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Diorhabda spp.
Saltcedar leaf beetles

Four species of *Diorhabda* have been released and established in North America for use against saltcedars. During the initial stages of the program, they were all classified as *D. elongata,* with seven ecotypes collected from across Eurasia and North Africa used in biocontrol. Following taxonomic revision, the ecotypes were divided between four *Diorhabda* species, with three ecotypes of *D. carinulata* (Fukang, Chilik, and Turpan), two ecotypes of *D. elongata* (Possidi and Crete) and a single ecotype each of *D. carinata* (Karshi) and *D. sublineata* (Tunisia) released in North America. The Possidi and Turpan ecotypes are not known to be established.

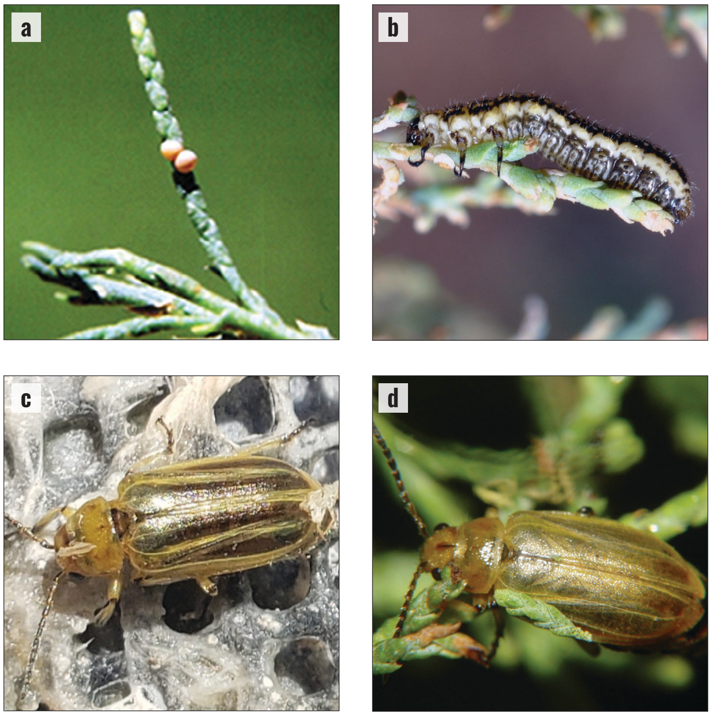

Figure 1. *Diorhabda* spp. (a) eggs; (b) larva; (c) adult (a: Roman Jashenko, Tethys Scientific Institute, Wikimedia.org CC0; b: William M. Ciesla, Forest Health Management International, Bugwood.org CC BY-3.0 US; c: David Vander Pluym, iNaturalist.org CC BY-NC 4.0; d: James L. Tracy, USDA ARS, Wikimedia.org CC0)

CLASSIFICATION

RANKING	SCIENTIFIC NAME	COMMON NAME
Kingdom	Animalia	Animals
Phylum	Arthropoda	Arthropods
Class	Insecta	Insects
Order	Coleoptera	Beetles
Family	Chrysomelidae	Leaf beetles
Genus	*Diorhabda*	Tamarisk leaf beetles
Species	*Diorhabda carinata* (Faldermann) *Diorhabda carinulata* (Desbrochers) *Diorhabda elongata* (Brullé) *Diorhabda sublineata* (Lucas)	Larger tamarisk beetle Northern tamarisk beetle Mediterranean tamarisk beetle Subtropical tamarisk beetle

DESCRIPTION

All four species are similar in appearance. Eggs of all species are tan, spherical, and laid as small clusters on saltcedar foliage (**Fig. 1a**). Larvae are up to 1 cm long, spotted grayish-black, and have distinct yellow or cream longitudinal stripes (**Fig. 1b**). Adults are 5½–6 mm long with tan to yellow bodies. Two dark stripes on each elytron are more obvious on some ecotypes (e.g., Chilik and Fukang; **Fig. 1c**) and less distinct on others (e.g., Crete, Karshi, and Tunisia; **Fig. 1d**).

