bay (coastal population) and, for some tests done at Albany, from alkali seeps from the Owens River floodplain near Independence, California (inland population). *F. palmeri* was grown in a greenhouse from juvenile plants collected near San Diego, California. For the endangered *F. johnstonii*, we obtained permits from the US Department of the Interior (USDI) Fish and Wildlife Service, Austin, Texas, and then took cuttings from plants growing near Laredo, Texas, which we rooted under an automatic misting machine in the greenhouse. *Tamarix* test plant species and accessions were grown from cuttings obtained from the field in areas of major infestations, as listed in the tables. *T. ramosissima* was obtained from along the Bighorn River near Lovell, Wyoming and along the Sevier River near Delta, Utah; *T. parviflora* from along Cache Creek near Esparto, California; and *T. aphylla* from Phoenix, Arizona and Uvalde, Texas. At Temple, the cuttings were placed in pots in a soil-sand-vermiculite mix and at Albany in a commercial potting mix, as described by DeLoach et al. (2003), and grown in the greenhouse and outdoor slat houses.

### 2.2. Cages

Host-range testing was done in several types of cages. White polyester organza mesh bags measuring 12 × 25 cm were slipped over a branch of a potted plant for bag tests at Temple and Albany (used in no-choice tests for both larvae and adults). The test insects were placed inside the bags and the open end tied around the stem.

Outdoor cages were located on the secured grounds of the Temple ARS laboratory. The cages were in an area of open sunlight, and on black, Houston Clay soil and the plants were watered by a drip irrigation system. The cages measured 3 × 3 × 2 (ht) m, and were constructed of 16 × 18 mesh tan Saran screening (Pak Unlimited, Norcross, Georgia) over an aluminum conduit frame. The bottom of the screen was bolted to a wooden frame, which was buried in the soil to a depth of 10–15 cm; access to the cage was through a zippered door. Test plants were planted in the soil or were in pots placed in or on the ground (Fig. 1A); a drip irrigation system watered the plants. To prevent infestations of the cages by fire ants (*Solenopsis invicta* Buren), the surrounding area was treated at regular intervals with Amdro (hydramethylnon). A permit authorizing testing of *D. e. deserticola* in these outdoor cages was received from USDA Animal and Plant Health Inspection Service (APHIS) in the spring of 1998.

At Temple, small aluminum screen cages (56 × 67 × 122 (ht) cm) with hinged doors were used for the adult no-choice tests, for multiple-choice Test A11 in a large, outdoor cage, and for paired-plant Test A15 in the quarantine laboratory. Similar sized small cages were used in greenhouse Test A13 at Albany. A medium-sized, aluminum screen-cage, 1.2 × 1.5 × 0.5 (ht) m, was used in greenhouse Test A12 of ovipositional selection at Temple. This cage was placed over a sheet of plywood with holes in which potted plants were suspended, which left the top of the pot level with the cage floor; the cage held 20 pots with the plants 30 cm apart, in a 4 × 5 plant grid (Fig. 1B). The wooden Berkeley boxes used at Albany were approximately 40-cm square; they had a sloped Plexiglas top, two muslin sleeves in the front, two screened 10-cm holes in each side, and an 8-cm wide screened slot across the back. The Temple boxes were similar, but 60 × 45 × 51 (ht) cm.

### 2.3. Source of insects

Details on the origin and identification of *D. e. deserticola* from Fukang, China used in these studies are provided in DeLoach et al. (2003). The beetles from eastern Kazakhstan were collected in May 2000 by our cooperators Prof. Ivan Mityaev and Dr. Roman Jashenko (Kazakhstan Academy of Sciences, Almaty) from a site of *T. ramosissima* near Chilik, 120 km ENE of Almaty.

### 2.4. Experimental design and testing procedure

#### 2.4.1. Larval no-choice tests

Larval survival and development was compared between *Tamarix* and *Frankenia* in four tests. The test conditions, test plants and beetles used in each test are summarized in Table 1. Larvae were placed in mesh bags and exposed to growing, potted plants. Tests L8, L10, and L11 were conducted at Albany in the quarantine greenhouse where temperatures ranged from 13.1 to 32.2 °C with a 14:10 light:dark photoperiod. Test L8 had three replications, each with one bag of five neonate larvae, on each of three test plant species. The larvae were obtained from eggs produced by second generation adults from beetles sent several months earlier from Fukang, China and collected there on *Tamarix* prob.

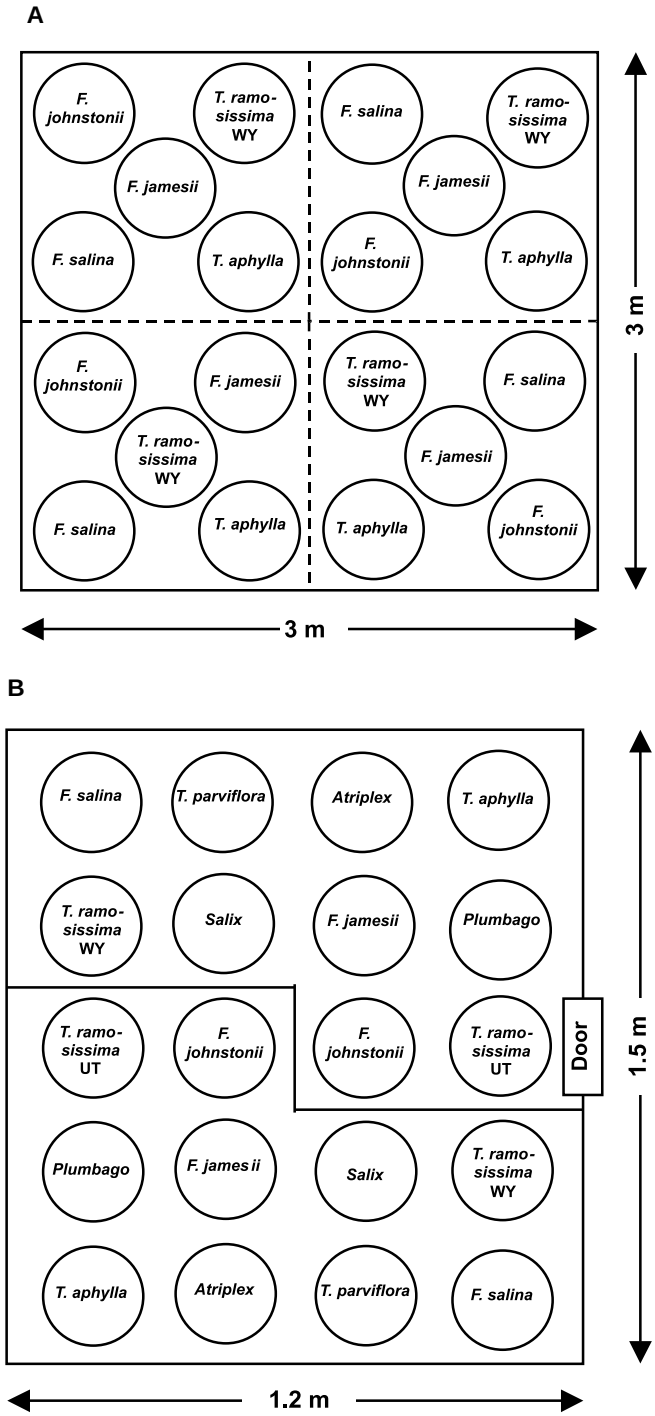


Fig. 1. Plot diagram for *D. e. deserticola* multiple-choice host-range and oviposition selection tests at Temple, Texas: (A) in the large outdoor cages (no physical barriers between quadrants); (B) greenhouse cage, the 2 replications separated by a screen partition.

*ramosissima* and other *Tamarix* species. These were reared in quarantine at Albany on *T. parviflora* DC. (Lone Pine, California). Test L10 was similar to Test L8, with three replications but each bag contained 12 neonates on each of six test plants. The neonate larvae tested were from beetles shipped from the Pueblo field nursery cages. Test L11 used neonate larvae placed on four test plants of each species, contained in mesh bags at a density of 10 larvae per bag. Larvae were obtained from a laboratory colony that had been started with beetles collected from field cages in Nevada and California. A thin layer of sand was poured into the bottom of each mesh bag to serve as a substrate for pupation. Test L9 at Temple had 9–11 replications, each replication

Table 1
Conditions and details of tests conducted and observations on *D. e. deserticola*

