Influences of the Tamarisk Leaf Beetle (*Diorhabda carinulata*) on the Diet of Insectivorous Birds Along the Dolores River in Southwestern Colorado

By Sarah L. Puckett and Charles van Riper III

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Abstract

We examined the effects of a biologic control agent, the tamarisk leaf beetle (*Diorhabda carinulata*), on native avifauna in southwestern Colorado, specifically, addressing whether and to what degree birds eat tamarisk leaf beetles. In 2010, we documented avian foraging behavior, characterized the arthropod community, sampled bird diets, and undertook an experiment to determine whether tamarisk leaf beetles are palatable to birds. We observed that tamarisk leaf beetles compose 24.0 percent (95-percent-confidence interval, 19.9-27.4 percent) and 35.4 percent (95-percent-confidence interval, 32.4-45.1 percent) of arthropod abundance and biomass in the study area, respectively. Birds ate few tamarisk leaf beetles, despite a superabundance of *D. carinulata* in the environment. The frequency of occurrence of tamarisk leaf beetles in bird diets was 2.1 percent (95-percent-confidence interval, 1.3- 2.9 percent) by abundance and 3.4 percent (95-percent-confidence interval, 2.6-4.2 percent) by biomass. Thus, tamarisk leaf beetles probably do not contribute significantly to the diets of birds in areas where biologic control of tamarisk is being applied.

Introduction

Riparian corridors, narrow belts of vegetation along streams and rivers, are crucial components of ecosystems in the Southwestern United States, owing to their importance to the perpetuation of water and wildlife in an otherwise-arid region (Knopf and others, 1988; Skagen and others, 1998). Although riparian vegetation contributes to only a small percentage of land cover in the Western United States, it is critically important for maintaining high richness and densities of birds in this region (Anderson and Ohmart, 1977; Krueper and others, 2003; Brand and others, 2010). However, anthropogenic changes to natural patterns of riverflow contribute to the susceptibility of riparian corridors to invasion by nonnative species (Baker, 1986; Mack and others, 2000). Naturalization of nonnative species alters ecosystem structure and function significantly and is considered one of the primary threats to rare and endangered species (Randall, 1996; Culliney, 2005). As a result, control of the populations of invasive species is commonly a management priority. Biologic control, or introduction of host-specific natural enemies to control nonnative pests, may be a sustainable and relatively inexpensive option for management of invasive species. Biologic control agents, however, may have adverse or unexpected effects on native species (Louda and others, 2003; Kimberling, 2004). Therefore, monitoring the interactions between biologic control agents and native communities is essential, so that the appropriateness of this control method and its overall success can be evaluated objectively (Blossey, 1999).

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Tamarisk (a.k.a. saltcedar, *Tamarix* spp.; Radford and others, 1965), a deciduous shrub native to drier regions of Eurasia and Africa, was introduced into the United States in the mid-1800s as an ornamental plant and to provide shade and erosion control. Aided by its capacity to grow in saline soil, its prolific seed production, and its tolerance for drought conditions, tamarisk now occupies ~400,000 to 600,000 ha of waterways and flood plains in the Western United States (Neill, 1985; Zavaleta, 2000; Gaskin and Schaal, 2002), particularly in areas where natural flood regimes have been altered (Warren and Turner, 1975; Cleverly and others, 1997; DiTomaso, 1998; Glenn and Nagler, 2005). Naturalization of this vigorous invader can culminate in substantial changes to the structure and function of streams (Stromberg and others, 2007), including reduction in water quantity due to an increase in evapotranspiration rates, degradation of habitat for some native species, increase in the frequency and severity of fire, and displacement of native vegetation (Anderson and Ohmart 1977; Shafroth and others, 2005). Several studies, however, have shown that tamarisk can also be an important habitat feature for various birds (Brown and Trosset, 1989; Hunter and others, 1988; Ellis, 1995). An emerging perspective suggests that the abundance of bird species is highest at intermediate abundances of tamarisk and native vegetation (van Riper and others, 2008). Regardless, controlling tamarisk appeals to many agencies, especially in light of its expanding geographic distribution (Duncan and others, 2004; Shafroth and Briggs, 2008; Barz and others, 2009).

Traditional strategies for controlling tamarisk include mechanical removal, fire, and herbicide. These techniques, each of which has its advantages and limitations, may affect growth of native vegetation in riparian communities (Hultine and others, 2010). A relatively new addition to management of tamarisk is biologic control. Tamarisk leaf beetles (*Diorhabda carinulata*; Desbrochers, 1870), originally from Eurasia, were selected as a biologic control agent for tamarisk, owing to their high host specificity, broad geographic range, and presumed ability to adapt to conditions in the United States. Biologic control of tamarisk, which was first implemented in 2001, has resulted in successful defoliations in Nevada, Utah, Colorado, and Wyoming (Dudley and DeLoach, 2004). Tamarisk plants produce new foliage after ~3-6 weeks, however, and multiple defoliation events per year are needed to affect mortality at a given site. In northern Nevada, tamarisk mortality reached 40 percent by the fourth year of consecutive defoliation events (Dudley and others, 2006), and 3 years of defoliation by tamarisk leaf beetles culminated in ~25-percent mortality of tamarisk at Big Springs, Tex. (Moran and others, 2009). Benefits of biologic control include relatively low cost once initial research and development have been completed, low maintenance, and automatic dispersal of agents. Some questions remain with this approach, however, because it involves introduction of nonnative organisms that can alter the structure of riparian communities.

Tamarisk leaf beetles are able to spread broadly and defoliate tamarisk on a grand scale (Paxton and others, 2011). Widespread loss of riparian vegetation, coupled with the addition of a potential food resource that is commonly superabundant, may affect native wildlife. Proponents of biologic control of tamarisk suggest that birds eat tamarisk leaf beetles and that the presence of *D. carinulata* in areas inhabited by tamarisk may enhance habitat quality for birds during defoliation (DeLoach and others, 2004; Dudley and DeLoach, 2004; Longland and Dudley, 2008). However, any beneficial response by birds to an increase in the abundance of prey depends upon palatability of the prey (Paxton and others, 2011).

Palatability in arthropods is generally predictable on the basis of coloration, behavior, and the presence of potential defensive compounds in host plants (Bowers and Farley, 1990). Although little is currently known about the palatability or nutritional value of *D. carinulata,* the tamarisk leaf beetle feeds almost exclusively on tamarisk, a plant rich in noxious substances (Dudley and DeLoach, 2004; Drabu and others, 2012). Of the chemical compounds that occur naturally in *Tamarix gallica L,* one of several *Tamarix* spp. naturalized in the Southwestern United States, ~50 percent are tannins, which are bitter, astringent, and able to function in a defensive role against herbivory in plants (see table 1; Levin, 1976; Coley, 1986). Two other compounds produced by several plant species for their insecticidal properties, germacrene D and benzyl benzoate, were also detected in *T. gallica* (Landegren and others, 1979; Arimura and others, 2004). Sequestration of the noxious or unpalatable compounds produced by tamarisk may provide *D. carinulata* with defense mechanisms against predation.

We decided to investigate how tamarisk leaf beetles influence native birds. Specifically, we used observational and experimental methods to determine whether and to what degree birds eat tamarisk leaf beetles. This interaction has implications for the success of biologic control of tamarisk, as well as for the welfare of avian communities in areas where biologic control is being applied. To answer these questions, we (1) determined in what substrates and to what heights birds forage, (2) determined the composition of the arthropod community at sites where birds forage, (3) evaluated the diets of insectivorous birds, and (4) tested the palatability of tamarisk leaf beetles to native avifauna. Additionally, we characterized the phenology of tamarisk to determine its availability of green-leaf, flower, and fruit coverage and to provide an index of damage to tamarisk by *D. carinulata* (brown leaves). We then compared these phenological data with avian use of tamarisk to track the response of birds to beetle damage and defoliation of tamarisk.