LIFE CYCLE

Overwintering adults emerge from the leaf litter in spring and feed on saltcedar foliage. After aggregation and mating in response to a male-produced aggregation pheromone, females lay 100–200 eggs in small groups of up to 25 on saltcedar foliage (**Fig. 1a**). Larvae hatch after about five days and feed on young saltcedar growth through three instars. Mature larvae move into the litter beneath saltcedar plants to pupate. Chilik and Fukang ecotypes were originally northern adapted, requiring long summer days characteristic of northern latitudes to remain reproductive and avoid premature diapause, which initially prevented their establishment at sites south of the 38th parallel. They have since evolved, and their changing photoperiod requirements now allow them to persist further south, even into northern Mexico. These two ecotypes tend to have two generations per year north of the 38th parallel. The remaining three species, *D. elongata, D. carinata,* and

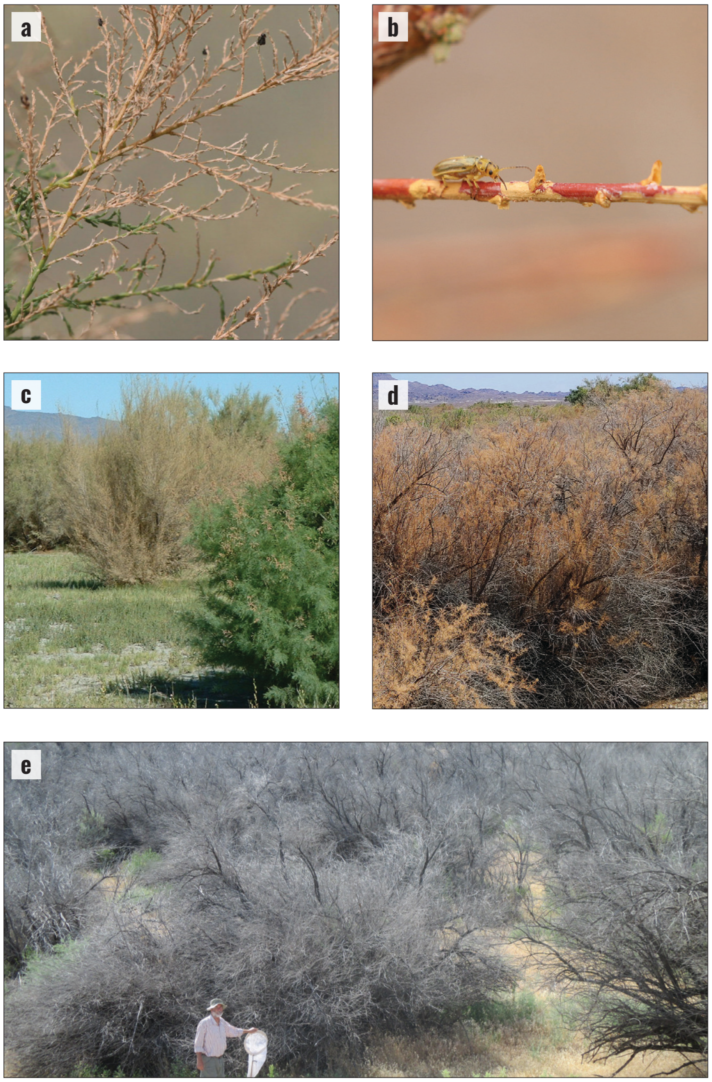

Figure 2. *Diorhabda* spp. (a) larval defoliation; (b) adult scraping damage to young twig; (c) first defoliation of plants, turning them straw-colored (background plants); (d) repeated defoliation causing branches to die; (e) repeated defoliation causing plant death (a: Whitney Cranshaw, Colorado State University, Bugwood.org CC BY-3.0 US; b: Forest Brown, iNaturalist.org CC BY-NC 4.0; c,e: Dan Bean, Colorado Department of Agriculture; d: Tom Dudley, University of California, Santa Barbara)

D. sublineata, have 3–5 generations per year. Adults of all *Diorhabda* overwinter in the leaf litter beneath tamarisk, or in other sheltered microhabitats near the host plant, and emerge in spring to feed, mate, and lay eggs.

DAMAGE

Larvae and adults feed on saltcedar foliage (**Fig. 2a**) and occasionally kill more foliage than they consume by scraping the bark off young twigs (**Fig. 2b**), resulting in stem desiccation. Newly defoliated plants (**Fig. 2c**) are straw-colored and quickly refoliate while plants that have been defoliated multiple times may die back, leaving dead gray branches (**Fig. 2d**). Plants may re-grow from the plant base, but repeated defoliation reduces metabolic reserves which leads to incremental dieback, eventually killing some plants (**Fig 2e**).