| Test #, location, outdoor cage[a] | Type of cage, location of test | Type of plants | Plant height | Type test: Multi-choice/ paired-choice/no-choice | Test plant species[b] | Dates of test | No. of beetles in a cage | Mean temperature, °C (range) | Rain (mm) |
|---|---|---|---|---|---|---|---|---|---|
| L8, Albany | Bag, greenhouse | Potted | N/A | NC | 2T, 1F | Nov.–Dec. 99 | 45 | 29.5 (24–32) | — |
| L9, Temple | Bag, outside | Planted/pot | N/A | NC | 3T, 3F | May–Jun. 00 | 283 | 25.4 (14–36) | 89 |
| L10, Albany | Bag, greenhouse | Potted | N/A | NC | 4T, 3F | Aug. 00 | 216 | 29.5 (24–32) | — |
| L11, Albany | Bag, greenhouse | Potted | N/A | NC | 1T, 2F | May–Jul. 01 | 120 | 29.5 (24–32) | — |
| A6, Temple, A | Lg, outside | Planted | Normal | MC | 2T, 3F | 8–16 May 00 | 95 | 24.5 (14–36) | 24 |
| A7, Temple, B | Lg, outside | Pot, buried | Normal | MC | 2T, 3F | 16–19 May 00 | 120 | 25.9 (16–33) | 8 |
| A8, Temple, A | Lg, outside | Planted | Low | MC | 2T, 3F | 22–26 May 00 | 98 | 27.1 (18–36) | 0 |
| A9, Temple, B | Lg, outside | Pot, surface | Normal and low | MC | 2T, 3F | 23–26 May 00 | 100 | 28.6 (20–36) | 0 |
| A10, Temple, B | Lg, outside | Pot, surface | Normal | MC | 3F + 2 | 2–8 Jun. 00 | 150 | 24.0 (15–34) | 23 |
| A11, Temple, C | Sm, outside | Pot | Normal | MC | 2T, 3F | 10–24 May 00 | 75, 75, 15 | 24.7 (14–36) | 34 |
| A12, Temple | Med, greenhouse | Pot | Normal | MC | 4T, 3F + 3 | 2–9 Jun. 00 | 50 × 6 | 23.8 (22–26) | — |
| A13, Albany | Sm, greenhouse | Pot | Normal | NC | 2T, 3F | 23 May–5 Jun. 00 | 20 × 15 | 20.7 (14–31) | — |
| A14, Albany | Med, greenhouse | Pot | Normal | MC | 2T, 3F + 1 | 1–13 Jun. 00 | 100 × 3 | 19.3 (14–31) | — |
| A15, Temple[c] | Sm, lab | Pot | Normal | PC | 1T, 3F | 2–21 Aug. 00 | 10 × 3 | 28.0 (27–29) | — |
| LA1, Temple[c] | Sm, lab | Pot | Normal | NC | 1T, 3F | 27 July–8 Aug. 00 | 10 × 4[d] | 28.0 (27–29) | — |
| LA2, Albany[c] | Sm, lab | Pot | Normal | PC | 1T, 1F | 10–20 Oct. 00 | 20 × 6 | 25 (constant) | — |
| Obs. F1, Pueblo, CO | Lg. cage outdoors | T planted, F pots | Normal | PC | 1T, 1F | Jun.–Jul. 00 | 500+ | — | — |
| Obs. F2, Bishop, CA | Lg. cage outdoors | T planted, F pots | Normal | PC | 1T, 1F | Jun.–Jul. 00 | 500+ | — | — |

[a] Tests numbered consecutively, continuing from DeLoach et al. (2003). L, larval test; A, adult test; LA, test with both larvae and adults; Obs. F, observations in field cages at release sites.
[b] T, *Tamarix* spp.; F, *Frankenia* spp., a number alone indicates plant species outside the Order Tamaricales.
[c] Photoperiod set at 16:8 light:dark at Temple and 15:9 light:dark at Albany.
[d] Not all replications had 10 beetles; see Section 2.

with four or five neonate larvae in one mesh bag on six potted test-plant species, one or two bags per plant which were held inside the large outdoor cages. These larvae also were reared from adults collected from a field-cage culture of Chinese Fukang beetles sent from Pueblo, Colorado.

### 2.4.2. Adult host-selection tests

Test conditions for all 12 adult tests are summarized in Table 1. Tests A6–A10 (Temple) were conducted in the large outdoor quarantine field cages during May and June 2000 using Chinese beetles sent from a field-cage culture near Pueblo, Colorado on July 7. The median natural day length during the tests was: 13 h 40 min in Test A6, 13 h 52 min in Test A7 and Test A10, 13 h 55 min in Test A8 and Test A9, and 14 h 16 min in Test A10 and Test A12. Temperature and rainfall during the outdoor tests was recorded each 30 min (Fig. 2). The cages were divided spatially into four quadrants; each quadrant contained five plants (Fig. 1A). Tests A6–A10 were conducted in two adjacent large cages, all test plants together in each cage. Randomly collected, unsexed adult beetles were placed in the center of the cage to begin each test. Plants were examined daily in the morning for the presence and number of adults and eggs. Data on alighting/resting and on ovipositional substrate selection are analyzed and presented separately in Section 3. For each observation, adults were counted and aspirated off the plants after which all eggs were removed from the plant foliage or cage walls and counted. The insects collected from the plants were re-released into the center of the cages by mid-morning. In Cage A, the test plants were removed from the pots and transplanted into the soil, with the original root-ball intact and level with the soil surface. In Cage B, the plants remained in pots. The pots were buried in the soil in Test A7 and set on the soil surface in Tests A9 and A10, thus increasing the height of the foliage above the soil by ca. 25 cm. The plants were arranged in each quadrant in a randomized complete block design that was re-randomized for each test in Cage B. A typical setup is described in Fig. 1A and was the layout of the plants in Cage A.

Tests A6 and A7 compared two species of *Tamarix* with each other and with three *Frankenia* species, all at their normal growth profiles, with the *Tamarix* foliage averaging about 60 cm higher than that of the *Frankenia* spp. Beetle response to plants of the same height was investigated in Test A8; saltcedar and athel (*T. aphylla*) were bent over and tied near the ground so that their foliage was ca. equal to the height of the *Frankenia* plants. Test A9 compared normal, upright saltcedar growth to saltcedar with the foliage tied down as in Test A8; however, all pots were placed on the soil surface, so plants were 25 cm higher than in Tests A6–A8. In these tests, the average heights of foliage above the pots were: *T. ramosissima* (tall plants 74 cm, tied down plants 13 cm), *F. johnstonii* (16 cm), *F. jamesii* (16 cm), and *F. salina* (8 cm).

Test A10 investigated beetle response to *Frankenia* when *Tamarix* plants were absent. Beetles were exposed to three *Frankenia* species and two unrelated plants, coyote willow (*Salix exigua* Nutall) from the Lower San Pedro River, Arizona, and *Plumbago capensis* Thundberg from a local plant nursery. Test A11 was conducted using three small screen cages within large outdoor Cage C, forcing the beetles into close contact with the *Frankenia* plants. One of each of the five potted test-plant species was placed in each of the small cages in a randomized complete block design. Three observations were made of beetle oviposition and presence on each of the plant species over a 2-week period, on May 11, May 15 , and May 24. The first two observations were made with 75 unsexed adults in each of the three cages. These beetles were removed after the second observation and 15 beetles were placed in each cage for the third and final observation, giving a mean of 55 beetles per observation.

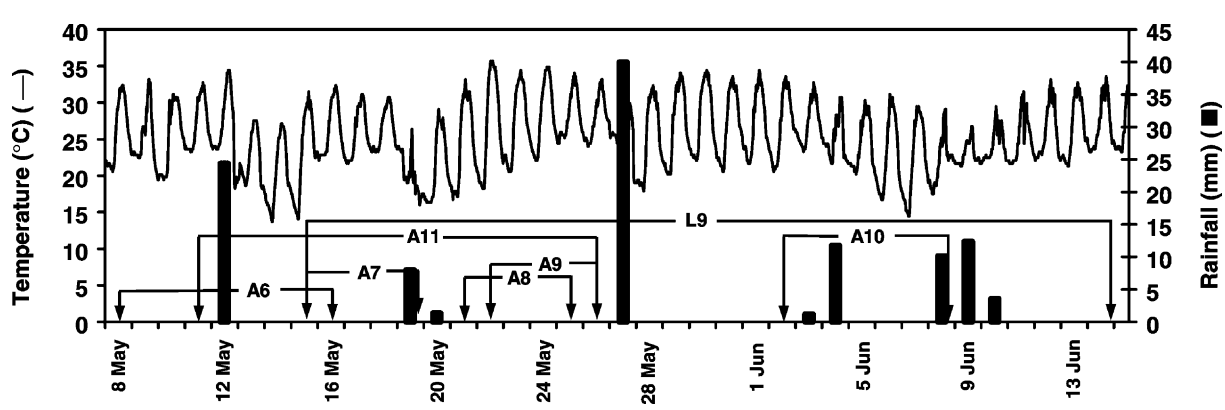


Fig. 2. Weather records during tests of *D. e. deserticola* in outdoor cages at Temple, TX, 2000: Test L9 is a larval no-choice bag test, and Tests A6–A11 are multiple-choice tests of adult alighting and oviposition.

In Test A12 (Temple), beetles shipped from Chilik, Kazakhstan in May were used for an ovipositional host-selection test. In the quarantine greenhouse, 10 potted plants were randomly placed in each side of a divided $1.2 \times 1.5 \times 0.5$ (ht) m screen cage. Plants were randomized in one side of the cage and a reverse arrangement of that was used on the other side as a replicate, with replicates separated by a screen partition (Fig. 1B). Fifty unsexed adult beetles were placed in each half of the cage and allowed to oviposit for a 3-day period, after which eggs were removed from the plant foliage and from the cage walls. The test was repeated three times during the period of 2–9 June (six replications); photoperiod was slightly more than 14 h daylight during this period. During this test, temperature in the greenhouse averaged 23.8 °C (21.5–26.1 °C), and relative humidity (RH) averaged 72% (50–93%).

Test A13 (Albany) was a no-choice test measuring ovipositional host preferences between two *Tamarix* spp. and three *Frankenia* spp. in the quarantine greenhouse (temperature 14–31 °C). Adult *D. e. deserticola* used for these tests were collected as overwintered adults near Fukang, China on ca. 10 May 2000 from *Tamarix* prob. *ramosissima*. One potted test plant was placed in a Berkeley box with 20 beetles (10 females and 10 males). Three replicates of each plant species were arranged in a randomized complete block design, with blocks of 5 cages corresponding to benches on the north, east, and south sides of the greenhouse (total of 15 cages). Beetles were exposed from 23 May to 5 June 2000, at which time they were removed and eggs were counted.

Test A14 (Albany) was a multiple-choice ovipositional preference test, with six species of test plants used per cage. This series was replicated in three cages (aluminum frame and screening, ca. $1 \times 1 \times 1.5$ m), with each cage containing 100 *D. e. deserticola*, 50 females and 50 males; however, only two *F. palmeri* plants were available, so one replicate lacked this plant. The exposure period was from 1 to 13 June, at which time the beetles were removed and the eggs counted.

Test A15 (Temple) was a paired-plant test in which a group of five male and five female beetles had a choice of alighting or ovipositing on either *T. ramosissima* or one of three *Frankenia* species in each cage. Adults were from larvae reared on the Lovell, Wyoming accession of *T. ramosissima*. The tests were conducted in the quarantine laboratory in three small aluminum screen cages, one for each plant pair. Four observations were made each day on beetle location and egg-laying and data were collected for 3 weeks. Only observable adults were counted in order not to unnecessarily disturb the beetles. During the test, temperatures averaged 28 °C (27–29 °C), RH averaged 70% (60–80%), and photoperiod was a constant 16:8 light:dark.