Methods

Study Area

The Dolores River, a tributary to the Colorado River, flows ~400 km through parts of southwest Colorado and southeastern Utah. Three study sites, at river miles 47, 54, and 97 (Slick Rock, Crocker-Bedford Ranch, and Bedrock, respectively, fig. 1), were selected along the Dolores River in southwestern Colorado to evaluate the use of tamarisk leaf beetles and tamarisk by birds and to estimate the availability of arthropod prey (see fig. 1).

Each study site covered ~4 ha of riparian corridor. Study sites were dominated by seven species of shrub: coyote willow (*Salix exigua*; Davis, 1952), desert olive (*Forestiera neomexicana*; Kearney and Peebles, 1960), sumac (*Rhus aromatic*; Booth and Wright ,1966), big sagebrush (*Artemisia tridentate;* Davis, 1952), rabbitbrush (*Chrysothamnus nauseosus*; Davis, 1952), greasewood (*Sarcobatus vermiculatus*; Davis, 1952), and exotic tamarisk (see table 2). Other, less common plants included fourwing saltbush (*Atriplex canescens*; Davis, 1952), boxelder (*Acer negundo*; Deam, 1940), Gambel-oak (*Quercus gambelii*; Kearney and Peebles, 1960), Siberian-elm (*Ulmus pumila*; McGregor and others, 1977), and mulefat (*Baccharis salicifolia*; Abrams, 1960). Cottonwood (*Populus* spp.; Kearney and Peebles, 1960) was rare at all sites, and pinyon (*Pinus edulis*; Kearney and Peebles, 1960) and juniper (*Juniperus* spp.; House, 1924) dominated scree along the canyon slope. Annual precipitation averaged ~30 cm at these sites, and summer temperatures ranged from 7°C to 35°C. Data were collected between June 1 and August 15, 2010, through 2012.

Vegetation

At each study site, we sampled vegetation within ten 0.04-ha (11.3-m radius) circular plots with their centers ~25 m from the bank and at 100-m intervals parallel to the river (James and Shugart, 1970). All trees (any woody species >7.5 cm in diameter at breast height [DBH]) were identified as to species, counted, and their DBHs measured to the nearest centimeter. Density, frequency, and dominance were estimated by species and averaged across plots for each study site.

We established one 22.6-m transect perpendicular to the river across each 0.04-ha plot to measure shrub density by species. All woody stems <7.5 cm in diameter that made contact with a 2-m rod, held at breast height parallel to the ground, were counted. The percentage of coverage of woody stems per hectare was calculated for seven dominant species of shrubs: coyote willow, desert olive, sumac, big sagebrush, rabbitbrush, greasewood, and tamarisk. Estimates of the availability of various shrub species were then compared with observations of foraging behavior to characterize the selection of different plants by birds.

Phenology

We sampled tamarisk phenology in 2010-12 to determine the availability of green-leaf, flower, and fruit coverage, as well as to provide an index of damage to tamarisk by *D. carinulata* (brown leaves). A 1-km transect was established through the middle of each study site, and observers walked each transect monthly, visually sampling a total of 100 tamarisk plants per transect for phenological patterns (after van Riper, 1980). Individual plants within 50 m of the transect were assessed by visualizing a full crown and estimating the proportion of the plant currently covered by green leaves, brown leaves, flowers, and fruit. Data from 100 plants per transect were averaged to obtain monthly stand conditions. We compared phenological data with avian use of tamarisk to assess the associations of birds to beetle damage and defoliation of tamarisk.

Focal Avian Species

We analyzed the diets of 25 bird species spanning nine families in the order Passeriformes (see table 3). All passerines were subject to diet analysis. However, to ensure that birds were responding to the vegetation and arthropod communities at each study site, only species of resident, breeding birds were used.

Avian Surveys

Point-count surveys (Reynolds and others, 1980; Ralph and others, 1993) were made monthly from June through August 2010-12 at 20 points per study site to characterize the avian community (see table 3). Counting stations with 100-m radii were established at 200-m intervals parallel to the river. Surveys began at sunrise and ended by 10:00 a.m., except during periods of rain or high winds. To minimize bias, observers alternated study sites, and starting points for avian surveys were reversed monthly. Observers waited 2 minutes upon arriving at a census point to minimize the effects of the disturbance created by approaching the station, then recorded all birds seen and heard for 5 minutes.

Foraging Behavior

Observations of foraging behavior were made along a 1-km transect at each study site during the 2010-12 seasons. For each foraging event, we recorded the substrate and height of the attack maneuver, which was defined as a directed movement toward a potential food item. Substrates included seven dominant species of shrub (coyote willow, desert olive, sumac, big sagebrush, rabbitbrush, greasewood, and tamarisk) and four supplemental substrates (air, grass, ground, and other). “Other” substrates, which were used rarely, included fourwing saltbush, mulefat, boxelder, pinyon, juniper, Gambel-oak, and Siberian-elm.

Each transect was walked at least once a week from sunrise to 10:30 a.m. The starting points for transects were reversed weekly to minimize bias associated with time of day, and all parts of transects received an approximately equal amount of coverage. When possible, the identity of prey taken by birds was recorded.

We used the location of first attack maneuver, as opposed to the location of first detection, when analyzing observations of foraging behavior (McGrath and others, 2009). Use of first attack maneuver specifically addresses the foraging location, whereas the location of first detection may provide information relative to other aspects of avian behavior (perching, singing, and searching). Additionally, use of the first attack maneuver reduces visual bias associated with foraging behavior in different plant species (Bell and others, 1990).

Percentage of use of all substrates was calculated for 14 bird families: Aegithalidae, Cardinalidae, Corvidae, Emberizidae, Fringillidae, Icteridae, Mimidae, Parulidae, Polioptilidae, Thraupidae, Troglodytidae, Turdidae, Tyrannidae, and Vireonidae. Observations of foraging maneuvers in supplemental substrates were excluded in the analysis of use versus availability but were used to characterize the foraging behavior of avian families. Heights of attack maneuvers were averaged within substrates to coordinate the collection of arthropods, such that the sampling location could be determined by the foraging behavior of birds.

One-way analysis of variance was used to test for differences in substrate use by all birds, and then within each avian family. We used repeated-measures analysis of variance that included date as a repeated measure to test for an interaction between use and availability of shrub species by birds at each study site. We corrected for multiple tests by using a Bonferroni adjustment. Between-subject measures were plant species, percentage of use/availability, and date. All interactions were included in the model. We also tested for differences in shrub-species use versus availability by using a paired *t*-test of the average preferences and availability of each shrub species for each month at each study site.

A mixed model for multiple regression was used to test for an effect of tamarisk phenology on avian use of tamarisk that included date as a repeated measure, phenology as a covariate, and avian family as a factor.

Arthropod Availability

Arthropods were sampled from eight plant species monthly from June through August 2010-11: coyote willow, desert olive, sumac, big sagebrush, rabbitbrush, greasewood, grass, and tamarisk. Sweep nets were used to collect arthropods at 10 plots spaced 100 m apart along the same 1-km transects used for foraging and phenologic observations. Sample collections were 25 vertical sweeps per plant species per plot at a height of 0 to 3 m above ground with a standard 38-cm-diameter canvas sweep net. Arthropod samples were collected from dawn to 10:00 a.m., concurrent with the collection of diet samples from birds.

