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Pollen Loads on Adult Insects from Tamarisk Flowers and Inferences about Larval Habitats
at Topock Marsh, Arizona

W. D. Wiesenborn,¹ S. L. Heydon,² and K. Lorenzen²

¹ Bureau of Reclamation, Lower Colorado Regional Office, P. O. Box 61470, Boulder City, Nevada 89006.

² Bohart Museum of Entomology, University of California, Davis, California 95616.

ABSTRACT: We identified adult insects aspirated from tamarisk, *Tamarix ramosissima* Ledebour (Tamaricaceae), flowers during May-August 2005 next to the Colorado River at Topock Marsh, Arizona. We compared tamarisk pollen loads and flower constancies, estimated as percentages of *T. ramosissima* pollen, of genera with >3 specimens. Insects from tamarisk flowers represented four orders, 16 families, and 37 genera. Detritus-feeding flies in Syrphidae were the predominant insects collected and comprised mostly of introduced *Syrphid pipiens* (L.). Bees were second most-frequently aspirated and predominated by introduced *Apis mellifera* L. Wasps comprised the highest diversity of genera and included parasitic Tiphidae and predaceous Vespidae and Sphecidae. Tamarisk pollen loads were greatest on *A. mellifera* and least on *S. pipiens*. All adult insects collected exhibited high flower constancies with tamarisk pollen averaging >91% of the pollen load in each genus. Introduced honey bees appear to be the most important pollinators of *T. ramosissima* at Topock Marsh based on their abundance, pollen loads, and flower constancies. Insects visiting *T. ramosissima* flowers require a variety of resources to reproduce such as cavities for nesting or soil for excavating burrows and insect prey or decomposed plants for feeding larvae.

KEY WORDS: Insecta, *Tamarix ramosissima*, pollination, flower constancy, larval diet.

Tamarix ramosissima Ledebour (Tamaricaceae) is a halophytic, deciduous shrub or tree facultatively dependent on shallow ground water (Brock, 1994; Di Tomaso, 1998). It is one of eight *Tamarix* species native to Eurasia and North Africa that have become naturalized in North America (Baum, 1967). Four deciduous species of *Tamarix*, collectively called tamarisk, are currently recognized in California (Wilken, 1993). Areal extent of tamarisk in the U.S. was estimated in 1961 to be 370,000 ha, mostly along stream channels in the Southwest (Robinson, 1965). Most tamarisk plants in the U.S. are *T. ramosissima*, *Tamarix chinensis* Loureiro, or their hybrids (Gaskin and Schaal, 2002, 2003). These two species also hybridize in the U.S. with the similar, but evergreen, introduced tree *Tamarix aphylla* (L.) Karsten (Gaskin and Shafroth, 2005). Leaves and stems on naturalized tamarisk support few species of insect herbivores, mostly the leafhopper *Opsius stactogalus* Fieber (Hemiptera: Cicadellidae) and the armored scales *Chionaspis* spp. (Hemiptera: Diaspididae), and their arthropod predators and parasites (Wiesenborn, 2005). Tamarisk's pervasiveness, water uptake, and low diversity of dependent wildlife have made it the target of classical biological control (DeLoach *et al.*, 2003; Milbrath and DeLoach, 2006).

Tamarisk reproduces sexually by self-pollinating or outcrossing (Gaskin and Schaal, 2002) or propagates vegetatively when buried stem segments sprout (Brock, 1994). *Tamarix ramosissima* flowers are small, with five 1-2 mm long white to reddish petals that are exceeded by the anthers and stigmas, clustered in 1.5-7 cm long spikes, and contain a nectar disk that subtends the superior ovary (Wilken, 1993). Tamarisk produces inflorescences during spring on previous-year or older branches and during summer on current-year branches (Baum, 1978), prolonging seed production and contributing to its invasiveness (DeLoach *et al.*, 2003).

Pollination of *Tamarix* by insects in North America has not been examined. A variety of insects visit tamarisk flowers. For example, a survey of *Tamarix* insects in southern Arizona found 12 families and six orders on flowers (Hopkins and Carruth, 1954). Insects on tamarisk flowers also provide an important food source for birds. Wiesenborn and Heydon (2007) compared diets of Southwestern Willow Flycatchers (*Empidonax traillii extimus* Phillips) (Passeriformes: Tyrannidae), an endangered bird (Sedgwick, 2000), breeding at three localities in Nevada and Arizona during 2004. Birds in western Arizona at Topock Marsh, where *T. ramosissima* predominates, most frequently ate Diptera comprised primarily of flower-visiting Syrphidae. Many species of holometabolous insects, such as flies and wasps, that visit flowers obtain nutrients from pollen and nectar only as adults. Abundances and species compositions of adult insects on tamarisk flowers likely result primarily from availabilities of food for immatures and resources for nesting.

In the present study, we identify adult insects found on *T. ramosissima* flowers at Topock Marsh and compare their pollen loads and flower constancies to estimate their potential for pollinating tamarisk. We also discuss resources other than tamarisk pollen or nectar required by these insects to complete their life-cycles and the contribution of Topock Marsh's wetland and riparian habitat to providing these resources.