#### 2.4.3. Effect of larval host on adult host selection

We conducted a no-choice test at Temple and a choice test at Albany using adults that as larvae had been reared on either *Frankenia* or *Tamarix* plants. Host selection for alighting/resting and for ovipositional response was measured for the no-choice test while only oviposition was recorded in the choice test. The objective of these tests was to determine any potential for *D. e. deserticola* to develop a biotype that might favor *Frankenia*.

Test LA1 (Temple) was a no-choice test conducted in small aluminum-screen cages in the quarantine laboratory, under identical temperature and light conditions as in Test A15. Adults used for baseline data (Treatments A–D) had been reared on the Lovell accession of *T. ramosissima*; adults used for experimental data (Treatments E–H) were from larvae reared from each of the three *Frankenia* species tested. Upon emergence of adults, five males and five females, if available, were placed in a screen cage with a potted test plant. Baseline data were from *Tamarix*-reared insects tested on *Tamarix* and on each of the *Frankenia* species (Treatments A–D). Beetles reared from *Frankenia* were exposed to the same *Frankenia* species on which they were reared; a group of beetles reared on *F. salina* were exposed to a *T. ramosissima* plant as a control of the experimental group (Treatments E–H). Not enough *F. salina* foliage was available for rearing adults on this species, so larvae were reared through the 2nd instar on *T. ramosissima* and then transferred to *F. salina* to complete their development.

Adults were exposed to a single potted test plant and maintained in a no-choice situation until the majority of beetles had died. Observations were made several times per day to note the presence of adult beetles on either the cage surface or on the plants, counting only observable adults as in Test A15. Both the cage surfaces and plant foliage were examined daily for the presence of eggs.

Sufficient numbers of beetles for the test were available for those insects reared from *T. ramosissima* and *F. salina*, but less than 10% of neonates survived to the adult stage on the other two *Frankenia* species. Only two males and two females were available to conduct the test with *F. jamesii*. For *F. johnstonii*, two males and two females were available at the start of the test and additional adults were added over time as they became available; ultimately, only nine beetles were used in this test, five males and four females, as these species proved to be very poor hosts and only this many could be reared.

Test LA2 (Albany) was conducted in Hotpack growth chambers set at 25 °C and 15 h daylength in the quarantine facility at Albany. Larvae had been reared on either the Cache Creek accession of *T. parviflora* or on *F. salina* plants obtained from Pt. Isabel, California. Ten male–female pairs of the ensuing adults were placed inside $30 \times 30 \times 30$ cm cages along with two test plants in each of six growth chambers; three chambers con-

tained adults reared from *T. parviflora* and the other three contained adults reared from *F. salina*. Beetles were exposed to the tests plants for 10 days, after which eggs were collected and the experiment stopped.

#### 2.4.4. Observations in field cages

Observations of 1st generation adults and their progeny were made in field cages at two of the proposed release sites; cages near Pueblo, Colorado (Obs. F1) measured $3 \times 3 \times 2$ (ht) m and $3 \times 7 \times 3$ (ht) m at the site near Bishop, California (Obs. F2). These cages contained plants of *T. ramosissima* that had been cut back and had resprouted. Adult beetles had overwintered in the cages at both sites and a large population of larvae and adults were present for observation. Potted plants of *F. jamesii* (Pueblo) or *F. salina* (Bishop) were placed in the cages during late spring.

### 2.5. Statistical analysis

Data from laboratory, greenhouse, and field tests were subjected to analysis of variance (ANOVA) using an independent samples *t* test or an ANOVA procedure with means separated by the LSD procedure using SPSS software (Norusis, 1988). Significance levels were set at $P < 0.05$ for all statistical analyses.

## 3. Results and discussion

The experiments described in this paper were devised and conducted to fully assess, under a variety of conditions and life stages, the potential of *D. e. deserticola* to accept and utilize *Frankenia* spp. as host plants. We conducted 16 tests and two field-cage observations (Table 1) to compare the response of *D. e. elongata* to *Tamarix* vs. *Frankenia*. Four no-choice tests were conducted with larvae (1 at Temple and 3 at Albany) and 10 choice or no-choice tests investigated adult host selection and ovipositional behavior (8 at Temple and 2 at Albany). An objective of two additional experiments was to determine if the larval host plant (*Frankenia* or *Tamarix*) would affect the subsequent choice of adults to feed or oviposit upon *Frankenia* plants.

### 3.1. Old world literature, museum host-range records, and field observations

In its native range, the literature reports *D. elongata* as feeding only upon two genera of the family Tamaricaceae, *Tamarix* and rarely on *Myricaria*, but not on *Frankenia* spp. anywhere within its native range (DeLoach et al., 2003). To further determine if *D. elongata* develops on *Frankenia* in the Old World, our cooperators Drs. Rouholla Sobhian and Alan Kirk (USDA-ARS European Biological Control Laboratory at Montferrier sur Lez, France) made visual searches and took sweep-net samples on *Frankenia thymifolia* Desfontaines growing near *Tamarix* spp. in Tunisia where *D. elongata* was abundant, but found no *D. elongata* on the *Frankenia*. This is the only location where we are aware of these two plants occurring in close proximity and where *D. elongata* is known to be abundant.

### 3.2. Larval tests—Tamarix vs. Frankenia

In this series of tests, we compared survival and development of neonate larvae forced to feed on specific test plants in mesh bags on potted, growing plants.

#### 3.2.1. Test L8 (Albany)

In this test in the greenhouse, survival from egg to adult was rather low (13–33%) on the two *Tamarix* species, but was 27% (4 of 15 neonate larvae) on *F. salina* (Table 2). This survival rate on *Frankenia*, being much higher than that found in 1992–1993 by DeLoach et al. (2003), stimulated the additional, more extensive testing of both larvae and adults on *Frankenia* spp.

#### 3.2.2. Test L9 (Temple)

In this test in mesh bags in the outdoor cages during May and June 2000, 56.0% of the neonate larvae produced adults on *T. ramosissima* from Lovell, Wyoming, 31.1% on *T. aphylla*, and 36.4% on *T. parviflora*. On the three *Frankenia* species, from 8.0 to 11.1% of the neonates produced adults, significantly less than on any of the *Tamarix* plants (Table 2). Larval mortality on the three *Tamarix* species was similar through all stages, but larvae on the *Frankenia* species died mostly during the 1st instar, with moderate mortality thereafter. Survival on *F. salina* in this test was half to one-third that seen in experiments done at Albany. This is most likely the result of the different test conditions at the two locations. Tests at Albany were all conducted in controlled greenhouse conditions, while the Temple test was conducted outside with daytime highs often near 35 °C (Fig. 2). These are temperatures that the coastal variety of *F. salina* used at Temple do not normally encounter and may have resulted in physiological stress and poor plant quality as well as differences in beetle response.

#### 3.2.3. Test L10 (Albany)

In this test, larvae had the greatest average survival to the adult stage on *T. ramosissima* and *T. parviflora*/*T. gallica* from Lone Pine, although mean survival on *Tamarix* species was not significantly different from that on the *Frankenia* species, due to large variations between replications (Table 2). *Frankenia palmeri* did not support larval development, but 14% of neonate larvae survived on both *F. jamesii* and on *F. salina* from Independence, California. Although more larvae survived to adult on

Table 2
Larval development of *D. e. deserticola* from neonates to the adult stage on *Frankenia* or *Tamarix*: no-choice tests in sleeve bags

| Test plants | Percent reaching adult stage[a] | | | |
|---|---|---|---|---|
| | Test L8, Albany, greenhouse (Nov.–Dec. 1999) | Test L9, Temple, field cage (May–Jun. 2000) | Test L10, Albany, greenhouse, (Aug. 2000) | Test L11, Albany, greenhouse (July 2001) |
| Family Tamaricaceae | | | | |
| *Tamarix aphylla* Esparto, CA | 33.3 ± 11.5a $n = 3$ | | 36.1 ± 26.8ab $n = 3$ | |
| *T. aphylla* Uvalde, TX | | 31.1 ± 22.6b $n = 9$ | | |
| *T. parviflora*/*T. gallica* Lone Pine, CA | | | 47.2 ± 17.4ab $n = 3$ | |
| *T. parviflora* Cache Creek, CA | 13.3 ± 11.5a $n = 3$ | 36.4 ± 28.0b $n = 11$ | 16.7 ± 22.1ab $n = 3$ | 7.5 ± 9.6b $n = 4$ |
| *T. ramosissima* Brawley, CA | | | 52.8 ± 9.6a $n = 3$ | |
| *T. ramosissima* Lovell, WY | | 56.0 ± 22.7a $n = 10$ | | |
| Family Frankeniaceae | | | | |
| *Frankenia jamesii* Pueblo, CO | | 11.1 ± 14.5c $n = 9$ | 13.9 ± 17.4ab $n = 3$ | |
| *F. johnstonii* Laredo, TX | | 8.0 ± 16.9c $n = 10$ | | |
| *F. palmeri* Tijuana Estuary, CA | | | 0.0 ± 0.0b $n = 3$ | 60.0 ± 0.0a $n = 4$ |
| *F. salina* Independence, CA | | | 13.9 ± 9.6ab $n = 3$ | |
| *F. salina* Point Isabel, CA | 26.7 ± 11.5a $n = 3$ | 10.0 ± 10.5c $n = 10$ | 22.2 ± 19.2ab $n = 3$ | 42.5 ± 26.3a $n = 4$ |

[a] For percent survival comparisons, 3 groups of 5 larvae were used in Test L8, 9–11 groups of 4–5 larvae each in Test L9, 3 groups of 12 larvae in Test L10, and 4 groups of 10 larvae in Test L11. Values are mean percentages ±SD. Values followed by the same letter in the same test are not significantly different ($P > 0.05$; LSD, one-way ANOVA).

the coastal *F. salina* from Point Isabel, this difference was not statistically different from larval survival on plants from the inland population at Independence.