FIELD IDENTIFICATION

Larvae and adults of *Diorhabda* spp. can be readily observed on saltcedar foliage and shoots throughout the growing season (**Fig. 3a,b**). Because of the close similarities in their morphologies and the extensive hybridization that has occurred, *Diorhabda* spp. and ecotypes are not easily differentiated from each other without genetic testing.

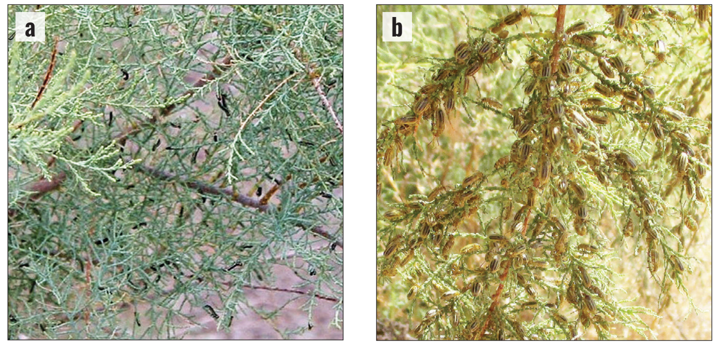

Figure 3. *Diorhabda carinulata* aggregating on saltcedar branches (a) larvae; (b) adults (a,b: Dan Bean, Colorado Department of Agriculture)

Two additional foliage-feeding insects (both unintentionally introduced) are established throughout saltcedars' invaded range in North America—the beetle *Coniatus splendidulus* and leafhopper *Opsius stactogalus*. Larvae and adults of *C. splendidulus* are cryptic but can be observed feeding on saltcedar foliage throughout the year. *Coniatus splendidulus* larvae can be differentiated by being bright green with black head capsules (**Fig. 10a**), and their adults are mottled green to brown (**Fig. 10d,e**) with a long snout pointing markedly downward. Pupation of *C. splendidulus* occurs in distinctive pupal baskets (**Fig. 10c**) attached to saltcedar foliage. Nymphs and adults of *O. stactogalus* feed by piercing saltcedar foliage with specialized stylets. Both can be readily differentiated from *Diorhabda* by being green (**Fig. 11a,b**) and ≤4 mm long.

PREFERRED HABITAT

The tamarisk beetles are tolerant of a variety of climate conditions and are established across most of the invasive range of saltcedar in North America. Flooding can cause periodic declines in the populations of saltcedar beetles.

HISTORY AND CURRENT STATUS

Chilik Ecotype of *Diorhabda carinulata*

This ecotype was introduced from Kazakhstan and released in Utah beginning in 2001. After successfully establishing, it spread rapidly both naturally to surrounding states and via intentional redistributions within Utah (**Fig. 4**). Populations may be large but can experience substantial bird predation, though they have still increased sufficiently to exert significant control of saltcedar. This is especially true along the Colorado River near Moab and the Virgin River to Lake Mead. Beetle populations often exhibit a boom-bust cycle over the course of three or more years. Repeated defoliation results in carbon starvation that reduces growth and causes incremental stem dieback, in some cases killing the host plant. For reasons not yet clear, saltcedar populations in some regions experience little permanent damage despite multiple defoliation events. Evolution in photoperiod requirements has allowed this ecotype to spread south of the 38th parallel. Flooding limits beetle populations.

Figure 4. Reported distribution of the Chilik ecotype of *Diorhabda carinulata* in the USA (Winston et al. 2023)

Fukang Ecotype of *Diorhabda carinulata*

The Fukang ecotype was introduced from Fukang, China and released in several western states beginning in 2001. It is now widespread (**Fig. 5**) and causes heavy defoliation at most release sites; however, spread from release sites varies by location. This ecotype has been very successful throughout Nevada where thousands of acres were defoliated by 2006. Repeated defoliation led to the death of 70% of plants within five years in some stands. It has also defoliated large stands of saltcedar in Wyoming, but elsewhere defoliation is more variable. Often as a site is defoliated, next-generation beetles disperse in search of food, and populations rebuild as saltcedar refoliates. However, at many locations with extensive defoliation, insect populations have declined, possibly owing to depletion of their sole food resource, allowing host plant recovery as part of a boom-bust cycle. Flooding and heavy predation can also limit agent populations. Evolution in photoperiod requirements has allowed this ecotype to spread south of the 38th parallel.