Materials and Methods

The study was located (34° 47' N, 114° 32' W; elevation 133 m) at Topock Marsh, Havasu National Wildlife Refuge, Mohave County, western Arizona. The marsh is a permanent impoundment next to the Colorado River that contains open water, vegetated islands, and large areas of emergent wetland plants primarily comprised of cattails (*Typha* sp. [Typhaceae]). Maximum temperatures during July average 42.6° C, and minimum temperatures during

December average 5.6° C, at nearby Needles, California (Western Regional Climate Center, 2006). We collected insects at three sites 1.3 km apart along both sides of a dirt road that bordered and crossed the marsh near its west edge. Percent covers of plant species at each site were estimated by summing canopy lengths measured with a tape along both sides of the road. The north site was 65% arrowweed (*Pluchea sericea* [Nuttall] [Asteraceae]), 19% screwbean mesquite (*Prosopis pubescens* Benth [Fabaceae]), 12% tamarisk, and 3% mule fat (*Baccharis salicifolia* Nuttall [Asteraceae]). The middle site was 56% arrowweed and 43% tamarisk. The south site was 93% tamarisk and 8% Russian thistle (*Salsola tragus* L. [Chenopodiaceae]). We identified all trees that we collected insects from as *T. ramosissima* by their acuminate leaves and minutely-toothed sepals (Wilken, 1993). A plant voucher (accession no. 59598) was deposited at the Niles Herbarium, University of Nevada, Las Vegas.

Adult insects on tamarisk flowers were collected on 12 dates every 1-2 weeks during 2 May - 8 Aug 2005. Sites were sampled in random order on each date. We arbitrarily selected six trees with flowers for sampling insects at each site on each date. A total of 15-24 trees at each site were sampled across dates, because individual trees did not flower continuously during the entire study period. We sampled each site three times during 0825-1844 MST on 2 May 2005 and once during 0659-1339 MST on the remaining dates. Each tree was observed for insects on flowers for 10 min. We aspirated insects on tamarisk flowers to maximize pollen-load collection and segregate pollen by insect specimen. Each aspirated insect fell into a separate 4-dram vial containing 70% EtOH. We rinsed the intake tube of the aspirator with water between collections. We attempted to aspirate all insects observed on flowers within reach except ants (Formicidae). Lepidoptera, likely difficult to aspirate, were not observed on tamarisk flowers. We recorded time of day and air temperature when each insect was aspirated.

Pollen on insects was mounted for examination with a compound microscope. Plant material (eg. petals, anthers) aspirated with the insect was removed from the vial, and the vial was vortexed for 30 seconds. EtOH from the vial was centrifuged for 10 min at 3K rpm and drawn off. We added 3 ml of water to the pollen residue, mixed the suspension, and poured it into a 100 ml Teflon[®] evaporating dish. We stirred 1 ml of 12.5% polyvinyl alcohol (Dafni, 1992) into the pollen suspension and dried it 2 h at 50° C. The dried film (diameter 57 mm) was peeled from the dish and sandwiched between two pairs of side-by-side microscope slides marked with 30 mm-long lines. We examined the film at 100X by scanning four randomly-selected lines and counted pollen grains. Scanning was stopped when >200 pollen grains were counted. We calculated the area (mm²) of film examined by measuring the field-of-view diameter with a stage micrometer and the length of the scan with the graduated mechanical stage. Counted pollen was classified as tamarisk or non-tamarisk. Tamarisk pollen was recognized by its size and shape, as described for *T. ramosissima* (in Afghanistan) and *T. chinensis* (in Mohave County, Arizona) by Baum *et al.* (1971). Pollen on insects also was compared with pollen that we collected from tamarisk, arrowweed, and screwbean mesquite at the study location, stored in 70% EtOH, and mounted. We described pollen from these species, and photographed tamarisk pollen, by examining films in immersion oil at 1000X. Pollen dimensions ($\pm 1 \mu$) at 400X were measured with an ocular micrometer. We identified collected insects to the lowest taxon possible and deposited vouchers at the Bohart Museum of Entomology, University of California, Davis. Body lengths of arbitrarily selected specimens were measured (± 0.1 mm) with an ocular micrometer.

Relative load of *T. ramosissima* pollen on each insect was calculated by dividing the number of tamarisk pollen grains counted by the area of film examined. Relative pollen loads were transformed $\log Y$ and compared among genera with >3 specimens with a one-way analysis of

variance followed by orthogonal contrasts tested against the pooled error (Steel and Torrie, 1980; calculated with SYSTAT version 10.2, Richmond, CA). We estimated the flower constancy of each insect as the proportion of its pollen load comprised of tamarisk pollen (Dafni, 1992). Proportions were transformed $2 \arcsin(Y^{1/2})$ and averaged within the same genera as above. We back transformed means to the original scale for reporting.