### 3.2.4. Test L11 (Albany)

The relatively high survival rate on *F. palmeri* (60.0 ± 0.0%) (Table 2), as compared to no survival in Test L10, was probably the result of better quality of test plants. This rate of survival was no different from the 42.5 ± 26.3% survival on *F. salina* in this test. Since *F. palmeri* is rare in California (it is a common Mexican species with distribution barely extending across the California border), the ability of *D. e. deserticola* to complete development on this species is of some concern. It is unclear why the larvae survived so poorly on *T. parviflora* in this test. The plant quality appeared to be good, and similar bags set up for colony production in the same greenhouse produced about 40% survival on this species during the period of this test.

## 3.3. Adult ovipositional attraction—Tamarix vs. Frankenia

Ten experiments compared host selection by adult *D. e. deserticola* and preference for *Frankenia* or *Tamarix*. At Temple, seven multiple-choice tests were conducted, six in outdoor cages using beetles from Fukang, China and one (Test A12) in the greenhouse using beetles from Chilik, Kazakhstan. Four tests in large outdoor cages (Tests A6–A9) compared one or two *Tamarix* species or accessions with three *Frankenia* species. One (Test A10), also in a large outdoor cage, tested whether oviposition on *Frankenia* would increase if *Tamarix* were removed. Another (Test A11) tested whether oviposition on *Frankenia* would increase in smaller, crowded outdoor cages. Three additional tests, also using the Chinese beetles, measured host selection in smaller cages in the greenhouse or laboratory: a choice and a no-choice test at Albany (Tests A13 and A14) that measured only oviposition and a paired-plant test at Temple (Test A15) that measured both alighting and oviposition.

### 3.3.1. Outdoor cage Tests A6–A11 (multiple-choice, Temple)

The first four multiple-choice tests in large outdoor cages (Tests A6–A9), where one or two *Tamarix* species or accessions were compared with all three *Frankenia* species in each cage (= test), were the most equal between-test comparisons that we made. In these four tests, adult females of *D. e. deserticola* from Fukang,

Table 3
Ovipositional selection by *D. e. deserticola* on *Tamarix* and *Frankenia* in multiple-choice tests in outdoor cages and greenhouse, Temple, TX, May–June 2000

| Plant species | Percent of total eggs laid within each test (total eggs laid) (mean # per plant per observation ±SD)[a] | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | Outdoor tests: beetles from Fukang, China | | | | | | Greenhouse:[b] | | |
| | Large cages | | | | | Small cages | Kazak beetles | Average[c] | |
| | Test A6, 8–16 May (9 obs.) | Test A7, 16–19 May (4 obs.) | Test A8, 22–26 May (5 obs.) | Test A9, 23–26 May (4 obs.) | Test A10, 2–8 June (7 obs.) | Test A11, 10–24 May (3 obs.) | Test A12, 2–9 June (3 obs.) | % of eggs laid | Normalized to 100% |
| *Tamarix ramosissima* (WY) | | | | | | | | | |
| Tall | 62.5 (1117) (31.0 ± 25.2a) | 50.1 (1123) (70.2 ± 46.4a) | — | 56.0 (549) (34.3 ± 35.3a) | — | 72.8 (830) (92.2 ± 61.8a) | 27.6 (253) (42.3 ± 48.0b) | | |
| Short | — | — | 79.9 (879) (44.0 ± 36.1a) | 44.0 (432) (27.0 ± 40.4a) | — | — | — | 56.41[d] | 45.71 |
| *T. ramosissima* (UT) | — | — | — | — | — | — | 18.7 (172) (26.8 ± 28.3bc) | | |
| *T. parviflora* | — | 49.9 (1120) (70.0 ± 38.2a) | — | — | — | — | 33.2 (305) (50.8 ± 26.4b) | 41.55 | 33.67 |
| *T. aphylla* | 34.8 (621) (17.3 ± 20.1b) | — | 17.2 (189) (9.5 ± 11.3b) | — | — | 25.4 (290) (32.2 ± 35.0b) | 19.8 (182) (30.3 ± 32.9bc) | 24.30 | 19.69 |
| *Frankenia jamesii* | 2.74 (49) (1.4 ± 4.1c) | 0.0 (0) (0 ± 0 b) | 2.91 (32) (1.6 ± 3.6b) | 0.0 (0) (0 ± 0b) | 0.0 (0) (0 ± 0b) | 1.75 (20) (2.2 ± 5.1bc) | 0.65 (6) (1.0 ± 2.5cd) | 1.15 | 0.93 |
| *F. salina* | 0.0 (0) (0 ± 0c) | 0.0 (0) (0 ± 0b) | 0.0 (0) (0 ± 0b) | 0.0 (0) (0 ± 0b) | 0.0 (0) (0 ± 0b) | 0.0 (0) (0 ± 0c) | 0.0 (0) (0 ± 0d) | 0.00 | 0.00 |
| *F. johnstonii* | 0.0 (0) (0 ± 0c) | 0.0 (0) (0 ± 0b) | 0.0 (0) (0 ± 0b) | 0.0 (0) (0 ± 0b) | 0.0 (0) (0 ± 0b) | 0.0 (0) (0 ± 0c) | 0.0 (0) (0 ± 0d) | 0.00 | 0.00 |
| *Atriplex canescens* | — | — | — | — | — | — | 0.0 (0) (0 ± 0d) | 0.0 | 0.0 |
| *Plumbago capensis* | — | — | — | — | 0.0 (0) (0 ± 0b) | — | 0.0 (0) (0 ± 0d) | 0.0 | 0.0 |
| *Salix exigua* | — | — | — | — | 0.0 (0) (0 ± 0b) | — | 0.0 (0) (0 ± 0d) | 0.0 | 0.0 |

Table 3 (*continued*)

| Plant species | Percent of total eggs laid within each test (total eggs laid) (mean # per plant per observation ±SD)[a] | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | Outdoor tests: beetles from Fukang, China | | | | | | Greenhouse:[b] | | |
| | Large cages | | | | | Small cages | Kazak beetles | Average[c] | |
| | Test A6, 8–16 May (9 obs.) | Test A7, 16–19 May (4 obs.) | Test A8, 22–26 May (5 obs.) | Test A9, 23–26 May (4 obs.) | Test A10, 2–8 June (7 obs.) | Test A11, 10–24 May (3 obs.) | Test A12, 2–9 June (3 obs.) | % of eggs laid | Normalized to 100% |
| Cage walls | 0.0 (0) (0 ± 0c) | 0.0 (0) (0 ± 0b) | 0.0 (0) (0 ± 0b) | 0.0 (0) (0 ± 0b) | 100.0 (144) (8.8 ± 10.3a) | 0.0 (0) (0 ± 0c) | 37.0 (533) (88.8 ± 49.2a) | — | — |
| Total eggs laid in test | 1787 | 2243 | 1100 | 981 | 144 | 1140 | 1451 | 8846 | 100.00 |

[a] Mean eggs per plant per observation are based on number of replications × observations during the test: Tests A6–A10, four replications in each cage × 4–9 daily observations; Test A11, three small cages (= replications) × 3 observations over 15 days; Test A12, two cages × 3 observations over 9 days. Means followed by the same letter within the same test are not significantly different ($P = 0.05$); LSD, one-way ANOVA.

[b] Calculations of percentages for each test plant in Test A12 are presented as the percent of the 918 eggs laid on the plants, excluding the 533 eggs laid on the cage walls.

[c] Average for all tests in which that test plant was included, giving equal weight to each test, excluding eggs laid on the cage walls.

[d] Percentage calculations for *T. ramosissima* use the average of the tall and short plants in Test A9 and of the two accessions in Test A12.

China laid 6030 (98.7%) of their total 6111 eggs on the *Tamarix* plants and only 81 eggs (1.3%) on the *Frankenia* plants (Table 3). Among the *Tamarix* species, they laid fewer eggs on *T. aphylla* (only 22–56% as many, in those two tests) as on *T. ramosissima*. In the one comparison with *T. parviflora* (Test A7), oviposition was not different from that on *T. ramosissima*.

In Test A10, the absence of *Tamarix* plants did not cause the females to lay more eggs on *Frankenia* or on the willow or *Plumbago* plants that substituted for the *Tamarix*; in fact, the females laid all 144 eggs on the screen sides of the cage rather than on any of the *Frankenia* foliage (Table 3). In Test A11, conducted in three small outdoor cages, females laid 72.8% of their eggs on *T. ramosissima*, 25.4% on *T. aphylla*, and only 1.75% on *F. jamesii*. The closer contact with the nonhost plants did not cause females to oviposit more on the *Frankenia* plants (Table 3) and relative attractance was actually less than in the big cages. If we compare the mean number of eggs laid per plant per observation between Test A11 (small cages) and the average of Tests A6 and A8 (large cages), the most equal comparison, females laid 2.5 times more eggs on *T. ramosissima* and 2.4 times more on *T. aphylla*, but only 1.5 times as many on *F. jamesii* in the small cages than in the large cages. This result was 1.6 times more eggs laid on *Tamarix* than on *F. jamesii*. Analysis of variance of the data revealed ovipositional differences between test plants to be highly significant, with $F$ values from 8.0 to 32.7 ($P < 0.001$) in each of Tests A6–A11 (Table 4).

Mean numbers of eggs laid on short and tall saltcedar plants were not statistically different when both growth forms were present in the same cage, although the total number of eggs laid on tall plants was greater (Test A9, Table 3). However, if tall plants were not present, females oviposited readily on short *Tamarix* plants (Test A8) and at least as frequently as when only tall plants were present (Test A6) ($t$ test, $P = 0.212$). When both *Frankenia* and short *T. ramosissima* were present in the same cage (Test A8), many more eggs were laid on *T. ramosissima*, even though plants were of equal height. Therefore, these data indicate that the low growth-form of *Frankenia* was not the basis for host discrimination by *D. e. deserticola*.