Turpan Ecotype of *Diorhabda carinulata*

This ecotype was introduced from Turpan, China, and a single open-field release of a small number was made in eastern Colorado in 2005, but they apparently failed to establish.

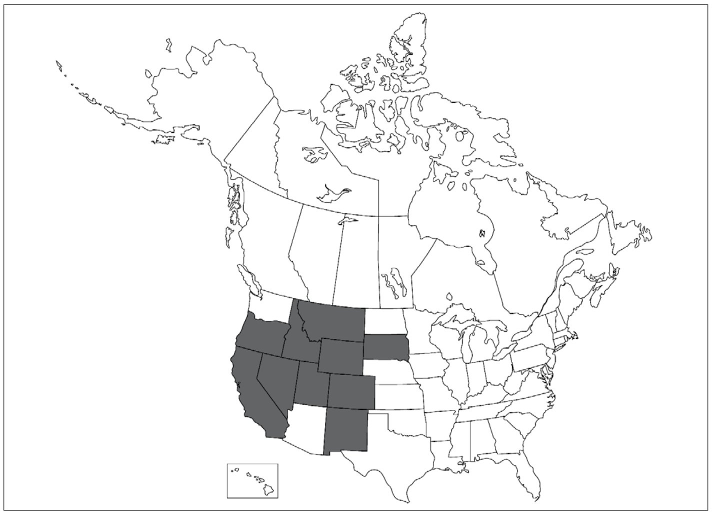

Figure 5. Reported distribution of the Fukang ecotype of *Diorhabda carinulata* in the USA (Winston et al. 2023)

Crete Ecotype of *Diorhabda elongata*

The Crete ecotype was introduced from Crete, Greece and released in California, New Mexico, and Texas beginning in 2003. It is currently weakly established in five states (**Fig. 6**), and its impact is variable. Large populations and increasing defoliation were observed in central Texas following initial releases, and they were still present fifteen years later, but mostly as hybrids with *D. carinata* and *D. sublineata*. Hybridization with *D. carinata* may have led to rapid expansion from Texas into Oklahoma and Kansas. (It also hybridizes with *D. sublineata* in New Mexico and Texas.) Populations subsequently crashed, likely due to extreme weather events. Though *D. elongata* exhibits a potential of boom/bust cycling in that region, most areas originally defoliated have not been extensively re-colonized to date, and populations generally remain low. This ecotype is established

Figure 6. Reported distribution of the Crete ecotype of *Diorhabda elongata* in the USA (Winston et al. 2023)

on smallflower tamarisk, *T. parviflora*, the dominant species in northern California, though it still prefers *T. ramosissima* in choice tests and has not provided control of *T. parviflora* in California to date. Flooding, freezing temperatures, and predation limit population growth throughout its range.

Possidi Ecotype of *Diorhabda elongata*

The Possidi ecotype was introduced from mainland Greece and released in north Texas in 2005. It became weakly established but was not found again after 2008 and is assumed to have died out.

Karshi Ecotype of *Diorhabda carinata*

This ecotype was collected from Uzbekistan and released in Texas beginning in 2006. Populations remained localized initially, but hybridization with *D. elongata* (Crete ecotype) may have led to rapid expansion in Texas, Oklahoma, and Kansas (**Fig. 7**). More recent surveys, however, indicate pure and hybrid *D. carinata* populations are uncommon, and so this ecotype has not caused long-term reductions in area-wide saltcedar growth and survival. Flooding and predation limit population growth.

Figure 7. Reported distribution of the Karshi ecotype of *Diorhabda carinata* in the USA (Winston et al. 2022)

Tunisian Ecotype of *Diorhabda sublineata*

This ecotype was introduced from Tunisia and released in Texas beginning in 2006. Populations expanded rapidly into New Mexico (**Fig. 8**) and Mexico, causing widespread defoliation and reductions of saltcedar cover. Populations subsequently contracted, and saltcedar infestations have recovered wherever beetle populations are low. Though *D. sublineata* exhibits a potential of boom/bust cycling, most areas originally defoliated have not been extensively re-colonized to date. Hybridization with *D. elongata* and *D. carinata* occurs, and hybrids are common at *D. sublineata* release sites in both New Mexico and Texas. In recent years, *D. sublineata* has been moving westward along the Gila River in Arizona after crossing from the Rio Grande drainage into the Colorado River drainage. Flooding and predation limit population growth.