Results

We collected 273 adult insects in four orders, 16 families, and 37 genera from *T. ramosissima* flowers at Topock Marsh (Table 1). Flower flies (Syrphidae) including *Palpada alhambra* (Hull), *Copestylum pallens* (Wiedemann), and the introduced *Syrirta pipiens* (L.) were most frequently collected. These syrphids were collected throughout the study period but mostly during early morning when air temperatures were low (Table 1). After flower flies, bees were most frequently collected and included the introduced honey bee, *Apis mellifera* L., the halictids *Lasioglossum* spp. and *Agapostemon melliventris* Cresson, the native bee *Melissodes tepida* Cresson, and several species of leaf-cutting bees (*Megachile*). Wasps were the third most-frequently aspirated taxon and included the tiphids *Paratiphia* and *Myzinum*, the paper wasp *Polistes fuscatus* (F.), the potter wasp *Pachodynerus praecox* (Saussure), and the sand wasp *Bembix melanaspis* Parker.

Tamarix ramosissima flowers at Topock Marsh produced pollen (Fig. 1) that was spheroidal (diameter 11-15, 13 ± 1 [SD] μ , $n = 20$) or prolate (length 15-20, 17 ± 1 μ , $n = 20$) and grainy with a smooth wall. Pollen ($n = 290$) from one inflorescence was 90% spheroidal and 10% prolate. Tamarisk pollen was furrowed, more strongly in prolate grains, in equatorial view and weakly tricolpate in polar view. Pollen from arrowweed and screwbean mesquite was larger. *Pluchea sericea* pollen was spheroidal (diameter 20-25, 23 ± 1 μ , $n = 20$) and grainy with a spiny wall. *Prosopis pubescens* pollen was spheroidal (diameter 20-28, 24 ± 2 μ , $n = 20$) or prolate (length 30-35, 32 ± 2 μ , $n = 10$) and grainy with a smooth wall.

Relative loads of *T. ramosissima* pollen on insects in genera with >3 specimens collected from tamarisk flowers varied among genera ($F = 66.8$, $df = 12,223$, $P < 0.001$; Fig. 2). Mean absolute loads of tamarisk pollen, extrapolated by multiplying mean relative pollen-loads by the total film area (2.6×10^3 mm²), ranged from 2.2×10^5 pollen grains on the introduced honey bee *A. mellifera* to 1.2×10^3 pollen grains on the introduced flower fly *S. pipiens*. Pollen loads were greater on native bees compared with wasps ($F = 20.5$, $df = 1,223$, $P < 0.001$). Within native bees, *Megachile* spp. and *M. tepida* carried more pollen than the halictids *A. melliventris* and *Lasioglossum* spp. ($F = 6.76$, $df = 1,223$, $P = 0.01$). Female Megachilidae have dense hairs on their abdominal sterna, the scopa, and *M. tepida* have dense hairs on their middle and hind legs. The halictids we collected lack these features, and *Lasioglossum* spp. were the smallest (mean length 4.7 mm, $n = 3$) insects aspirated from flowers. Pollen loads on wasps generally were related to body size. Pollen loads were greatest on *Myzinum* spp. (*Myzinum* prob. *frontalis* mean length 13.8 mm, $n = 2$) and *P. fuscatus* (14.4 mm, $n = 2$) followed by *Paratiphia* sp. (8.4 mm, $n = 2$) and *P. praecox* (9.4 mm, $n = 2$). Flower flies carried less tamarisk pollen than wasps and native bees ($F = 57.4$, $df = 1,223$, $P < 0.001$). Pollen loads on flower flies also were related to body size. *Palpada alhambra* (mean length 9.7 mm, $n = 2$) carried the most tamarisk pollen followed by *C. pallens* (7.9 mm, $n = 2$) and the thin-bodied *S. pipiens* (6.3 mm, $n = 3$).

Proportions of *T. ramosissima* pollen on insects from tamarisk flowers varied among genera (Fig. 3). Flower constancies were high, with mean proportions of tamarisk pollen exceeding 91% of each genus's pollen load. Flower constancies may have been overestimated, because

Table 1. Adult insects collected from *Tamarix ramosissima* flowers during 2005 at Topock Marsh, Arizona.