Differences between the four quadrants (replications, or location within the large cages) were very small and never significant. However, the difference over time in the number of eggs laid per day during the 4–9 days of each test was significant in Test A8 (Table 4). In this experiment, numbers of eggs laid during the successive days of the test were 8, 94, 296, 406, and 298; this difference was significant because of the low rate of oviposition during the first 2 days of the test (when the females were still young) and the steady increase in eggs laid during the remainder of the test.

Table 4
Analysis of variance for different effects on plant selection for presence and oviposition of adult *D. e. deserticola* at Temple, TX[a]

| Source of variation | Outdoor tests | | | | | | | | | Greenhouse |
|---|---|---|---|---|---|---|---|---|---|---|
| | Large cages | | | | | | | | Small cages | |
| | Test A6 | | | | Test A7[b] | Test A8[b] | Test A9[b] | Test A10[b] | Test A11[b] | Test A12[b] |
| | Degrees of freedom | Sum of squares | *F* | *P* | *P* | *P* | *P* | *P* | *P* | *P* |
| *Main effects* | | | | | | | | | | |
| Presence | 4 | 2096 | 43.89 | 0.001 | 0.001 | 0.001 | 0.001 | 0.001 | 0.001 | — |
| Oviposition | 4 | 27,696 | 32.70 | 0.001 | 0.001 | 0.001 | 0.001 | 0.001 | 0.001 | 0.001 |
| *Interactions* | | | | | | | | | | |
| Presence × time | 8 | 13 | 0.07 | 0.999 | 0.999 | 0.803 | 0.698 | 0.699 | 0.634 | — |
| Presence × quadrant | 3 | 37 | 0.52 | 0.667 | 0.295 | 0.694 | 0.315 | 0.976 | 0.998 | — |
| Oviposition × time | 8 | 3391 | 1.18 | 0.313 | 0.475 | 0.047[c] | 0.138 | 0.420 | 0.122 | 0.103 |
| Oviposition × quadrant | 3 | 166 | 0.15 | 0.929 | 0.374 | 0.832 | 0.657 | 0.911 | 0.808 | 0.966 |

[a] See Tables 3 and 6 for experimental design and data.
[b] For brevity, degrees of freedom, sum of squares, and *F* are omitted here.
[c] Significance was due to a steady increase in the number of eggs laid during the test. Mean number of eggs laid per plant from day 1 to day 5 were 0.4, 4.7, 14.8, 20.3, and 14.9; $P = 0.05$; LSD, one-way ANOVA.

#### 3.3.2. Test A12, Kazakhstan beetles (Temple, greenhouse)

This was the only experiment performed with *D. e. deserticola* adults reared from Kazakhstan beetles, and investigated ovipositional preference only. Female selection of plants for egg laying was not different from that of the Chinese beetles. Excluding eggs laid on cage walls, the total percentage of all eggs laid on the two accessions of *T. ramosissima* from Wyoming and Utah was 46.3%, on *T. parviflora* 33.2%, on *T. aphylla* 19.8%, on *F. jamesii* 0.65%, and none were laid on *F. salina* and *F. johnstonii* (Table 3). The percentage of total eggs that were laid on each of the *Tamarix* species was lower in Test A12 than in Tests A6–A9 and A11 because females in Test A12 distributed their eggs between four *Tamarix* species and accessions rather than between only two as in the previous tests. These differences between plants were highly significant (Table 4).

#### 3.3.3. Overall comparisons (Tests A6–A12)

Averaging oviposition across all tests (Table 3) estimated overall ovipositional preferance of *D. e. deserticola* females. Averaging all values for *T. ramosissima* (but using the average of the tall and short plants in Tests A9 and of the two accessions in Test A12, excluding the eggs laid on the cage in Test A12, and giving equal weight to each test) gives an average 56.4% for the six tests. Similar values for *T. parviflora* (2 tests) was 41.6%, for *T. aphylla* (4 tests) was 24.3%, and for *F. jamesii* (6 tests) was 1.15%. Normalizing to 100% gives values of 45.7% for *T. ramosissima*, 33.7% for *T. parviflora*, 19.7% for *T. aphylla*, only 0.93% for *F. jamesii*, and zero for the other plants tested. Although the values are not statistically valid because of the different comparisons in each test, this probably is the most realistic estimate of the relative attractiveness of these plants for oviposition (Table 3).

#### 3.3.4. Tests A13–A14 (Albany, greenhouse)

Two additional oviposition tests were conducted at the Albany laboratory (Table 5). Test A13 revealed that *T. parviflora* elicited the greatest egg-laying response by females, with athel receiving significantly fewer eggs, and with very few or no eggs laid on the three *Frankenia* species. Females laid more eggs on the sides of the cage than on the *Frankenia* plants, which suggests that the *Frankenia* plants were no more attractive for oviposition than the surrounding inert substrates. Test A14 was a multiple-choice test that exposed beetles to all test plants used in the no-choice test. In this test, females again laid more eggs on *T. parviflora*, half as many on *T. aphylla*, but only 10 eggs on the *F. palmeri* plant and none on *F. salina* or *F. jamesii*. Three times as many eggs were laid on the cage walls as on the *Frankenia* plants (Table 5).

### 3.4. Adult alighting response—Tamarix vs. Frankenia

We assumed the alighting response to include alighting, resting, and feeding responses, but we did not measure these parameters separately; the actual measure was our observation of the presence of adult beetles "sitting" or "resting" on the plants. Measurement of feeding was not practical because of the morphology of *Tamarix* foliage and the difficulty in accurately quantifying the varying feeding responses to different growing plants.

#### 3.4.1. Tests A6–A11 (Temple)

The first four multiple-choice tests in large outdoor cages (Tests A6–A9), that compared one or two species or accessions of *Tamarix* with all three species of *Frankenia* in each cage (= test), were the most equal between-test comparison that we made. In these four tests, adults of *D. e. deserticola* from Fukang, China were observed almost entirely on the *Tamarix* plants

Table 5
Ovipositional host selection by adult *D. e. deserticola* for oviposition on host and nonhost plants: choice and no-choice tests in the greenhouse at Albany, California, May–June 2000[a]

| Test plant | % of total eggs laid (mean number of eggs per plant per day ±SD) | | |
|---|---|---|---|
| | Test A13, no-choice[a] | | Test A14, choice[b] |
| | Laid on plant | Laid off plant (cage) | |
| *Tamarix parviflora* Ft. Hunter-Liggett, CA | 64.5 (14.9 ± 3.1a) | 2.8 (0.6 ± 0.2a) | 54.7 (4.4 ± 1.6a) |
| *T. aphylla* Esparto, CA | 18.0 (4.2 ± 1.1b) | 2.5 (0.6 ± 1.0a) | 30.1 (2.4 ± 2.7ab) |
| *Frankenia salina* Pt. Isabel, CA | 0.0 (0.0 ± 0.0c) | 2.2 (0.5 ± 0.6a) | 0.0 (0.0 ± 0.0b) |
| *F. palmeri* Tijuana Estuary, CA | 1.8 (0.4 ± 0.7bc) | 2.8 (0.6 ± 0.6a) | 3.5 (0.4 ± 0.6b) |
| *F. jamesii* Pueblo, CO | 1.9 (0.4 ± 0.5bc) | 3.5 (0.8 ± 0.9a) | 0.0 (0.0 ± 0.0b) |
| *Prunus dulcis* (Almond, Nursery, CA) | — | — | 0.0 (0.0 ± 0.0b) |
| Cage/inert substrate | — | 13.9 (Total %) | 11.8 (0.9 ± 0.4b) |
| Female days in test | | | 1800 |
| Total eggs laid in test | | | 289 |

[a] Conducted in 0.4 × 0.4 × 0.4 m glass-topped cages, each cage containing one of each test plant and 20 beetles (10♂ and 10♀) for 13 days, replicated 3 times simultaneously; means marked with the same letter within a column are not significantly different ($P = 0.05$; Tukey–Kramer HSD, one-way ANOVA).

[b] Conducted in 1 × 1 × 1.5 m screen cages, each containing all 6 test plants and 100 beetles (50♂ and 50♀) for 12 days, replicated 3 times simultaneously, except for *F. palmeri* for which only 2 plants (replications) were available.

(1365 of the total 1371 observations, or 99.56%) and only six beetles were observed on the *Frankenia* plants (0.44% of the total) (Table 6). Among the *Tamarix* species, 46.7% as many adults were observed on *T. aphylla* in Tests A6 and A8 as on the *T. ramosissima* plants. In the one comparison, fewer beetles also were observed on *T. parviflora* (64.7% as many) as on *T. ramosissima* (Table 6).

In Test A10, the absence of *Tamarix* plants did not increase beetle presence on the *Frankenia* plants or on the willow and *Plumbago* plants. In fact, they instead preferred the screen sides of the cage (106 beetles) rather than the *Frankenia* plants (2 beetles) (Table 6). Also, in Test A11, the forced closer contact of the beetles with the nonhost plants in small cages did not increase their attraction to the *Frankenia* plants. Beetles were never observed on the *Frankenia* plants in this test, but 117 were observed on the *Tamarix* plants (Table 6).

Height of the test plants did influence the number of beetles resting on *Tamarix*. When tall and short forms of saltcedar were present within the same cage (Test A9), significantly (2.7 times) more beetles were found on the tall plants than on the short plants. However, if tall *Tamarix* plants were not present, beetles were attracted more often to the short *Tamarix* plants (Test A8), but were attracted to tall plants when only this growth form was present (Test A6, Table 6). Clearly then, the beetles seek out the taller growth forms of saltcedar, but can still colonize short forms of their host plant. As with oviposition, the short growth form of *Frankenia* was not the basis for its not being selected as an alighting substrate. Using an ANOVA procedure, $F$ values for differences in plant selection ranged from 23.7 to 72.8 ($P < 0.001$) in each test. Differences in presence on the plants over time or by quadrant were small and never approached significance (Table 4).