In Mexico, the beetle naturally spread across the Rio Grande by 2009. It is now established in Chihuahua Coahuila and can be found up to 124 mi (200 km) from USA release sites. Although this species can have high impacts locally in Mexico, populations vary and have recently contracted, similar to contractions in the USA.

Figure 8. Reported distribution of the Tunisian ecotype of *Diorhabda sublineata* in the USA (Winston et al. 2022)

Fluctuation in Density and Range of *Diorhabda* spp.

Populations of *Diorhabda* spp. undergo boom and bust cycles, which may result in major defoliation events followed by one or more years in which beetles are scarce or absent from an area. Adults mate and oviposit in aggregations in response to a male-produced pheromone, a behavior that often results in high *Diorhabda* densities and complete defoliation of tamarisk stands. Sometimes, however, *Diorhabda* may fail to achieve high densities and then disappear from areas where they had previously been abundant. These fluctuations have been noted in populations of all four species and in settings ranging from the northern boundaries of establishment in Wyoming, south to Texas and Mexico. Since their introduction, the range limits of *Diorhabda* spp. have also also shifted, due to evolution and to hybridization among species and ecotypes.

The underlying causes of population cycles remain poorly understood, although it has been shown that predation by ants can severely impact populations, and a strong correlation has also been noted between record freezing late winter temperatures in Texas and an abrupt crash in *Diorhabda* populations. Because *Diorhabda* spend time in the leaf litter both as pupae and overwintering adults, they are susceptible to the periodic flooding typical of western rivers. Additional studies and long-term tracking of *Diorhabda* populations will be required to better understand population dynamics.

Diorhabda spp. Hybridization Status

Extensive hybridization between *D. carinata, D. sublineata,* and *D. elongata* has been detected in the field throughout the North American ranges of the three species, wherever populations have come into contact with one another. Hybridization involving *D. carinulata* has been limited to genetic exchange between the Fukang and Chilik ecotypes, with almost no interspecific hybrids formed. The hybrid status of populations in Texas and New Mexico remains dynamic, although the genetic makeup of most hybrids is dominated by *D. carinata* and *D. sublineata*, with *D. carinata* appearing to be more prevalent at northern sites and *D. sublineata* at southern sites. As populations become more locally adapted, the underlying genetic makeup will likely remain dynamic. Much like the host plant *T. ramosissima/chinensis*, *Diorhabda* beetles are losing the distinct species boundaries that they had in the native range.

Southwestern Willow Flycatcher

The southwestern willow flycatcher (*Empidonax traillii* ssp. *extimus*; **Fig. 9**), an endangered bird in the USA, utilizes saltcedar in some areas where its natural habitat has been displaced by this weed. In 2009, a lawsuit was filed against USDA APHIS due to the possible negative impacts this biocontrol program could have on the bird by defoliating some of its adventive breeding habitat. A moratorium was enacted, preventing further releases and redistributions of the saltcedar leaf beetles. The moratorium remains in place for interstate movement and release of *Diorhabda* spp., and redistribution to federal lands remains prohibited. To abide by the limitations of the original permit (not to release beetles within 200 miles or 322 km of known nesting of the southwestern willow flycatcher in saltcedar), the states of Arizona and New Mexico do not allow beetle introduction or redistribution. Releases in other states are legal, though redistributions across state lines are not permitted.

Figure 9. The southwestern willow flycatcher is an endangered bird in the USA that uses saltcedar where its natural habitat has been enroached by this weed (Andrew N, iNaturalist.org CC BY-NC 4.0)

NONTARGET EFFECTS

Spillover feeding has been observed on the exotic ornamental *Tamarix aphylla* in the USA and Mexico, but only in cases where nearby invasive saltcedars are heavily consumed. In these instances, oviposition is minimal, impact is temporary, and the affected *T. aphylla* grow with resumed vigor the following year. Slight adult and larval feeding were also observed on the native *Frankenia salina* in open field tests, though this was deemed temporary spillover after the target host saltcedar had been fully defoliated by high beetle populations.