Family ^a	Genus or species	<i>n</i>	Collection date first-last; mean	Mean MST ^{b,c}	Mean air ° C ^c
Rhopalidae ^{He}	<i>Liorhyssus hyalinus</i> F.	2	8-15 Jul; 11 Jul	0819	28
Reduviidae ^{He}	<i>Zelus</i> sp.	1	1 Aug	1057	37
Dermestidae ^C	<i>Novelsis uteana</i> Casey	2	25-25 May	1019	36
	<i>Cryptorhopalum</i> sp.	1	15 Jul	1012	37
	<i>Trogoderma</i> sp.	1	2 May	1150	32
Coccinellidae ^C	<i>Hippodamia convergens</i> Guerin	3	2-2 May	1020	30
Lagriidae ^C	<i>Statira</i> sp.	1	8 Jul	0659	19
Tiphidae ^{Hy}	<i>Myzinum</i> prob. <i>frontalis</i>	8	7 Jun-8 Aug; 27 Jul	1002	33
	<i>Myzinum maculatum</i> F.	1	25 May	0911	28
	<i>Paratiphia</i> sp.	16	8 Jul-8 Aug; 24 Jul	1007	34
Scoliidae ^{Hy}	<i>Campsomeris tolteca</i> Saussure	1	25 May	0946	34
Vespididae ^{Hy}	<i>Stenodynerus</i> sp. nr. <i>blandus</i>	2	1-8 Aug; 4 Aug	0853	34
	<i>Stenodynerus microstictus</i> Viereck	1	25 Jul	1108	35
	<i>Pachodynerus praecox</i> (Saussure)	6	2 May-8 Aug; 15 Jul	0935	33
	<i>Polistes fuscatus</i> (F.)	11	2 May-8 Aug; 2 Jul	1002	33
Sphecidae ^{Hy}	<i>Tachytes</i> sp.	1	25 Jul	0749	30
	<i>Oxybelus</i> sp.	1	15 Jul	0906	31
	<i>Bembix melanaspis</i> Parker	4	1-8 Aug; 4 Aug	0941	35
	<i>Aphilanthops</i> sp.	1	25 May	0940	34
	<i>Cerceris macswaini</i> Scullen	2	1-8 Aug; 4 Aug	0842	34
Halictidae ^{Hy}	<i>Nomia nevadensis</i> Cresson	1	8 Jul	0855	27
	<i>Agapostemon melliventris</i> Cresson	7	27 Jun-1 Aug; 7 Jul	0905	27
	<i>Lasioglossum</i> spp.	13	2 May-15 Jul; 5 Jun	0914	28
Andrenidae ^{Hy}	<i>Andrena fracta</i> Casad & Cockerell	1	2 May	1630	33
Megachilidae ^{Hy}	<i>Megachile chilopsidis</i> Cockerell	1	20 Jun	0934	30
	<i>Megachile concinna</i> Smith	2	8-15 Jul; 11 Jul	0903	32
	<i>Megachile frugalis</i> Cresson	3	25 Jul-8 Aug; 3 Aug	0955	34
Ceratinidae ^{Hy}	<i>Ceratina arizonensis</i> Cockerell	1	25 May	1100	37
Apidae ^{Hy}	<i>Melissodes tepida</i> Cresson	8	25 May-8 Aug; 12 Jul	0957	32
	<i>Centris rhodopus</i> Cockerell	1	1 Jun	0843	28
Syrphidae ^D	<i>Apis mellifera</i> L.	55	2 May-8 Aug; 1 Jun	1127	30
	<i>Toxomerus marginatus</i> Say	1	7 Jun	1021	26
	<i>Eupeodes volucris</i> Osten Sacken	1	2 May	1830	27
	<i>Eupeodes</i> sp.	1	2 May	1836	26
	<i>Melangyna</i> sp.	3	2-2 May	0929	29
	<i>Copestylum pallens</i> (Wiedemann)	14	19 May-8 Aug; 30 Jun	0824	27
	<i>Parhelophilus</i> sp.	2	27 Jun-1 Aug; 14 Jul	0802	27

	<i>Lejops</i> sp.	1	15 Jul	0720	28
	<i>Palpada alhambra</i> (Hull)	33	2 May-8 Aug; 22 Jul	0828	30
	<i>Syritta pipiens</i> (L.)	54	2 May-8 Aug; 2 Jul	0839	28
Muscidae ^D	<i>Coenosia occidentis</i> Stein	3	2-2 May	1239	25
Sarcophagidae ^D	<i>Amobia</i> sp.	1	25 Jul	1132	34

^aSuperscript letters are orders: C, Coleoptera; D, Diptera; He, Hemiptera; Hy, Hymenoptera.

^bMountain Standard Time.

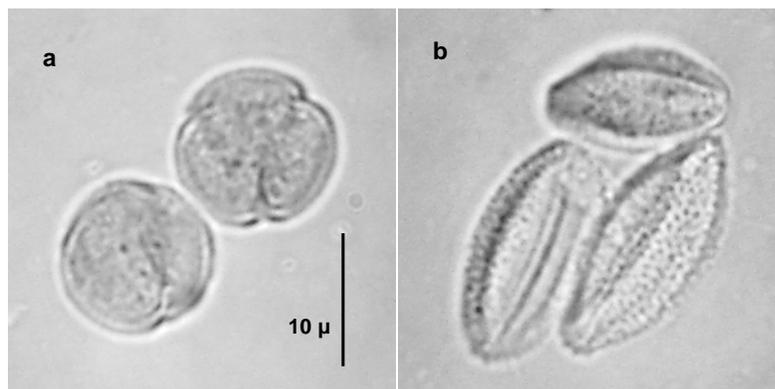
^cAt time of collection.

more pollen may have been collected during each visit to an inflorescence on tamarisk than on other plant species due to tamarisk's smaller pollen size. Flower constancies were highest on the introduced honey bee, halictid bees, the tephritid wasp *Paratiphia* sp., and flower flies. Flower constancies were lowest on the native bees *Megachile* spp. and *M. tepida* and the vespid wasp *P. praecox*.