Arthropods collected by sweep net were transferred to vials and preserved in 70-volume-percent ethanol. Later, in the laboratory, arthropods were identified as to order, then as to level of morphologically distinct taxa, which were categorized as morphospecies. When a range of size classes within a morphospecies was noted (for example, Lepidoptera larvae), similar-size individuals were placed into subgroups. Body lengths were measured to the nearest 0.05 mm from the frons to the tip of the abdomen with an ocular micrometer fitted to a dissecting binocular microscope (Rogers and others, 1977). Voucher specimens of all morphospecies were placed into a reference collection.

The purpose of sampling the arthropod community was to quantify arthropod abundance and biomass from dominant plant species and then to compare these measures with arthropod prey observed in the diets of birds. Additionally, we compared the arthropod community in tamarisk with the arthropod communities of native plant species, where arthropod abundance is the number of individual arthropods, biomass is the estimated dry weight (in milligrams) of arthropods collected per sample or per 25 sweeps, and species richness is the number of morphospecies detected per sample. Samples were averaged among plant species within each sampling period and study site. The arthropod community was subdivided into 10 general categories: *D. carinulata*, Araneae (spiders), Coleoptera (beetles), Diptera (flies), Hemiptera: Heteroptera (true bugs), Hemiptera: Auchenorrhyncha (leafhoppers), Hymenoptera (ants and wasps), Lepidoptera (largely caterpillars), Orthoptera (grasshoppers), and other (Acari, Isoptera, Mantidae, Neuroptera, Phasmatodea, Thysanoptera, Thysanura, and Trichoptera). We used a generalized regression equation that permits an estimate of dry weight (in milligrams) based on length (in millimeters) to calculate biomass for each morphospecies group (Rogers and others, 1976).

One-way analysis of variance was used to test for differences in mean abundance and biomass among arthropod categories. Repeated-measures analysis of variance with Bonferroni adjustments was used to test for overall differences in mean arthropod abundance, biomass, and species richness among plant species, with date as the repeated measure and plant species, abundance, biomass, and species richness as between-subject measures.

We tested for the influence of plant species on the abundance and biomass of distinct arthropod categories by using repeated-measures analysis of variance, with date as the repeated measure. Between-subject effects were arthropod category, date, and plant species.

Avian Diet

Diet samples were collected from 25 bird species in nine families in the order Passeriformes. Birds were captured with passive mist netting in 2010-11, whereby 6- and 12-m mist nets (30-mm mesh) were erected adjacent to stands of tamarisk at each of the three study sites (fig. 1) and opened 1 hour after sunrise to ensure that birds had sufficient time to forage before capture. In addition to taking diet samples, all birds were identified as to species, aged, sexed, and banded with U.S. Geological Survey aluminum leg bands.

Immediately upon capture, we used a modified irrigation technique that has proved effective in sampling both hard- and soft-bodied arthropods to acquire gizzard contents from birds (Moody, 1970; Laursen, 1978; Rosenberg and Cooper, 1990). This protocol was approved by the University of Arizona Institutional Animal Care and Use Committee (protocol #11-273). A 3-cm^3 syringe was filled with warm water, and a French feeding tube was attached to its head; the size of the bird determined the inner diameter of the tube used (3.5 Fr = 1.2 mm, 5 Fr = 1.7 mm, 8 Fr = 2.7 mm). French feeding tubes are soft, resilient, and completely flexible; one end of the feeding tube is flared to fit a syringe, whereas the other end has a smooth, rounded tip to prevent injury to the animal. Tubing was guided slowly and gently along the roof of the bird’s mouth and into the esophagus. No force was needed, and care was taken to align the tube at the junction of the esophagus and body cavity to allow for easy insertion. The bird was then inverted to prevent water from entering its trachea, and water was pushed into its digestive tract at a rate of $1\text{cm}^3/\text{s}$. As fluid was forced into the digestive tract, excess fluid plus crop and gizzard contents were collected in a plastic dish positioned beneath the bird for this purpose. Regurgitated contents were transferred to a vial and preserved with 70-volume-percent ethanol.

Later, in the laboratory, diet samples were placed in a petri dish and sorted under a variable-power dissecting microscope. Arthropod fragments were identified to the lowest taxonomic level possible, according to Tatner (1983), Ralph and others (1985), Moreby (1987), and Borror and others (1989). Common features used to identify items in the diet are listed in table 4. Some of these structures are shown in figure 2.

The minimum number of individual arthropods in each sample was estimated by counting single body parts (for example, head capsules, dorsal sclerites, ovipositors) and pairs of corresponding body parts (for example, antennae, legs, mandibles, wings) of a known number in the intact arthropod (Jenni and others, 1989; Rosenberg and Cooper, 1990). Fragments of elytra could generally be used to identify and count beetles, in the same way that fangs could be used to quantify spiders.

A reference collection assembled from concurrent arthropod sampling was critical for identifying fragmented arthropods. Arthropods from the reference collection were macerated to facilitate matches between parts observed in diet samples and fragments taken from known, intact specimens. The piecemeal form of the evidence made it impossible to establish individual weights or volumes of arthropod prey. However, multiplying the numbers of prey items observed in the diet by the known weights of similar arthropods in the reference collection allowed for an indirect estimate of biomass (Tatner, 1983). Consequently, the percentages both by number of individuals (abundance) and by estimated biomass were used to describe the relative contributions of arthropod categories to avian diet.

Percentages of the abundance and biomass of food items in gizzard contents within each avian family were pooled and calculated for 11 food-item categories: *D. carinulata*, Araneae (spiders), Coleoptera (beetles), Diptera (flies), Hemiptera: Heteroptera (true bugs), Hemeptera: Auchenorrhyncha (leafhoppers), Hymenoptera (ants and wasps); Lepidoptera (largely caterpillars), Orthoptera (grasshoppers), other (Neuroptera and Trichoptera), and seed (fruit and seed taken from vegetation). Seeds were used to characterize the diets of avian families, but were excluded in the analysis of use versus availability of arthropod prey. One-way analysis of variance was used to test for differences in the mean percentage of use of all food-item categories by birds in general and within each avian family.

Because birds do not forage on all arthropods, we identified preferred species of arthropod prey from the diets of birds. We then tested for the influence of both total and preferred arthropods available in the environment on the arthropod prey observed in the diets of birds by using repeated-measures analysis of variance, with date as the repeated measure. Between-subject effects were arthropod category, arthropod source (total and preferred available, used), and date.

Palatability Experiment

Yellow-breasted chats (*Icteria virens*; Linnaeus, 1758) were chosen for a palatability experiment because they are insectivorous, abundant in the study area, and potential consumers of *D. carinulata*. Over a period of 3 months, from June 1 to August 15, 2011, a total of 10 yellow-breasted chats were captured with mist nets, aged, sexed, and banded with U.S. Geological Survey aluminum legbands. Captive chats were held individually for the duration of the experiment (2 hours) in small enclosures covered with fine mesh (0.3 by 0.3 by 0.3 m) and provided with shelter, an artificial perch, and with free access to water. Experimental protocol was approved by the University of Arizona Institutional Animal Care and Use Committee (protocol 11-273).

Adult tamarisk leaf beetles were collected in the field on the day of each experiment. Mealworms, larvae of the beetle (*Tenebrio molitor*; Linnaeus, 1758), were store bought and maintained for the duration of the field season at 1.6°C. Mealworms were removed from storage the evening before use and allowed to acclimate to ambient temperatures. All insects were presented live to experimental birds.