### 3.4.2. Overall comparisons (Tests A6–A11)

Normalizing to a total of 100% for all test plant species in Tests A6–A11, and weighting each test equally, 43.8% of the beetles were observed on *T. ramosissima*, 28.7% on *T. parviflora*, 27.0% on *T. aphylla*, and 0.50% on the three *Frankenia* species together (Table 6). This probably provides the most realistic estimate of the relative attraction of these plants, and agrees closely with the normalized percentage of eggs laid on these test plants in the same tests (Table 3).

### 3.4.3. Test A15 (Temple)—paired-plant test: alighting and ovipositional response

Beetle oviposition and host-finding response were tested in small cages in the quarantine laboratory in a paired-plant, choice experiment at Temple (Test A15) (Fig. 3). Adult host-plant selection for alighting was

Table 6
Presence (alighting/resting/feeding response) of adult *D. e. deserticola* from Fukang, China on *Tamarix* or *Frankenia* plants: multiple-choice tests in outdoor cages at Temple, TX, May–June 2000

| Plant species | Percent of total number of beetles observed on plants (total beetles) (mean per plant per observation ± SD)[a] | | | | | | Average[b] | |
|---|---|---|---|---|---|---|---|---|
| | Large cages | | | | | Small cages | | |
| | Test A6 (9 obs.) | Test A7 (4 obs.) | Test A8 (5 obs.) | Test A9 (4 obs.) | Test A10 (7 obs.) | Test A11 (3 obs.) | % of adults | Normalized to 100%[b] |
| *Tamarix ramosissima* (WY) | | | | | | | | |
| Tall | 55.9 (278) (7.7 ± 6.2a) | 60.6 (238) (14.9 ± 11.1a) | — | 72.1 (160) (10.0 ± 6.2a) | — | 41.9 (49) (5.4 ± 3.3b) | | |
| Short | — | — | 91.1 (236) (11.8 ± 6.9a) | 26.6 (59) (3.7 ± 5.0b) | — | — | 59.76[c] | 43.79 |
| *T. parviflora* | — | 39.2 (154) (9.6 ± 3.6b) | — | — | — | — | 39.19 | 28.72 |
| *T. aphylla* | 43.9 (218) (6.1 ± 4.6b) | — | 8.5 (22) (1.1 ± 1.5b) | — | — | 58.1 (68) (7.6 ± 3.6a) | 36.83 | 26.99 |
| *Frankenia jamesii* | 0 (0) (0 ± 0c) | 0.25 (1) (0 ± 0c) | 0.39 (1) (0.1 ± 0.2b) | 0.45 (1) (0.1 ± 0.3c) | 0.93 (1) (0.1 ± 0.3b) | 0 (0) (0 ± 0c) | 0.34 | 0.25 |
| *F. salina* | 0.20 (1) (0 ± 0c) | 0 (0) (0 ± 0c) | 0 (0) (0 ± 0b) | 0.45 (1) (0.1 ± 0.3c) | 0.93 (1) (0.1 ± 0.3b) | 0 (0) (0 ± 0c) | 0.26 | 0.19 |
| *F. johnstonii* | 0 (0) (0 ± 0c) | 0 (0) (0 ± 0c) | 0 (0) (0 ± 0b) | 0.45 (1) (0.1 ± 0.3c) | 0 (0) (0 ± 0b) | 0 (0) (0 ± 0c) | 0.08 | 0.06 |
| *Plumbago* | — | — | — | — | 0 (0) (0 ± 0b) | — | 0.0 | 0.00 |
| *Salix exigua* | — | — | — | — | 0 (0) (0 ± 0b) | — | 0.0 | 0.00 |
| Cage walls | 0 (0) (0 ± 0c) | 0 (0) (0 ± 0c) | 0 (0) (0 ± 0b) | 0 (0) (0 ± 0c) | 98.1 (106) (6.6 ± 3.1a) | — | — | — |
| Total number observed | 497 | 393 | 259 | 222 | 108 | 117 | 1596 | 100.00 |

[a] Mean number of adults per plant per observation is based on number of replications × observations during the test: Tests A6–A10, four replications in each cage × 4–9 daily observations; Test A11, three small cages (= replications × three observations over 15 days). Means followed by the same letter within the same test are not significantly different ($P = 0.05$; LSD, one-way ANOVA).
[b] Average percentage of all tests in which that test plant was included, giving equal weight to each test, and excluding adults present on the cage walls.
[c] Average percentage of all tests with *T. ramosissima*, using the average of tall and short plants in Test A9.

very different between each of the three *Frankenia* species and *Tamarix*. The beetles quickly sought out and probably fed on the *Tamarix* plants (Figs. 3A–C). However, a maximum average of only one beetle was observed a few times over the course of 3 weeks of observations on *F. jamesii* and *F. johnstonii* (Figs. 3B and C), but no feeding or damage to the plants was ever observed; beetles were never observed on the *F. salina* foliage (Fig. 3A). Beetles clearly preferred to remain on the *Tamarix* foliage in all three cages.

Oviposition was first observed on the third day of this experiment; in the 21 days of observations, the majority of eggs were laid on the *Tamarix* foliage with an occasional egg mass collected off of the cage walls and one egg mass laid on the *F. salina* foliage (Figs. 3D–F). During the 10 days of oviposition in the *F. salina* test, an average of $19.5 \pm 10.8$ eggs per day were laid on *Tamarix*, $1.0 \pm 3.2$ per day on *F. salina* and $4.8 \pm 6.2$ eggs per day were laid on the cage walls (Fig. 3D). Oviposition was observed on 6 days in the *F. jamesii* test, with an average of $14.2 \pm 7.5$ eggs per day on *Tamarix*, none on *F. jamesii* and $1.8 \pm 4.5$ eggs per day laid on the cage (Fig. 3E). Females laid eggs on 16 days during the *F. johnstonii* test, $13.4 \pm 4.9$ eggs per day on *Tamarix*, none on *F. johnstonii* and $0.4 \pm 1.5$ eggs per day on the cage walls (Fig. 3F). For each test, significantly more eggs were laid on *Tamarix* foliage than on any of the other substrates (*F. salina* test, $P = 0.0001$, one-way ANOVA; *F. jamesii* test $P = 0.006$, Independent Samples *t* test; *F. johnstonii* test $P = 0.001$, Independent Samples *t* test). Overall, females laid 497 eggs in 88 clusters on *Tamarix* foliage, 65 eggs in 10 clusters on the cage walls, the one cluster of 10 eggs on *F. salina*, and none on the foliage of the other two *Frankenia* species. Although females were actively laying eggs while in close confines with *Frankenia* plants, the results of this experiment suggest that females will not seek to lay eggs on these plants.

### 3.5. Effect of larval host on adult host selection

The potential of *D. e. deserticola* to adapt to and harm native North American species of *Frankenia* was examined in Tests LA1 (no-choice) and LA2 (choice). Results of both tests failed to demonstrate that the use of *Frankenia* spp. as the larval host results in a greater propensity for adults to prefer *Frankenia* for subsequent feeding or oviposition.

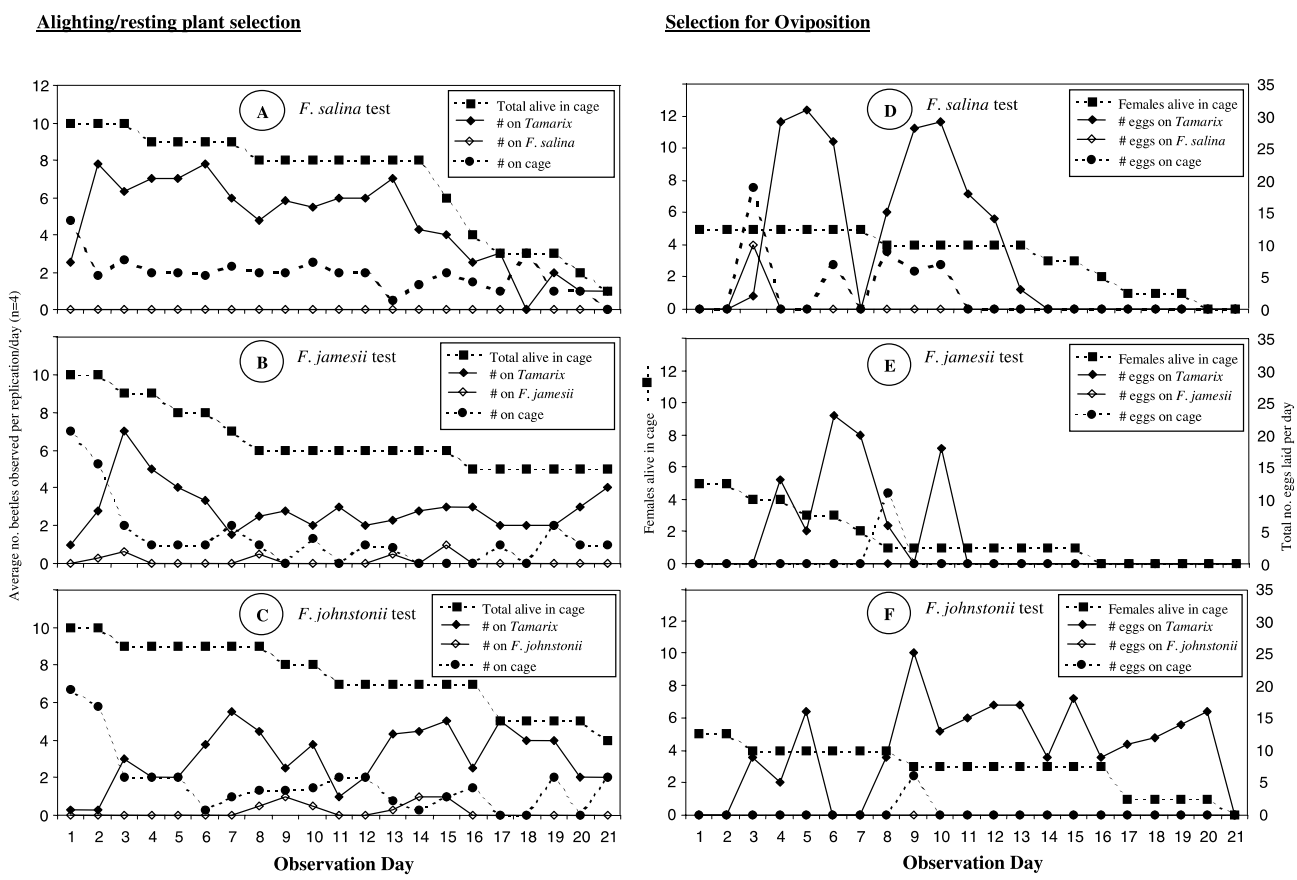


Fig. 3. Paired-plant test of host selection and oviposition between *Frankenia* and saltcedar larval host on plant selection by adult *D. e. deserticola* from larvae reared on *Tamarix* (Test A15), conducted in small cages in the laboratory, Temple.