UNAPPROVED BIOCONTROL AGENTS

Two accidentally introduced species are now widely established on saltcedars in North America. Care should be taken when transferring approved agents to ensure that unapproved species are not also included in transferred material.

Coniatus splendidulus

(Coleoptera: Curculionidae)

DESCRIPTION AND LIFE CYCLE

Overwintering adults emerge in early spring and feed on the tips of new saltcedar shoots. After mating, females lay eggs near stem tips or on flower buds. Eggs are small, yellow, and oval-shaped. Larvae are highly cryptic, closely resembling the green scale-like leaves of saltcedars, albeit with black head capsules (**Fig. 10a,b**). They feed on saltcedar foliage and flower tissue through four instars. Larvae pupate within woven baskets attached to saltcedar leaves (**Fig 10c**). Adults are ~3 mm long with robust bodies, large eyes, thick legs, and thick snouts pointing strongly downward. The elytra have distinct grooves. Adults vary from mottled brown (**Fig. 10d**) to iridescent green (**Fig. 10e**). Because larvae and adults can be difficult to find, searching for the presence of pupal baskets is often the best way to confirm the insect's presence. There may be 3–4 generations per year, though the adults of each generation are capable of living >12 months. Adults overwinter in plant litter beneath saltcedars.

HISTORY AND CURRENT STATUS

Another species in this genus, *C. tamarisci*, was studied as a potential biological control agent for saltcedar in the USA, though it was never released. *Coniatus splendidulus* was first recorded in Arizona in 2006 from an unknown mode of introduction. It has since spread naturally throughout much of western North America. It was first recorded in Chihuahua, Mexico in 2016 and in Baja California in 2017. The beetle's overall abundance and impact in the USA are largely unknown as its spread is relatively recent, and individuals are cryptic in behavior; however, impact is likely minor. In Colorado, large populations have been observed emerging prior to *Diorhabda* spp. emergence in the spring, and feeding on regrowth of saltcedars in the fall, after *Diorhabda* have entered diapause. In Chihuahua, very high numbers have been observed, and this weevil is believed to cause significant damage, though this has not been quantified. Its overall abundance and impact in Baja California are unknown. **This weevil is not approved for redistribution in the USA.**

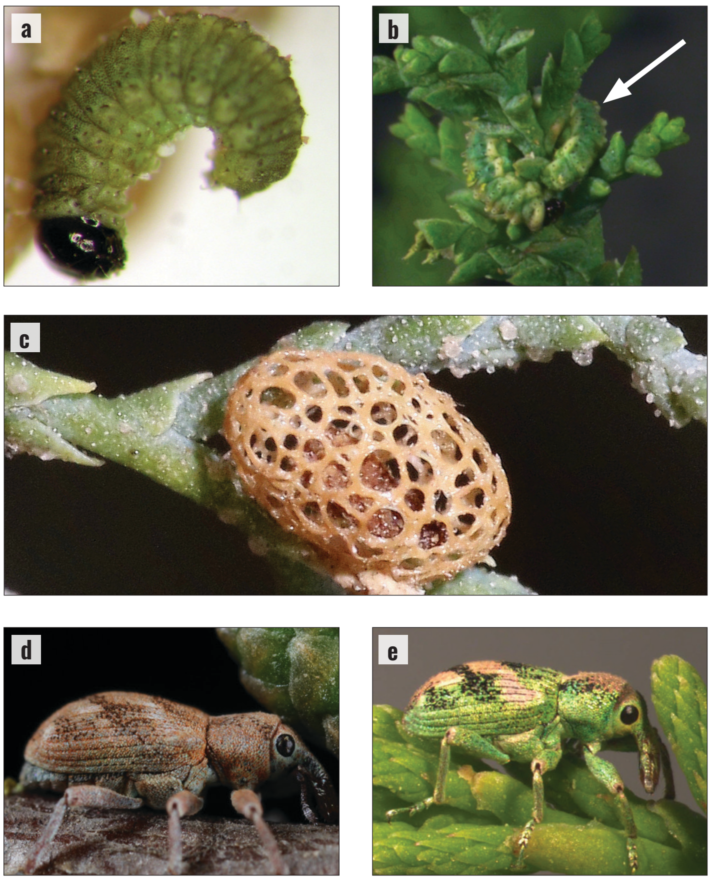

Figure 10. *Coniatus splendidulus* (a) larva; (b) cryptic larva wrapped around saltcedar stem (white arrow); (c) pupal basket; (d) brown adult; (e) green adult (a: Jason Eckberg; b,e: Zeynep Özsoy, Colorado Mesa University; c: James Bailey; d: Nathan Taylor; a,c,d: iNaturalist.org CC BY-NC 4.0)