Upon capture, chats were randomly assigned to either control or treatment groups. The control group was offered 20 mealworms, and the treatment group offered 20 adult tamarisk leaf beetles. The control group consisted of three adults, all female, and two hatch-year birds, whose sex was unknown. The treatment group included two adults, both female, and three hatch-year birds. Consumption of mealworms by birds was used to demonstrate that capture and containment in enclosures does not inhibit foraging behavior by wild chats. Consumption of food items was measured by the number of individual insects missing or partially eaten from enclosures at the conclusion of the experiment.

A two-sample *t*-test was used to test for differences in the mean number of prey items eaten between control and treatment groups.

Results

Foraging Behavior

In general, birds foraged most often in desert olive (16.5percent; 95-percent-confidence interval, 6.3-26.7 percent), followed by tamarisk, air, ground, other, willow, grass, sumac, greasewood, sagebrush, and rabbitbrush ($F_{10,\,198}$ =1.89; two-sided *p*-value, 0.0479 from a one-way-analysis-of-variance *F*-test). Birds foraged preferentially within a zone ~0 to 3 m off the ground (see table 5).

Of 14 avian families, 6 preferred certain substrate types (see table 6). Emberizidae preferentially foraged on the ground (35.5 percent) and in grass (18.7 percent) more than in all other substrates ($F_{10,\,198}$ = 1.89; two-sided *p*-value, 0.0479 from a one-way-analysis-of-variance *F*-test). Fringillidae foraged in desert olive (46.6 percent) and on the ground (25.6 percent) ($F_{10,\,198}$ = 2.62; two-sided *p*-value, 0.0052), Parulidae foraged in willow (22.8 percent) and desert olive (22.8 percent) ($F_{10, 198} = 3.88$; two-sided *p*-value, <0.0001), Polioptilidae foraged in tamarisk (28.0 percent) ($F_{10, 198} = 2.76$, two-sided *p*-value, 0.0033), and Turdidae foraged in desert olive (63.6 percent) ($F_{10, 198} = 2.07$; two-sided *p*-value, 0.0281). Finally, Tyrannidae foraged in air (57.0 percent) more than in all other substrates ($F_{10, 198} = 6.31$; two-sided *p*-value, <0.0001).

The selection of foraging substrates within bird families was affected by the interaction between plant species, availability, and date ($F_{48, 1227.40} = 2.38$; two-sided *p*-value, <0.0001 from a repeated-measures-analysis-of-variance *F*-test; see table 7). Birds foraged most often in desert olive (26.6 percent; 95-percent-confidence interval, 6.1-47.0 percent), followed by tamarisk, willow, sumac, greasewood, sagebrush, and rabbitbrush. In general, birds foraged more in desert olive than expected, given its availability ($t_{18} = 2.97$; two-sided *p*-value, 0.0081 from a paired *t*-test). Birds foraged less in willow, given its availability ($t_{18} = 11.59$; two-sided *p*-value, <0.0001; see fig. 3).

No evidence was obtained that the phenology of tamarisk affected its use by birds (green leaf, $F_{1, 208.32} = 0.18$; two-sided *p*-value, 0.669; brown leaf, $F_{1, 192.65} = 0.82$; two-sided *p*-value, 0.367; flower $F_{1, 223.43} = 0.12$; two-sided *p*-value, 0.734; fruit, $F_{1, 210.33} = 0.14$; two-sided *p*-value, 0.712 from a repeated-measures-analysis-of-variance *F*-test).

Arthropod Availability

A total of 18,855 individual arthropods representing 141 morphospecies in 17 orders were collected from eight plant species. We noted a difference in the mean abundance of arthropod categories in the study area (see fig. 1) in general ($F_{9, 1110} = 13.40$, two-sided *p*-value <0.0001 from a one-way analysis of variance *F*-test). *D. carinulata* was collected most commonly (24.0 percent; 95-percent-confidence interval, 19.9-27.4 percent) followed by Auchenorrhyncha, Hymenoptera, Coleoptera, Diptera, Araneae, Heteroptera, other, Lepidoptera, and Orthoptera (see table 8).

Additionally, *D. carinulata* contributed the most to total biomass of arthropods in the study area (35.4 percent; 95-percent-confidence interval, 32.4-45.1 percent), followed by Orthoptera, Hymenoptera, Auchenorrhyncha, Coleoptera, Lepidoptera, Heteroptera, other, Diptera, and Araneae (see table 9).

Plant species affected the abundance of arthropods collected per sample ($F_{7, 17.36} = 2.77$; two-sided *p*-value, 0.04 from a repeated-measures-analysis-of-variance *F*-test). Total arthropod abundance in tamarisk was higher than in all other plant species, whereas arthropod abundance was similar among native plant species. However, when tamarisk leaf beetles were excluded, arthropod abundance in tamarisk was lower than in willow and rabbitbrush but comparable to that in other plant species ($F_{76, 931} = 3.47$; two-sided *p*-value, <0.0001 from a repeated-measures-analysis-of-variance *F*-test; see fig. 4).

Abundance within each arthropod category was affected by plant species ($F_{63, 297.72} = 6.89$; two-sided *p*-value, <0.0001 from a repeated-measures-analysis-of-variance *F*-test; see fig. 5). In tamarisk, *D. carinulata* was more abundant than any other arthropod category ($F_{9, 130} = 20.56$; two-sided *p*-value, <0.0001 from a one-way-analysis-of-variance *F*-test). On average, *D. carinulata* composed 73.6 percent of the arthropod abundance in tamarisk (95-percent-confidence-interval, 66.8-80.3 percent).

Biomass of arthropods was affected by plant species ($F_{118, 891} = 6.90$; two-sided *p*-value, <0.0001 from a repeated-measures-analysis-of-variance *F*-test). Total arthropod biomass in tamarisk was higher than in all other plant species, whereas no significant difference was detected in arthropod biomass among native plant species. When the tamarisk leaf beetle was excluded, arthropod biomass in tamarisk was again lower than that in willow and rabbitbrush but comparable to that in other plant species ($F_{116, 891} = 4.46$; two-sided *p*-value, <0.0001 from a repeated-measures-analysis-of-variance *F*-test).

Similarly, biomass within each arthropod category was affected by plant species ($F_{63, 309.84} = 5.31$; two-sided *p*-value, <0.0001 from a repeated-measures-analysis-of-variance *F*-test; see fig. 13). The biomass of *D. carinulata* in tamarisk was greater than that of all other arthropod categories ($F_{9, 130} =$

16.68; two-sided *p*-value, <0.0001 from a one-way-analysis-of-variance *F*-test). On average, the biomass of *D. carinulata* composed 87.7 percent of the total biomass of arthropods in tamarisk (95-percent-confidence intervals, 78.9-96.4 percent). No significant difference was detected in the abundance or biomass of the other arthropod categories in tamarisk.

Mean richness of arthropod morphospecies was also affected by plant species ($F_{7,\,24.31}$ = 3.57; two-sided *p*-value, 0.009 from a repeated-measures-analysis-of-variance *F*-test). Arthropod richness in tamarisk was lower than that in willow and sagebrush, but higher than that in greasewood (fig. 14). On average, samples from tamarisk contained 4.0 fewer arthropod morphospecies than those from willow (two-sided *p*-value = 0.0007; 95-percent-confidence interval, 1.3- 6.7 percent), 2.5 fewer morphospecies than those from sagebrush (two-sided *p*-value, 0.0091; 95-percent-confidence interval, -0.16 to 5.21 percent), and 1.4 more morphospecies than those from greasewood (two-sided *p*-value, 0.0425; 95-percent-confidence interval, -1.30 to 4.08 percent).