In Test LA1 (no-choice, Temple), baseline results (adults from larvae reared on *Tamarix*) yielded a maximum average of two beetles per day (average of the four daily observations) present on the foliage of *F. jamesii* (Fig. 4B), and we once observed an average of two beetles and once one beetle on the foliage of *F. salina* (Fig. 4A). We never observed beetles on the foliage of *F. johnstonii* (Fig. 4C). No evidence of adult feeding or feeding damage on any of the *Frankenia* plants was seen, while up to 6–8 adults were observed on the cage screening and on the cage floor. All adults died after about a week and failed to lay eggs; we never observed any mating by these beetles. In contrast, in the cage with a plant of *T. ramosissima*, beetles lived twice as long and we observed a maximum average of 7–9 adults on the plant and only one or two on the cage after the first day (Fig. 4D). We frequently observed mating in this cage, beginning on day 4. The females began ovipositing on the plants on day 7, laid between 34 and 56 total eggs per day for the next 4 days, and laid 225 eggs during the course of the test; few or no eggs were laid on the cage screening. Oviposition declined on day 12, when one mass of eggs was laid on the cage and one on the saltcedar foliage, after which only one female remained alive, and we terminated the test.

Adults from larvae reared on *Frankenia* spp. yielded similar results, but these adults did not appear as vigorous as those obtained from larvae reared on *Tamarix*. Adults were never observed on the foliage of *F. salina* or *F. jamesii* (Fig. 4E and F). We did observe a maximum average of two beetles per day on *F. johnstonii* over several days (Fig. 4G). Adults also fed and caused minor damage to the foliage of *F. johnstonii*, although it did not sustain them. The majority of beetles in tests on the three *Frankenia* plants, however, remained on the cage floor and screening. No oviposition occurred on *Frankenia*, either on the plants or anywhere within the cages; mating by the beetles was not observed during any of these tests. The experimental group that had been reared on *F. salina* rapidly found the *Tamarix* plant and remained on it (Fig. 4H). Beetles were often observed on the *Tamarix* plant and most lived more than 11 days; a maximum of five or six adults were seen on the plant and only one or two on the cage screen or floor after the second day. Oviposition began after about a week, with eggs laid only on the foliage. Mating by the beetles was first observed on day 6 of the test, and the first eggs appeared 2 days later with a total of 26 eggs laid during the course of this test (Fig. 4H).

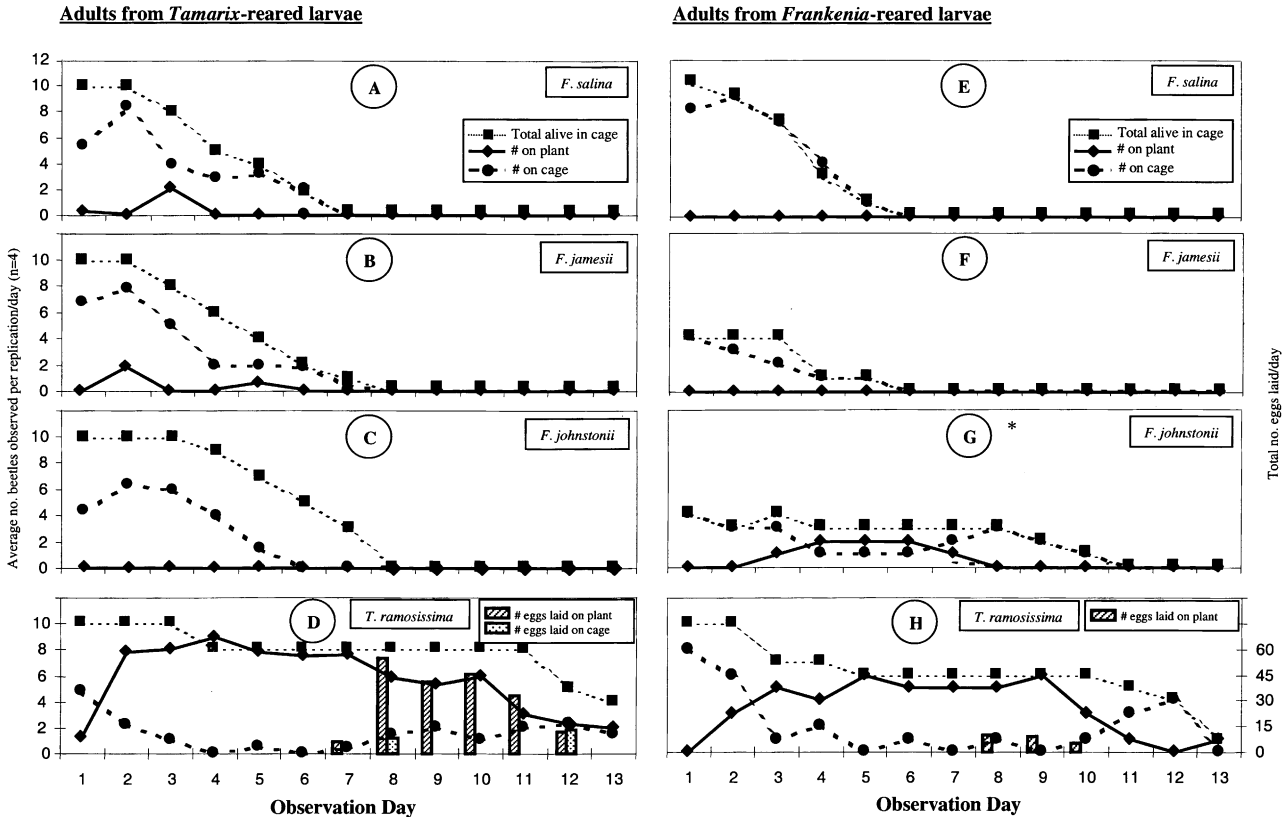


Fig. 4. No-choice test of alighting/resting and oviposition response to *Frankenia* and saltcedar by adult *D. e. deserticola* when reared from larvae on *Tamarix* or respective *Frankenia* spp. (Test LA1). *Additional adults were added after the start of this test, 2 on day 3 and one each on days 5–7. Conducted in small cages in the laboratory, Temple.

Oviposition and survival were distinctly different between adults reared as larvae on *Tamarix* vs. *Frankenia* plants (compared by Independent Samples *t* test). Between observation days 7 to 13 (allowing 6 days for ovary development), females of the *Tamarix*-reared group (Fig. 4D) laid a significantly higher average number of eggs per day ($32.0 \pm 23.2$) as compared to females reared as larvae on *Frankenia* (Fig. 4H) ($3.7 \pm 5.0$; $P = 0.008$). Adults reared as larvae on *Frankenia* and then exposed to the *Frankenia* plants laid no eggs. The *F. johnstonii* tests could not be included in the comparison of longevity, as additional beetles were added to this test as they became available (Figs. 4C and G). Also, because differing numbers of beetles were available between the two *F. jamesii* tests, this comparison was made by the daily average percent alive of the original total (Figs. 4B and F). No significant differences were noted between longevity of adults reared as larvae on *Tamarix* or *Frankenia* when these adults were then exposed to *F. salina* ($P = 0.654$) or *F. jamesii* ($P = 0.778$). However, *Frankenia*-reared adults on saltcedar had an average survival of $6.2 \pm 2.3$ adults per day, significantly less than the $7.9 \pm 1.8$ adults per day of *Tamarix*-reared adults on saltcedar ($P = 0.037$) (Figs. 4D and H).

In comparing survival within these two groups of adults (using one-way ANOVA), the average number alive each day among *Tamarix*-reared adults (Figs. 4A–D) did not differ statistically for those adults exposed to the three *Frankenia* species (Figs. 4E–H) and ranged between $3.0 \pm 4.0$ and $4.2 \pm 4.5$, while the subset of adults allowed to feed on saltcedar averaged $7.9 \pm 1.8$ adults alive, a significantly higher average ($P = 0.004$) (Figs. 4A–D). Survival data for beetles reared on *Frankenia* showed evidence that longevity is similarly reduced. For these adults, the average percentage alive each day when exposed to *F. salina* and *F. jamesii* did not differ statistically and ranged between $23.1 \pm 37.7$ and $26.9 \pm 42.6\%$, while the subset of adults allowed to feed on saltcedar averaged $61.5 \pm 23.0\%$ of the adults alive each day, a significantly higher average ($P = 0.016$) (Figs. 4E–H).

Adults from larvae reared on *Tamarix* or *Frankenia* (Figs. 4A–D) behaved similarly in both alighting response and in ovipositional response when placed on *Frankenia* plants (Figs. 4E–H). When adults from *Frankenia*-reared larvae were placed on *Tamarix* plants, they lived for a shorter time and laid only 11.5% as many eggs (Fig. 4H) as adults from *Tamarix*-reared larvae (Fig. 4D). In fact, we found no indication of the development of a biotype that displayed an increased preference for *Frankenia*. Rearing larvae on *Frankenia* appeared to have a deleterious effect on the ensuing adults, reducing their longevity and reproduction.