Discussion

Tamarix ramosissima at Topock Marsh appears to be pollinated mostly by introduced *A. mellifera*. Introduced honey bees were most frequently collected, observed during spring and summer, individually specific to tamarisk flowers, and carrying the greatest amount of *T. ramosissima* pollen. Expansion of *T. ramosissima* in the U.S. may have been facilitated by the earlier introduction of *A. mellifera*, because the spread of introduced plants has been associated with introduced bees (Hanley and Goulson, 2003). The native bees *M. frugalis* and *M. tepida* carried large tamarisk-pollen loads but are unlikely to pollinate many tamarisk plants due to their low numbers. The native syrphid *P. alhambra* also may be an important pollinator of *T. ramosissima* at Topock Marsh and similar localities where nearby marshes support its larval development. *Palpada alhambra* were frequently aspirated, found during the entire study period, individually specific to *T. ramosissima* flowers, and carrying a moderate amount of tamarisk pollen. The low pollen loads on *S. pipiens* likely decrease their ability to pollinate a large proportion of tamarisk flowers despite their apparent abundance. The frequency of self-pollination, affecting reliance on pollinators, has not been determined in *Tamarix*.

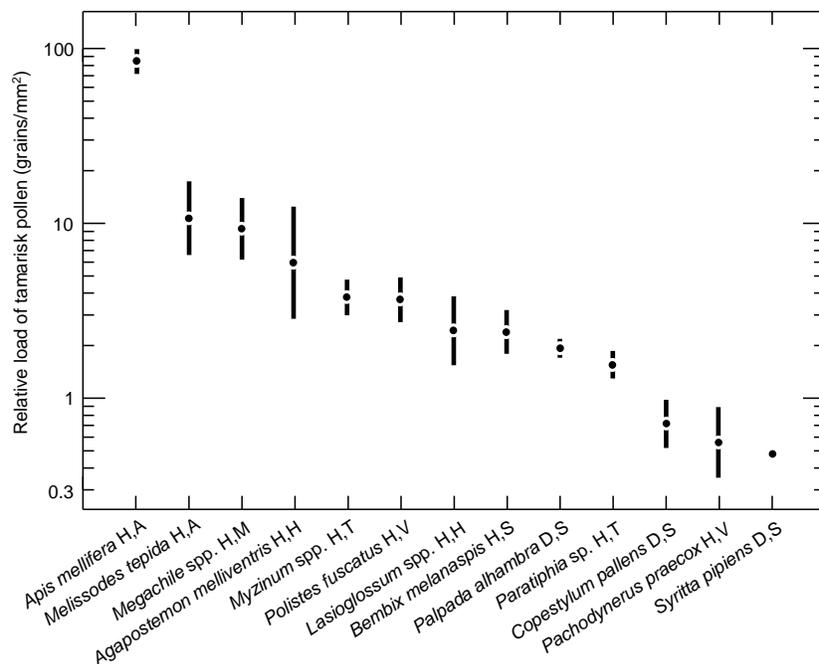
Fig. 1. Pollen from *Tamarix ramosissima* flowers at Topock Marsh, Arizona. Brightfield photomicrographs at same scale. a. Spheroidal pollen grains, upper grain in polar view and lower grain in equatorial view. b. Prolate pollen grains in equatorial view.



Families of insects collected from *T. ramosissima* flowers at Topock Marsh differed from those collected from tamarisk flowers in southern Arizona by Hopkins and Carruth (1954). They collected Thripidae (Thysanoptera); Reduviidae and Aphidae (Hemiptera); Apidae, Pompilidae, and male Mutillidae (Hymenoptera); Scarabaeidae (Coleoptera); Papilionidae, Nymphalidae, and Pieridae (Lepidoptera); and Anthomyiidae and Sciomyzidae (Diptera). Only *A. mellifera* was found on tamarisk flowers in southern Arizona and at Topock Marsh.

Species of adult insects collected on *T. ramosissima* flowers at Topock Marsh expectedly reflect, in part, the diversity of larval habitats. Butterflies were not observed at our study sites, because host plants likely were not available. The Hymenoptera that we collected can be divided by larval diet into bees (Halictidae, Megachilidae, and Apidae) and wasps (Tiphidae, Vespidae, and Sphecidae). Bees feed their larvae nectar and pollen that can be obtained from tamarisk. The larvae of wasps generally require insects as food, and because tamarisk supports a low diversity of insect herbivores (Wiesenborn, 2005), insect prey or hosts must be obtained from other nearby sources. Both tiphids, *M. prob. frontalis* and *Paratiphia* sp., are external parasites of soil-dwelling larvae in Scarabaeoidea (Brothers and Finnamore, 1993). Female *B. melanaspis* provision larvae with a variety of flies and sometimes damselflies (Alcock and Gamboa, 1975). The potter wasp *P. praecox* and paper wasps (*Polistes* spp.) provision their larvae with captured caterpillars (Richards, 1978; Krombein, 1979).