Avian Diet

Diets of 188 individual birds spanning 25 species and nine families in the order Passeriformes were analyzed in this study. We identified 520 arthropod prey items from diet samples, representing 76 arthropod morphospecies from 10 orders.

The frequency of occurrence by abundance of food-item categories in the diets of birds varied significantly among avian families ($F_{10,\,144}$ = 4.04; two-sided *p*-value, <0.0001 from a one-way-analysis-of-variance *F*-test). Overall, seed (17.0 percent), Coleoptera (14.4 percent), and Hymenoptera (13.0 percent) were most abundant. Seeds were detected in the diets of four avian families (Cardinalidae, Emberizidae, Fringillidae, and Parulidae) and contributed significantly to the diets of Cardinalidae (51.7 percent, $F_{10,\,143}$ = 2.10; two-sided *p*-value, 0.0277), Emberizidae (61.1 percent, $F_{10,\,143}$ = 3.08; two-sided *p*-value, 0.0014), and Fringillidae (96.7 percent, $F_{10,\,143}$ = 2.57; two-sided *p*-value, 0.0069). Parulidae ate more Hymenoptera (27.9 percent) and Coleoptera (23.7 percent) than all other food-item categories ($F_{10,\,143}$ = 2.10; two-sided *p*-value, <0.0001). No difference was detected in the frequency of occurrence of food items in Icteridae, Mimidae, Polioptilidae, Tyrannidae, or Vireonidae (table 10).

By biomass, birds generally ate significantly more Lepidoptera (29.0 percent) than any other food-item category ($F_{10,\,1375}$ = 3.07; two-sided *p*-value, 0.0007 from a one-way-analysis-of-variance *F*-test). Fringillidae preferred seed (98.2 percent, $F_{10,\,143}$ = 2.58; two-sided *p*-value, 0.0066), whereas Parulidae ate more Coleoptera (24.5 percent) than all other food-item categories ($F_{10,\,143}$ = 2.91; two-sided p-value = 0.0024). No preferential use of food items was detected in Cardinalidae, Emberizidae, Icteridae, Mimidae, Polioptilidae, Tyrannidae, or Vireonidae (table 11).

When seed was excluded from analysis, the interaction between arthropod category and availability by abundance (total and preferred) affected the frequency of occurrence of arthropod categories in the diets of birds ($\mathrm{F}_{18,\,155.14}$ = 2.47; two-sided *p*-value, <0.0001 from a repeated-measures-analysis-of-variance *F*-test; fig. 15). Birds ate fewer Auchenorrhyncha than expected, given their availability. More Coleoptera, Heteroptera, and Araneae were eaten by birds than expected, given their availability in the total and preferred arthropod communities. Finally, fewer *D. carinulata* were eaten by birds (2.1percent; 95-percent-confidence interval, 1.3-2.9 percent) than expected, given its availability in both the total (24.0 percent; 95-percent-confidence interval, 19.9- 27.4 percent) and preferred (16.8 percent; 95-percent-confidence interval, 13.0- 20.6 percent) arthropod communities.

The percentage by biomass of arthropod categories in the diets of birds was affected by the availability of arthropods by biomass (preferred and total) ($\mathrm{F}_{10,\,155.14}$ = 2.47; two-sided *p*-value, 0.009 from a repeated-measures-analysis-of-variance *F*-test; fig. 16). Orthoptera were eaten less than expected, whereas Coleoptera and Lepidoptera were eaten more than expected, given their availability in the total and preferred arthropod communities. Again, fewer *D. carinulata* were eaten by birds (3.4 percent; 95-percent-confidence interval, 2.6-4.2 percent) than expected, given its availability by biomass in both the total (35.4 percent; 95-percent-confidence interval, 32.4-45.1 percent) and preferred (30.1 percent; 95-percent-confidence interval, 23.8-36.5 percent) arthropod communities.

D. carinulata was observed in the diets of 11 of 188 birds (5.9 percent; 95-percent-confidence interval, 4.1-7.7 percent). Overall, the frequency of occurrence of *D. carinulata* in the diets of birds was 2.1 percent (95-percent-confidence interval, 1.5-2.7 percent) by abundance and 3.4 percent (95-percent-confidence interval, 2.6-4.2 percent) by biomass. Four bird species from two families (Parulidae and Tyrannidae) ate *D. carinulata*: yellow-breasted chat, yellow warbler (*Dendroica petechial*; Gmelin, 1789), common yellowthroat (*Geothlypis trichas*; Linnaeus, 1766), and Cordilleran flycatcher (*Empidonax occidentalis*; Nelson, 1897). Most of the *D. carinulata* eaten by birds (8/11) were by yellow-breasted chats (72.7 percent; 95-percent-confidence interval, 46.4-99.0 percent). However, the frequency of occurrence of *D. carinulata* in the diets of yellow-breasted chats was only 3.3 percent (95-percent-confidence interval, 2.2-4.4 percent) by abundance (fig. 17) and 5.6 percent (95-percent-confidence interval, 4.1-7.1 percent) by biomass (fig. 18). Only adult beetles were observed in the diet samples collected from birds; no *D. carinulata* larvae were detected.

Palatability Experiment

No evidence was obtained of a difference in selection between the number of *D. carinulata* and mealworm prey items eaten by captive chats (two-sided *P*-value, 0.678 from a two-sample *t*-test; *t*-value = 0.431, DF = 7.194). Yellow-breasted chats ate 42 and 30 percent of the tamarisk leaf beetles and mealworms offered during the experiment, respectively.

Hatch-year and adult chats ate 66.7 and 5.0 percent of the tamarisk leaf beetles offered during the experiment, respectively (two-sided *p*-value, 0.221 from a two-sample *t*-test; *t*-value = 1.54, DF = 3). On average, hatch-year birds ate 61.7 percent more *D. carinulata* than did adult birds (95-percet confidence interval, -65.7 to 189.0 percent; fig. 19). No evidence was obtained of a difference between the proportion of mealworm prey items eaten by hatch-year and adult birds (two-sided *P*-value, 0.432 from a two-sample *t*-test; *t*-value = 0.906, DF = 3).

Discussion

The purpose of this study was to provide a better understanding of how a biologic control agent, the tamarisk leaf beetle, affects native birds. Our results can be summarized as follows. (1) Birds foraged more often in tamarisk relative to several species of native shrubs, and approximately in proportion to the availability of tamarisk in the environment, (2) Tamarisk leaf beetles contributed to 24.0 percent of the abundance and 35.4 percent of the biomass of arthropods in the study area (see fig. 1), and to 73.6 and 87.7 percent of the abundance and biomass of arthropods in tamarisk, respectively. Arthropod abundance and biomass are high in tamarisk, but the community is dominated by tamarisk leaf beetles. Morphospecies richness of arthropods in tamarisk was comparable to that in native plant species. (3) Birds ate few tamarisk leaf beetles, despite a superabundance of *D. carinulata* in the environment. Overall, the frequency of occurrence of tamarisk leaf beetles in the diets of insectivorous birds was 2.1 percent by abundance, and 3.4 percent by biomass. Four species of birds (yellow-breasted chat, common yellowthroat, yellow warbler, and Cordilleran flycatcher) from two families (Parulidae and Tyrannidae) ate tamarisk leaf beetles, though less than their availability or biomass by abundance in the environment. (4) Captive yellow-breasted chats ate tamarisk leaf beetles in a palatability experiment, although adult birds ate fewer tamarisk leaf beetles than did hatch-year birds.