Opsius stactogalus

(Hemiptera: Cicadellidae)

DESCRIPTION AND LIFE CYCLE

Overwintering eggs, oviposited under the thin bark of tamarisk stems, hatch in the spring. Nymphs develop through five instars before reaching the adult stage in about one month. Nymphs are small and pale green (**Fig. 11a**); adults are bright green and about 4 mm long (**Fig. 11b**). *Opsius stactogalus* are multivoltine with 3–4 generations per year, depending on the length of the growing season. They are known to build up high populations late in the season, and damage to tamarisk is often visible as a yellowing of foliage. All stages feed on phloem tissue using specialized stylets.

HISTORY AND CURRENT STATUS

Opsius stactogalus is a *Tamarix* specialist with widespread distribution in North America, where it is known to have been established since the early 1900s. The leafhopper was introduced unintentionally, probably along with intentional introductions of the host plant, from its native range in the warmer parts of Eurasia. The leafhopper may damage tamarisk, especially late in the season when populations can increase dramatically, and particularly on drought-affected plants. Damage is readily visible as yellowing foliage (**Fig. 11c,d**), but typically impact is minimal because damage occurs late in the season, often just prior to naturally occurring winter senescence. Wasp parasitism may limit some *O. stactogalus* populations and impact. **This leafhopper is not approved for redistribution in the USA.**

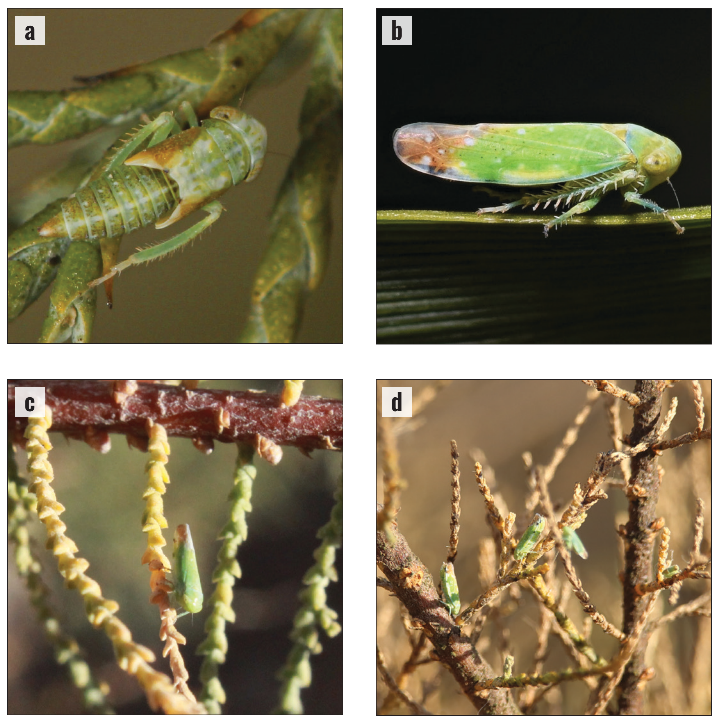

Figure 11. *Opsius stactogalus* (a) nymph; (b) adult; (c,d) adults and feeding damage (a: Simon Thevenin; b: Marcel Nadal; c: Leonardo Hernández Escudero; d: Orlandomontes; a–d: iNaturalist.org CC BY-NC 4.0;)

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NAISMA is a network of professionals challenged by invasive species: land managers, water resource managers, state, regional, and federal agency directors and staff, researchers, and nonprofit organizations. NAISMA's members are a diverse group of individuals and organizations who are involved in implementing invasive species management programs at all scales. Our mission is to support, promote, and empower invasive species prevention and management in North America. Our vision is to have North America's lands and waters protected from invasive species. NAISMA's programs aim to provide the support, training, and standards needed by the professional invasive species management community.

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