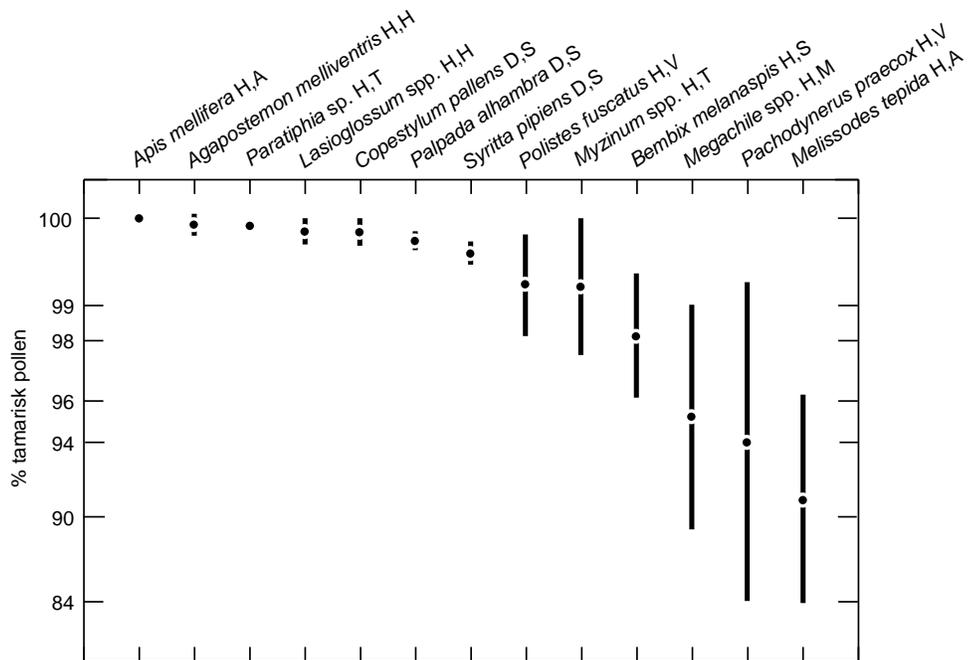
Fig. 2. Relative loads of *Tamarix ramosissima* pollen (grains/mm² of mounting medium examined) on insects in genera with >3 specimens collected from *T. ramosissima* flowers at Topock Marsh, Arizona. Means (points) ± SE's (lines) within genera were back transformed from data transformed log Y and plotted on transformed scale. Letters after genera are orders (D, Diptera; H, Hymenoptera) followed by families (A, Apidae; H, Halictidae; M, Megachilidae; S, Syrphidae; T, Tiphidae; V, Vespidae).



Availabilities of suitable nesting sites, in addition to food sources, influence the diversities of bee communities (Potts *et al.*, 2005). Several bees collected at Topock Marsh are ground nesters. Most halictid bees including *Agapostemon* and *Lasioglossum* dig burrows in soil for larval cells. *Melissodes tepida* females in Idaho dig clusters of shallow, branching burrows among stems and roots of saltgrass, *Distichlis stricta* (Torrey) Rydberg (Poaceae), place one larval cell at the end of each branch, and provide larvae with diverse pollen (Triplett and Gittins, 1988). Suitabilities of ground nesting sites are affected by numerous soil factors including texture, hardness, moisture level, slope, and insolation (Potts *et al.*, 2005). Nesting sites in soil also would be important for other Hymenoptera that we collected. For example, *B. melanaspis* requires sandy soil as a substrate for digging solitary burrows as deep as 114 cm (Alcock and Gamboa, 1975).

Several of the bees and wasps found at Topock Marsh require above-ground cavities of various sizes for nesting. Tamarisk is not prone to forming hollow stems and is a poor host for wood boring insects, so other plants are required by these cavity nesters for either their holes or nest lining materials. The potter wasp *P. praecox* utilizes the cavities created when pith rots out of plant stems (Parker and Bohart, 1966). *Agapostemon* bees sometimes exploit cavities made by other, unrelated insects (Roberts, 1969) with *A. melliventris* utilizing mud nests vacated by *Sceliphron* wasps (Hurd, 1979). Leaf-cutting bees (*Megachile* spp.) use excised circles of leaves or petals to construct larval cells that are stacked within narrow cavities (Hurd, 1979). Leaves

Fig. 3. Percentages of pollen loads comprised of *Tamarix ramosissima* pollen on insects in genera with >3 specimens collected from *T. ramosissima* flowers at Topock Marsh, Arizona. Means (points) \pm SE's (lines) within genera were back transformed from proportions transformed $2 \arcsin (Y^{1/2})$ and plotted on transformed scale. Letters after genera are orders (D, Diptera; H, Hymenoptera) followed by families (A, Apidae; H, Halictidae; M, Megachilidae; S, Syrphidae; T, Tiphiidae; V, Vespidae).



and petals on *Tamarix* likely are too small, requiring leaf-cutting bees at Topock Marsh to obtain nest material from other plant species. Introduced honey bees form large, social colonies within artificial or natural cavities, such as inside rotting tree trunks or limbs or beneath rocks. They require water, obtained directly or from nectar, for cooling their nests during summer.