Avian Use of Tamarisk

Observations of foraging behavior along the Dolores River (see fig. 1), where average coverage of tamarisk was approximately 15 percent (range, 5- 33 percent; table 2), suggests that birds foraged significantly more in tamarisk than in several species of native shrubs. Only ~16 percent of foraging maneuvers by birds occurred in tamarisk when all substrates were included in analysis. Avian use of tamarisk in this study indicates that tamarisk can provide some of the necessary vertical structure, foliar cover, and food resources for birds that use riparian vegetation (van Riper and others, 2008).

We observed no effect of tamarisk phenology and defoliation on the foraging behavior of birds. Data on phenology and defoliation patterns were recorded monthly and so may not reflect the nuances associated with changes in leaf, flower, fruiting, and defoliation of tamarisk and the subsequent effect on use of tamarisk by birds. However, we also observed no effect of time, indirectly a measure of phenologic change and defoliation, on the abundance or biomass of arthropods collected from tamarisk. The patchy distribution of tamarisk at the study sites (see fig. 1, table 2), coupled with defoliation and refoliation patterns that were distributed in space and time, may have allowed the arthropod community in tamarisk to retain some of its richness and abundance. Effects of defoliation on the foraging behavior by birds that breed in monocultures of tamarisk may be more severe (Paxton and others, 2011).

Naturalization of tamarisk in the Southwestern United States has been implicated in the degradation of riparian corridors (Shafroth and others, 2005; Stromberg and others, 2007; Brand and others, 2010). The presence of tamarisk in riparian regions purportedly lowers the habitat quality for some native plants and animals (DeLoach and others, 2003) but not for others, such as the southwestern willow flycatcher (*Empidonax traillii extimus*; Durst and others, 2006). Insectivorous and frugivorous birds show the greatest intolerance for tamarisk, whereas groundfeeders, granivores, and species that feed largely on other plant species appear to be unaffected by its presence (Cohan and others, 1978).

Recent research, however, suggests that the abundance of some bird species can be highest at intermediate levels of tamarisk (40-60 percent), owing to the complex vegetation structure and potentially greater abundance and biomass of arthropods provided by heterogeneous stands of tamarisk (van Riper and others, 2008). In the Mohave Desert on the Muddy River in Nevada, species richness of birds was predicted best by total vegetation volume (Fleishman and others, 2003), and a diverse and abundant community of breeding birds was observed in tamarisk along the Pecos River in New Mexico (Livingston and Schemnitz, 1996). As long as the vegetation community retained structural diversity, the presence of tamarisk did not negatively affect the species richness of native birds (Fleishman and others, 2003).

Use of tamarisk by birds in the current study may be explained by the increase in vegetation height and volume associated with the addition of tamarisk to the riparian vegetation community, which potentially increases both the number of feeding strategies that can be supported and the total volume of arthropod food available. Additionally, some functional redundancy may exist with regard to structure within the vegetation community. Some birds do not have a strong preference for the plant species in which they forage, so long as availability of arthropod prey is comparable (Fleishman and others, 2003). For example, stands of tamarisk created by the construction of Glen Canyon Dam were ecologically equivalent to native vegetation for some riparian birds. Birds nested in areas that were structurally similar among sites dominated by tamarisk and by native plant species (Brown and Trosset, 1989; Yard and others 2004).

Colonization of tamarisk potentially helps maintain a relatively diverse vegetation community under ecologically altered conditions where native species, such as willow and cottonwood, are no longer successful. Tamarisk provides structure for some animal species that may otherwise disappear after the decline of native plant species (Anderson, 1998). Along Queen Creek in Arizona, construction of an earthfill dam in 1960 has culminated in the striking growth of an artificial riparian-gallery forest of Goodding's willow (*Salix gooddingii*) and tamarisk (Szaro and DeBano, 1985). Bird communities responded to the greater structural diversity in the riparian interior and riparian edge. Thus, bird density within this riparian island was 3 times that on the adjacent desert upland, and 10 species were observed only in the riparian area (Szaro and DeBano, 1985). In places where tamarisk monocultures have formed, removal can drastically reduce habitat availability for some bird species and especially when tamarisk is the only riparian vegetation. Where tamarisk has ecological value, it should be carefully managed, and not necessarily eradicated (Livingston and Schemnitz, 1996; Barz and others, 2009).

The Arthropod Community in Tamarisk

The effect of tamarisk on arthropods, an important food resource for many birds, can profoundly affect birds that breed in riparian regions. We observed that tamarisk supports a higher abundance and biomass of arthropods than do many native plant species (see figures 6 and 7). High arthropod abundance in tamarisk, however, was almost entirely the product of superabundance of tamarisk leaf beetles. When tamarisk leaf beetles were excluded, abundance and biomass of arthropods were lower in tamarisk than in willow and rabbitbrush but comparable to those in other plant species.

Species richness in tamarisk was comparable to that in most native plant species. Arthropod richness in tamarisk was lower than that in willow and sagebrush but higher than that in greasewood.

Currently, five hypotheses have been presented with regard to the species richness and biomass of arthropods in areas dominated by tamarisk (reviewed for aerial arthropods by Durst and others, 2008).

1. Tamarisk supports arthropod communities with lower biomass and diversity relative to native vegetation (Liesner, 1971; Yong and Finch, 1997; DeLoach and others, 2000; Dudley and DeLoach, 2004).
2. Arthropod biomass is high in tamarisk, but the arthropod community is dominated by a nonnative leafhopper, *Opsius stactogalus*, that was introduced with the tamarisk (Yard and others, 2004; Wiesenborn, 2005).
3. The arthropod community supported by tamarisk is as diverse as that in native vegetation, and arthropod biomass is potentially higher, owing largely to the profuse and long-lasting flowering of tamarisk. The abundance of this flower and nectar resource attracts nonresident bird species from neighboring riparian and upland vegetation (Ellis and others, 2000; Drost and others, 2003).
4. The biomass and species richness of the arthropod community are intermediate in areas with both tamarisk and native species because elements of both vegetation communities are present (Haddad and others, 2001; Durst and others, 2008).
5. Biomass and species richness are actually higher in mixed vegetation because of the higher diversity relative to native or exotic monocultures (van Riper and others, 2008).

Results of the current study support the third hypothesis: the arthropod community sustained by tamarisk was as diverse as that in native vegetation, and arthropod biomass was higher. However, greater arthropod biomass in tamarisk was not the product of profuse and long lasting flowering in tamarisk but instead was caused by superabundance of tamarisk leaf beetles. Moreover, introduction of tamarisk leaf beetles to the Southwestern United States has the potential to alter vegetation structure and, consequently, arthropod communities in this region.

Avian Use of *D. carinulata* As a Food Resource

Information related to the diets of birds is an important aspect of any ecologic study of avian communities or individual species. Such data are vital when evaluating the role of birds as potential consumers of arthropod prey (Ford and others, 1982). We observed that the use of arthropod categories by birds varied with the availability of these arthropods, by both abundance and biomass.

On the Colorado River in Colorado, Hymenoptera contributed to a large proportion of the diets of six species of warblers. Ants composed 82 percent of the diet of yellow-breasted chats (Yard and others, 2004). Similarly, in the current study, Parulidae ate more Hymenoptera (27.85 percent) and Coleoptera (23.73 percent) by abundance than all other food-item categories.