In Test LA2 at Albany, beetles reared on *Tamarix* had emerged and were actively ovipositing for several weeks prior to their use in this oviposition choice test. *Frankenia*-reared beetles had recently emerged and had just begun laying eggs. During the 10 days of the test, a total of 22 eggs were laid and 53% mortality occurred among the older *Tamarix*-reared females as compared to 156 eggs and only 2% female mortality of the younger beetles reared on *Frankenia*. Comparison of eggs laid between the two treatments was therefore made on a percentage of the total eggs laid, with no significant difference between treatments observed (Table 7). However, in both treatments, significantly more females selected *Tamarix* foliage for oviposition over *Frankenia* plants or the cage walls. Females reared from *Frankenia*-fed larvae laid as many eggs on the cage walls as on *Frankenia*, but the *Tamarix*-reared adults laid none on the cage.

Table 7
Influence of parental host of *D. e. deserticola* on adult oviposition choice at Albany (Test LA2)[a]

| Parental host | Percent eggs laid on substrate[b] | | |
|---|---|---|---|
| | *T. parviflora* | *F. salina* | Cage walls |
| *Tamarix parviflora* Cache Creek, CA | $89.9 \pm 17.6$a | $10.1 \pm 17.6$b | $0.0 \pm 0.0$b |
| *Frankenia salina* Point Isabel, CA | $80.6 \pm 19.5$b | $9.9 \pm 9.6$b | $9.5 \pm 11.8$b |

[a] Three replicates of 10 male and 10 female beetles were released in cages containing the 2 test plants; eggs were counted after 10 days.

[b] Values are mean percentages ± SD. Values followed by the same letter within a row are not significantly different ($P < 0.005$; LSD one-way ANOVA); percent egg laying on a substrate did not differ by parental host ($0.23 > P < 0.98$; Independent Samples *t* test).

### 3.6. Host-plant selection in field cages at proposed release sites

In addition to the above tests, *Frankenia* plants were included in nursery field cages at two proposed field release locations. At the Pueblo, Colorado, site (Obs. F1), our collaborator Debra Eberts (Ecological Research and Investigations Group, USDI Bureau of Reclamation, Denver, Colorado) established two cages, one with two and one with three potted plants of *F. jamesii* located among the large plants of *T. ramosissima* growing naturally in the soil inside the big cage. During the summer of 2000, she observed that adults and larvae had increased to high populations and had severely defoliated the *Tamarix* plants; hundreds of starving larvae and adults were crawling and flying about inside the cages searching for food. An examination on 15 June (60–65% saltcedar defoliation at this time) revealed no feeding or eggs on the *Frankenia* plants in the cage with two plants, and two eggs on one of the plants, and no feeding on *Frankenia* in the cage with three plants. At this time, larvae were so abundant they were falling to the ground off of the cage screening, some of them landing on the *Frankenia* plants, but only slight feeding

was noted on these plants. A subsequent observation on 6 July (saltcedar 80% defoliated) revealed several 3rd instar larvae and an adult feeding on one of the *Frankenia* plants. Their feeding damaged about 10% or less of the foliage on this plant, with 50% localized damage on one or two branches. In our cages at the Owens Valley site in California (Obs. F2), several *F. salina* plants inside the cage were undamaged by the beetles, which had caused heavy defoliation of the saltcedar plants.

## 4. Summary and conclusions

Our tests reported here demonstrate that larvae of *D. e. deserticola* develop well on *Tamarix* but that *Frankenia* is less suitable for larval development (Tests L8–L11). Survival of larvae on *F. salina* in tests at Albany was greater than in tests at Temple, possibly due to differing experimental conditions and host-plant quality. However, adults only rarely choose *Frankenia* for either alighting/resting or for oviposition.

In the four multiple-choice tests in large outdoor tests at Temple (Tests A6–A9), where the most equal comparisons were made, females laid 6030 eggs (98.7%) of the total 6111 eggs on *Tamarix* plants and only 81 eggs (1.3%) on the *Frankenia* plants. Among the *Tamarix* plants, they laid an average 39% as many on *T. aphylla* and the same percentage on *T. parviflora* as on *T. ramosissima*. When averaged across all seven tests (Tests A6–A12), the females laid 45.7% of the total 8846 eggs on *T. ramosissima*, 33.7% on *T. parviflora*, 19.7% on *T. aphylla*, 0.93% on *F. jamesii*, and none on *F. salina* or *F. johnstonii*. In these same tests, from 1596 total observations over 44 days, 43.8% of the adult beetles were resting on *T. ramosissima*, 28.7% on *T. parviflora*, and 27.0% on *T. aphylla*, and only 8 beetles (0.5%) were observed on the three *Frankenia* species together.

Adults in Test A10 did not oviposit on, and only 2 beetles were observed on, *Frankenia* plants when the *Tamarix* plants were removed and only *Frankenia* and two nonhost plants remained in the cage. All eggs and all but the 2 adults were found on the screen sides of the cage. Also, when the beetles were tested in small outdoor cages (Test A11), the more crowded conditions and closer contact with the plants did not cause the beetles to be more attracted to *Frankenia* for either oviposition or alighting/resting. The ovipositional response of adult beetles from Kazakhstan (Test A12) did not differ from that of the beetles from Fukang, China, evaluated in the other tests. Additional no-choice, paired-plant-choice, and multiple-choice tests at Albany and Temple (Tests A13–A15) produced similar results.

In Tests LA1 and LA2, adults produced from larvae reared on *Frankenia* plants (only 0–27% of these larvae produced adults) showed no increase in attraction to or oviposition on *Frankenia*, when compared with adults produced from larvae reared on *Tamarix*. These adults from *Frankenia*-reared larvae had shrunken abdomens, were not attracted to *Frankenia* plants, produced few if any eggs, and had reduced longevity when placed in cages with the three *Frankenia* species. However, adults from larvae reared on *Tamarix* readily found and fed on a saltcedar plant, produced many eggs, and lived twice as long as adults exposed only to *Frankenia*. Test LA1 indicated that *D. e. deserticola* has no propensity to develop a strain that has a greater selection for *Frankenia* or a greater survival or reproductive rate on *Frankenia*.

In releases into field cages by our collaborator at Pueblo, Colorado (Obs. F1) and by us at Owens Valley, California (Obs. F2), larvae only slightly or never damaged *Frankenia* plants inside the cages, even when *D. e. deserticola* populations increased greatly and defoliated the *Tamarix* plants, leaving hundreds of starving adults and larvae crawling about inside the cage searching for food. These observations cast considerable doubt that this insect can maintain a population on, or develop one that will exhibit any significant 'host substitution' onto *Frankenia* spp (cf. Marohasy, 1996).

The families Tamaricaceae and Frankeniaceae have different centers of origin and species diversity, with *Tamarix* primarily central Asian and *Frankenia* primarily Australian and South American. The insect herbivores also have coevolved separately on these genera. Kovalev (1995) stated that nearly all of the central Asian insects of *Tamarix* do not include *Frankenia* in their host range.

A consideration of all the above factors predicts a very low rate of attack, no significant damage, and probably no continuing attack on *Frankenia* by *D. e. deserticola* in the open field. We also believe the potential for *D.e. deserticola* to develop a strain that prefers *Frankenia* under natural field conditions to be unlikely. We expect the effects of *D. e. deserticola* on *Frankenia* in the United States to be the same as its effect on *Frankenia* in Asia and Tunisia, i.e. essentially zero. Thus, we have requested approval for this beetle to be released from the field cages and into the open environment at approved release sites in North America as a biological control agent for saltcedar.

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## References

Baum, B.R., 1978. The Genus *Tamarix*. Israel Academy of Sciences and Humanities, Jerusalem, Israel.

Crins, W.L., 1989. The Tamaricaceae in the southeastern United States. J. Arnold Arboretum 70, 403–425.

DeLoach, C.J., Lewis, P.A., Herr, J.C., Carruthers, R.I., Tracy, J.L., Johnson, J., 2003. Host specificity of a leafbeetle, *Diorhabda elongata deserticola* (Coleoptera: Chrysomelidae) from Asia, for biological control of saltcedars (*Tamarix*: Tamaricaceae) in the western United States. Biol. Control 117–147.

DeLoach, C.J., Carruthers, R.I., Lovich, J.E., Dudley, T.L., Smith, S.D., 2000. Ecological interactions in the biological control of saltcedar (*Tamarix* spp.) in the United States: Toward a new understanding. In: Spencer, N.R. (Ed), Proceedings of the X International Symposium on Biological Control Weeds, 4–14 July 1999. Montana Statue University, MT, pp. 819–873.

Gaskin, J.F., Schaal, B.A., 2002. Hybrid *Tamarix* widespread in US invasion and undetected in native Asian range. In: Proceedings of the National Academy of Science, 99, pp. 11256–11259.

Good, R., 1974. The Geography of the Flowering Plants. Longman, London.

Kovalev, O.V., 1995. Co-evolution of the Tamarisks (Tamaricaceae) and Pest Arthropods (Insecta; Arachnida: Acarina) with Special Reference to Biological Control Prospects. In: Proceedings of Zoological Institute, Russian Academy of Sciences, St. Petersburg, Russia, vol. 29. Pensoft Publishers, Moscow.

Lewis, P.A., DeLoach, C.J., Knutson, A.E., Tracy, J.L., 2003. Biology of *Diorhabda elongata deserticola* (Coleoptera: Chrysomelidae), an Asian leafbeetle for biological control of saltcedars (*Tamarix* spp.) in the United States. Biol. Control 101–116.

Marohasy, J.J., 1996. Host shifts in biological control: Real problems, semantic difficulties or poor science? Int. J. Pest Manage. 42, 71–75.

Norusis, M.J., 1988. SPSS/PC+ V2.0 Base Manual. SPSS Inc., Chicago, IL.

Rusanov, F.N., 1949. The Middle Asian tamarisks. Izv. Akad. Nauk Uzbek SSR, Tashkent (in Russian).

Spichiger, R., Savolainen, V., 1997. Present state of Angiospermae phylogeny. Candollea 52, 435–455.

Whalen, M.A. 1980. A Systematic Review of the New World Species of *Frankenia* (Frankeniaceae). Doctoral dissertation, University of Texas, Austin, TX.

Whalen, M.A., 1987. Systematics of *Frankenia* (Frankeniaceae) in North and South America. Syst. Bot. Monogr. 17, 1–93.