Decaying plant tissue provides nest material or larval food for some wasps and flower flies that visit *T. ramosissima* flowers. Paper wasps (*Polistes* spp.) are eusocial and construct hanging nests with macerated plant fibers pulled from splintered wood (Richards, 1978). *Copestylum* larvae live in decaying plant material, primarily cacti (Cole, 1969; Vockeroth and Thompson, 1987). *Syrpitta* larvae inhabit wet, decaying organic material such as manure or rotting vegetation (Rotheray, 1993). Larvae of *C. pallens* and *S. pipiens* at Topock Marsh likely develop on decaying emergent marsh vegetation, especially *Typha*. Emergent *Typha* stems and leaves senesce during fall and regrow from submerged rhizomes during spring. Larvae of several syrphid genera are associated with rotting *Typha* (Rotheray, 1993). Larvae of *S. pipiens* and other syrphids developing along the edge of Topock Marsh also may be provided with dung. We have seen or heard feral hogs, *Sus scrofa* L. (Artiodactyla: Suidae), wallowing at the marsh's edge near our study sites. Standing water within Topock Marsh likely supports larvae of *P. alhambra*. Larvae of syrphids in Eristalini, including *Palpada*, are aquatic and feed on detritus and microorganisms (Ferrar, 1987). Syrphidae adult males consume mostly nectar for energy, whereas adult females consume primarily pollen for egg maturation (Haslett, 1989).

Insect species collected from *T. ramosissima* flowers at Topock Marsh are eaten by birds. Fecal samples from Willow Flycatchers at Topock Marsh contained parts of the syrphids *C. pallens*, *P. alhambra*, and *S. pipiens* (Wiesenborn and Heydon, 2007). These flower flies likely are available as prey during the breeding season due to their long seasonal occurrence, relative abundance, and activity during early morning when air temperatures are low and flycatchers are active and feeding. After Diptera, flycatchers at Topock Marsh most frequently ate Odonata (damselflies and dragonflies, the largest insects eaten) followed by Hemiptera and Hymenoptera. *Apis mellifera*, common visitors to tamarisk flowers but generally avoided by birds due to their stings, were not eaten by flycatchers. Flycatchers most frequently ate Diptera and Hymenoptera (including Halictidae) in similar numbers alongside the Virgin River in southern Nevada, where water is not impounded, emergent wetland plants are less abundant, and tamarisk is mixed with the native willow *Salix exigua* (Wiesenborn and Heydon, 2007). The high abundances of decaying wetland plants and flowering tamarisk trees at Topock Marsh likely combine to produce and sustain large populations of detritus-feeding syrphids that provide insectivorous birds with food.

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Literature Cited

Alcock, J., and G. J. Gamboa. 1975. The nesting behavior of some sphecoid wasps of Arizona, including *Bembix*, *Microbembix*, and *Philanthus*. *Journal of the Arizona Academy of Science*

- 10: 160-165.
- Baum, B. R. 1967. Introduced and naturalized tamarisks in the United States and Canada (Tamaricaceae). *Baileya* 15: 19-25.
- Baum, B. R. 1978. *The Genus Tamarix*. Israel Academy of Sciences and Humanities; Jerusalem; xii + 209 pp.
- Baum, B. R., I. J. Bassett, and C. W. Crompton. 1971. Pollen morphology of *Tamarix* species and its relationship to the taxonomy of the genus. *Pollen et Spores* 13: 495-521.
- Brock, J. H. 1994. *Tamarix* spp. (salt cedar), an invasive exotic woody plant in arid and semi-arid riparian habitats of western USA. Pp. 27-44. In de Waal, L. C., L. E. Child, P. M. Wade, and J. H. Brock (eds.), *Ecology and Management of Invasive Riverside Plants*. Wiley; New York, New York; x + 217 pp.
- Brothers, D. J., and A. T. Finnamore. 1993. Superfamily Vespoidea. Pp. 161-278 In Goulet, H., and J. T. Huber (eds.), *Hymenoptera of the World: an Identification Guide to Families*. Publication 1894/E, Agriculture Canada, Biosystematics Research Centre; Ottawa, Ontario; 668 pp.
- Cole, F. R. 1969. *The Flies of Western North America*. University of California Press; Berkeley; 693 pp.
- Dafni, A. 1992. *Pollination Ecology: a Practical Approach*. Oxford University Press; New York, New York; xv + 250 pp.
- DeLoach, C. J., P. A. Lewis, J. C. Herr, R. I. Carruthers, J. L. Tracy, and J. Johnson. 2003. Host specificity of the leaf beetle, *Diorhabda elongata deserticola* (Coleoptera: Chrysomelidae) from Asia, a biological control agent for saltcedars (*Tamarix*: Tamaricaceae) in the Western United States. *Biological Control* 27: 117-147.
- Di Tomaso, J. M. 1998. Impact, biology, and ecology of saltcedar (*Tamarix* spp.) in the southwestern United States. *Weed Technology* 12: 326-336.
- Ferrar, P. 1987. *A Guide to the Breeding Habits and Immature Stages of Diptera Cyclorrhapha* (part 1: text). Entomonograph vol. 8, E. J. Brill/Scandinavian Science Press; Leiden, Holland; 478 pp.
- Gaskin, J. F., and B. A. Schaal. 2002. Hybrid *Tamarix* widespread in U.S. invasion and undetected in native Asian range. *Proceedings of the National Academy of Sciences USA* 99: 11256-11259.
- Gaskin, J. F., and B. A. Schaal. 2003. Molecular phylogenetic investigation of U.S. invasive *Tamarix*. *Systematic Botany* 28: 86-95.
- Gaskin, J. F., and P. B. Shafroth. 2005. Hybridization of *Tamarix ramosissima* and *T. chinensis* (saltcedars) with *T. aphylla* (athel) (Tamaricaceae) in the southwestern USA determined from DNA sequence data. *Madroño* 52: 1-10.
- Hanley, M. E., and D. Goulson. 2003. Introduced weeds pollinated by introduced bees: Cause or effect? *Weed Biology and Management* 3: 204-212.
- Haslett, J. R. 1989. Adult feeding by holometabolous insects: pollen and nectar as complementary nutrient sources for *Rhingia campestris* (Diptera: Syrphidae). *Oecologia* 81: 361-363.
- Hopkins, L., and L. A. Carruth. 1954. Insects associated with salt cedar in southern Arizona. *Journal of Economic Entomology* 47: 1126-1129.
- Hurd, Jr., P. D. 1979. Superfamily Apoidea. Pp. 1741-2209. In Krombein, K. V., P. D. Hurd, Jr., D. R. Smith, and B. D. Burks. *Catalog of Hymenoptera in America North of Mexico*, vol. 2. Smithsonian Institution Press, Washington, D.C. xvi + pp. 1199-2209.