Of 188 birds, only 11 ate tamarisk leaf beetles. The total frequency of occurrence of tamarisk leaf beetles in the diets of birds was 2.1 percent by abundance and 3.4 percent by biomass. Four bird species from two families (Parulidae and Tyrannidae) ate tamarisk leaf beetles*:* yellow-breasted chat, yellow warbler, common yellowthroat, and Cordilleran flycatcher. Of the birds that ate *D. carinulata*, ~75 percent were yellow-breasted chats. Notably, only a single tamarisk leaf beetle was detected in the diets of individual birds that ate *D. carinulata*, and only adult beetles were observed in diet samples; no tamarisk leaf beetle larvae were detected. This result may have been an artifact of the differential digestion of hard- and soft-bodied prey (Ford and others, 1982). However, Lepidoptera larvae were commonly observed in diet samples, suggesting that tamarisk leaf beetle larvae were not eaten by birds. Overall, fewer tamarisk leaf beetles were eaten by birds than expected, given their availability by abundance and biomass in the arthropod community.

Importantly, only insectivorous birds ate tamarisk leaf beetles. Species that tend toward more frugivorous and granivorous diets (for example, Cardinalidae, Emberizidae, Fringillidae, Turdidae) probably will not use *D. carinulata* as a significant food resource, nor will tamarisk leaf beetles likely contribute to the diets of Columbiformes like the mourning dove (Dudley and DeLoach, 2004). Groundfeeders, granivores, and bird species that feed largely in other habitat types (for example, agriculture) have been observed to use tamarisk as cover (Cohan and others, 1978). Therefore, observations of these bird species in tamarisk do not in themselves indicate that birds are eating tamarisk leaf beetles.

Use of tamarisk leaf beetles as a food resource by birds has implications for the welfare of avian communities in areas where biologic control is in place. *D. carinulata* can potentially affect native birds positively or negatively through changes in food abundance and vegetation structure. In places where avian populations increased after the arrival of biologic control agents, this success was attributed to an increase in the abundance of defoliating insects as prey and to environmental changes due to defoliation (Paxton and others, 2011).

The gypsy moth (*Lymantria dispar*), for example, is a prolific nonnative arthropod whose populations are capable of massive increases in numbers, similar to those of the tamarisk leaf beetle. Gypsy moths exploit a wide range of deciduous and coniferous host trees (Liebhold and others, 1992). Several warblers feed readily on early and late instars of gypsy-moth larvae (Whelan and others, 1989). However, given a simultaneous choice between gypsy-moth larvae and alternative prey, birds showed a preference for the alternative. Such may also be true for tamarisk leaf beetles and may explain the presence of *D. carinulata* in the diets of birds and why it occurs at such low frequencies.

Analysis of the gizzard contents from 557 birds of 17 species showed that 24 percent contained gypsy-moth remains (Smith, 1985), much higher than the frequency of occurrence of *D. carinulata* in the diets of birds in the current study. Gypsy moths, however, are an important food item for only a few predators and appear to be a low-preference food item that constitutes only a fraction of most avian diets. Predators were opportunistic feeders, and the selection of gypsy-moth prey was largely a function of the availability of other food items. Defoliation of vegetation by gypsy moths may affect the diversity and density of predators and, thus, the dynamics of predator-prey relations (Smith, 1985). Defoliation of tamarisk by *D. carinulata* may have a similar effect on the distributions and densities of the arthropods that occur in tamarisk and, thus, on the birds that forage in tamarisk.

Although few birds eat gypsy-moth larvae, potentially because of their hair-like setae, native cuckoos are commonly considered hairy-caterpillar specialists, enabling them to take advantage of nonnative gypsy moths, and may have a facultative effect on this native species (Barber and others, 2008). Yellow-breasted chats may have a similar and relatively singular capacity to prey upon tamarisk leaf beetles.

Palatability of *D. carinulata* to Birds

Results of our palatability experiment indicate that (1) yellow-breasted chats will eat tamarisk beetles in captivity when no other food resource is available; (2) overall, no difference is evident between the percentages of tamarisk beetles and mealworm prey eaten by chats; and (3) hatch-year birds ate more tamarisk beetles than did adult birds (66.7 versus 5.0 percent, respectively).

Thus, our results demonstrate that the tamarisk leaf beetle is not a preferred food resource for adult chats. Although coleopterans make up a significant percentage of the diets of riparian birds in the Southwest (Yard and others, 2004), *D. carinulata* is a member of the family Chrysomelidae. Many beetles in this family produce secondary chemicals distasteful to some birds (Rowell-Rahier and Pasteels, 1986; Hilker and Kopf, 1994; Pasteels and others, 1995; Rowell-Rahier and others, 1995; Labeyrie and others, 2003). Furthermore, tamarisk leaf beetles feed almost exclusively on tamarisk, a plant rich in noxious substances (Drabu and others, 2012). Thus, the tamarisk leaf beetle may exploit chemical defenses derived from its host plant that make it unpalatable to some degree, which birds learn as they encounter this food item while foraging.

The spectrum of palatability within chemically defended arthropods, as well as the persistent need for trial-and-error learning, may explain the large number of tamarisk leaf beetles eaten by young, naïve birds in this study (Brower, 1958a, 1958b; Brower and others, 1968). For example, a range of unpalatability among several species of European ladybird beetles (Coccinellidae) was detected when they were given as food to nestling blue tits. Chemical defense in these beetles ranged from a toxic effect that made nestlings severely ill or retarded their development, to unpalatability with no observable toxic effects (Marples, 1993). Palatability of tamarisk leaf beetles to birds may lie somewhere along a similar spectrum-- not so noxious that beetles are inedible, but distasteful enough to discourage predators when more palatable prey are available. Alternatively, the diets of young willow flycatchers contained higher numbers of odonates and beetles in comparison with the diets of adult birds (Drost and others, 2003). The greater number of tamarisk leaf beetles eaten by hatch-year chats may be a product of a disparity in experience and food choice among age classes in birds.

Despite the huge variety of defensive chemicals that occur in arthropods, recognizable patterns exist among physiologic and life-history traits that are suggestive of toxicity and unpalatability, including aposematism, gregariousness, and monophagy (Pasteels and others, 1983). Aposematism, a strategy for predator deterrence that combines a warning signal with unpalatability, contributes to high visibility in unpalatable insects. These insects are commonly eye-catching, colored in blatant schemes of black, orange, yellow, or white (Bowers, 1992). The combination of yellow and black, in particular, contributes to conspicuousness when placed against a natural green-and-brown background, and some birds demonstrate an innate reluctance to peck at black-and-yellow prey (Cott, 1940; Schuler and Hess, 1985). When laid, tamarisk leaf beetle eggs are initially bright yellow but soon dull to a light tan. All three larval instars are black, the second with an indistinct and the third with a conspicuous yellow lateral stripe (fig. 20). Pupae remain a uniform yellow color throughout their development. Upon emerging, adults are yellowish-green, with two dark-brown stripes on each elytron (Lewis and others, 2003). The black-and-yellow motif used by tamarisk leaf beetle larvae may be a warning signal advertising unpalatability.

Gregariousness, association of individuals with large numbers of their kind, is a strategy for predator avoidance that contributes to individual fitness in various ways (Cott, 1940). Several hypotheses explain this phenomenon in aposematic insects. Aposematic insects, no longer constrained to a solitary lifestyle because of their heightened defenses, become gregarious for reasons unrelated to chemical defense (for example, ready acquisition of mates). Alternatively, gregariousness is an aposematic strategy in its own right. The behavior may enhance the effectiveness of chemical defense or be a warning signal that advertises unpalatability through amplification of aversion to aposematic insects by naïve predators and through speed and memorability of avoidance learning (Gamberale and Tullberg, 1998). Gregariousness generally is more common in aposematic insects than in cryptic and palatable species (Eisner and Kafatos, 1962; Jarvi and others, 1981).