- Krombein, K. V. 1979. Superfamily Vespoidea. Pp. 1469-1522. In Krombein, K. V., P. D. Hurd, Jr., D. R. Smith, and B. D. Burks. *Catalog of Hymenoptera in America North of Mexico*, vol. 2. Smithsonian Institution Press, Washington, D.C. xvi + pp. 1199-2209.
- Milbrath, L. R., and C. J. DeLoach. 2006. Host specificity of different populations of the leaf beetle *Diorhabda elongata* (Coleoptera: Chrysomelidae), a biological control agent of saltcedar (*Tamarix* spp.). *Biological Control* 36: 32-48.
- Parker, F. D., and R. M. Bohart. 1966. Host-parasite associations in some twig-nesting Hymenoptera from western North America. *Pan-Pacific Entomologist* 42: 91-98.
- Potts, S. G., B. Vulliamy, S. Roberts, C. O'Toole, A. Dafni, G. Ne'eman, and P. Willmer. 2005. Role of nesting resources in organising diverse bee communities in a Mediterranean landscape. *Ecological Entomology* 30: 78-85.
- Richards, O. W. 1978. *The Social Wasps of the Americas excluding the Vespinae*. British Museum (Natural History), London; vii + 580 pp.
- Roberts, R. B. 1969. Biology of the bee genus *Agapostemon* (Hymenoptera: Halictidae). *University of Kansas Science Bulletin* 14: 689-719.
- Robinson, T. W. 1965. Introduction, spread and areal extent of saltcedar (*Tamarix*) in the western states. US Geological Survey Professional Paper 491-A; iii + 12 pp. + map.
- Rotheray, G. E. 1993. *Colour Guide to Hoverfly Larvae (Diptera, Syrphidae) in Britain and Europe*. *Dipterists Digest* no. 9; 156 pp.
- Sedgwick, J. A. 2000. Willow Flycatcher (*Empidonax traillii*). Pp. 1-32 In Poole, A., and F. Gill (eds.), *The Birds of North America*, Number 533. The Birds of North America, Philadelphia, Pennsylvania.
- Steel, R. G. D. and J. H. Torrie. 1980. *Principles and Procedures of Statistics: a Biometrical Approach* (2nd ed.). McGraw-Hill; New York, New York; xxi + 633 pp.
- Triplett, D. C., and A. R. Gittins. 1988. Nesting, mating and foraging habits of *Melissodes (Melissodes) tepida tepida* Cresson in Idaho (Hymenoptera: Anthophoridae). *Proceedings of the Entomological Society of Washington* 90: 462-470.
- Vockeroth, J. R., and F. C. Thompson. 1987. Syrphidae. Pp. 713-743. In McAlpine, J. F. (ed.), *Manual of Nearctic Diptera*, vol. 2. Monograph No. 28, Agriculture Canada, Biosystematics Research Centre; Ottawa, Ontario; vi + pp. 677-1332.
- Western Regional Climate Center. 2006. Western U.S. climate historical summaries. Desert Research Institute; Reno, Nevada. www.wrcc.dri.edu/Climsum.html (accessed 30 March 2006).
- Wiesenborn, W. D. 2005. Biomass of arthropod trophic levels on *Tamarix ramosissima* (Tamaricaceae) branches. *Environmental Entomology* 34: 656-663.
- Wiesenborn, W. D., and S. L. Heydon. 2007. Diets of breeding Southwestern Willow Flycatchers in different habitats. *Wilson Journal of Ornithology* (in press).
- Wilken, D. H. 1993. Tamaricaceae: tamarisk family, P. 1080. In Hickman, J. C. (ed.), *The Jepson Manual: Higher Plants of California*. University of California Press; Berkeley, California; xvii + 1400 pp.