Defensive chemicals also commonly function as intraspecific signals, and aposematic beetles have been known to emit aggregation pheromones (Roth and Eisner, 1962; Pasteels and others, 1983). *D. carinulata* is a gregarious species; a single tamarisk plant can foster hundreds of feeding beetles, whereas surrounding plants can contain none. Plants colonized by a small number of feeding beetles can be quickly (<30 minutes) joined by numerous other beetles (Cossé and others, 2006). Two compounds, (2E, 4Z)-2,4-heptadienal and (2E, 4Z)-2,4-heptadien-1-ol, are produced almost exclusively by male beetles (Cossé and others, 2005). These aldehydes have been shown to have a stimulating effect on both male and female beetles, provoking both sexes to swarm toward the source of the pheromone.

Insect herbivores that forage on only one or a few host plants are potentially more predictable to predators (Pasteels and others, 1983). As a result, scores of chemical, mechanical, and behavioral defensive mechanisms have arisen in monophagous arthropods (Rowell-Rahier and Pasteels, 1986). According to the requirements of a biologic control agent, extensive laboratory and outdoor cage testing suggest that the host range of *D. carinulata* is almost completely restricted to tamarisk (Lewis and others, 2003; Moran and others, 2009). The ovipositing female is the most highly selective life stage, and eggs are laid in masses on tamarisk. All three larval instars and adult beetles feed on tamarisk.

Although we cannot conclude whether or not tamarisk leaf beetles are completely unpalatable, given what is currently known about their physiology and the results of our feeding experiment, inferences are possible on the basis of relevant data. Tamarisk leaf beetles are large, conspicuous insects, and early life stages exhibit morphologies consistent with those of aposematic arthropods. The beetle is highly gregarious and secretes chemicals that elicit aggregation in conspecifics. Tamarisk leaf beetles are monophagous and feed almost exclusively on tamarisk, a plant rich in noxious substances (Drabu and others, 2012). Thus, tamarisk leaf beetles may exploit chemical defenses derived from its host plant, rendering it partially unpalatable to avian predators.

Conclusions

Biologic control is potentially an environmentally sound and effective option for management of some invasive species. However, this approach calls for the introduction of additional nonnative organisms that can contribute to changes in the existing structure of native communities. Extensive defoliation of tamarisk caused by tamarisk leaf beetles and the resulting widespread loss of riparian vegetation may have a considerable impact on birds that breed in riparian regions dominated by tamarisk.

Although addition of tamarisk leaf beetles to arthropod communities in the Southwestern United States contributes to a superabundance of potential prey items, any beneficial response by birds to an increased abundance of prey depends upon palatability of that prey. Tamarisk leaf beetles are monophagous and feed almost exclusively on *Tamarix* spp. Sequestration of the noxious compounds produced by this plant as a defense against herbivory may provide tamarisk leaf beetles with a similar defense against predation.

Our data indicate that tamarisk leaf beetles contributed little to the diets of birds along the Dolores River in southwestern Colorado, despite a high availability of the beetles. Thus, tamarisk leaf beetles could be less useful as a supplement to avian diet while defoliation of tamarisk takes place than predicted by advocates of their release (Dudley and DeLoach, 2004; Longland and Dudley, 2008). Low rates of predation on beetles by native avifauna may facilitate population growth in this biologic control agent and contribute to management of tamarisk. It seems unlikely, however, that the negative effects of large-scale defoliation in areas dominated by tamarisk will be compensated for by the use of tamarisk leaf beetles as a food resource by birds.

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Appendix 1. Figures and Tables

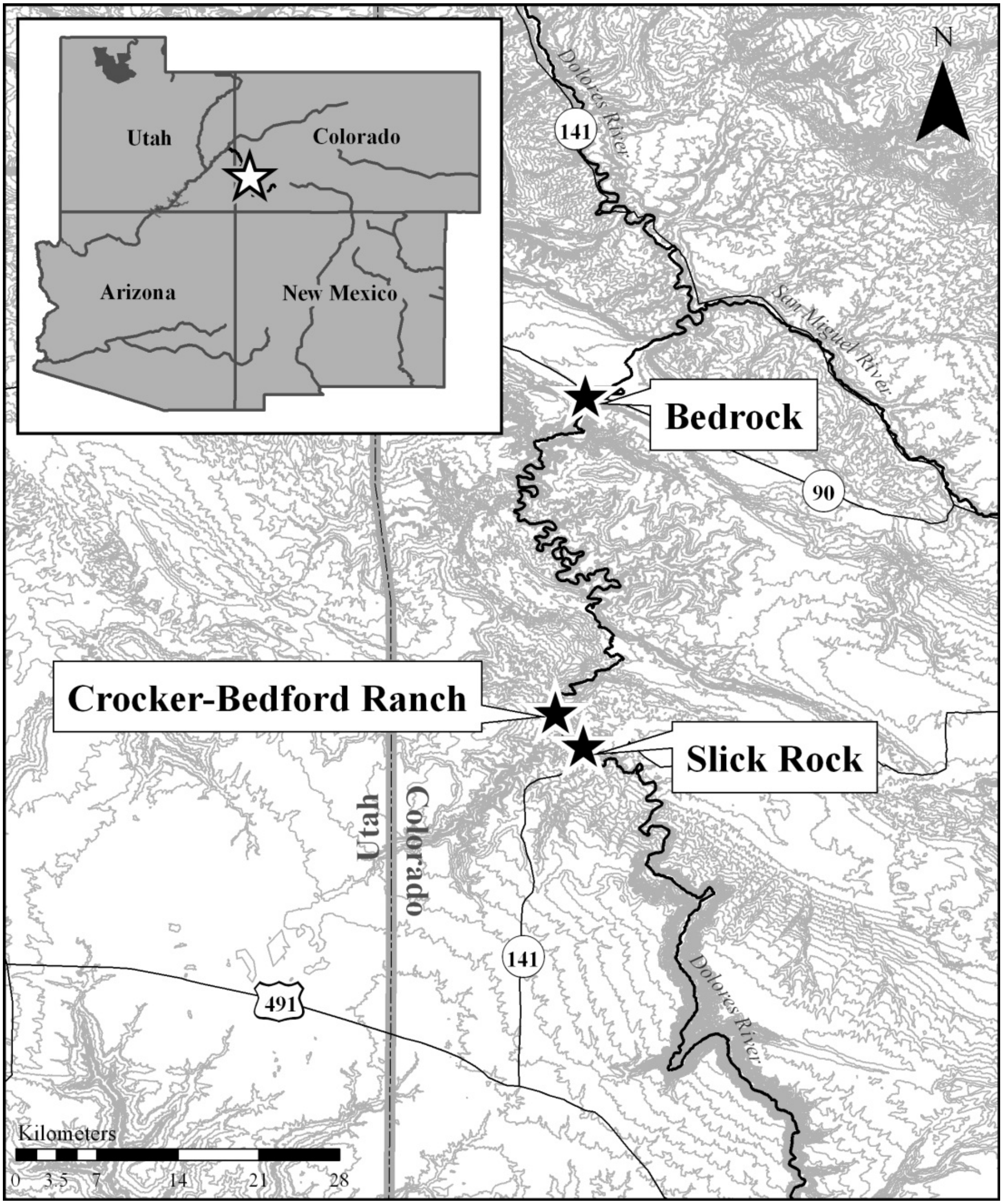
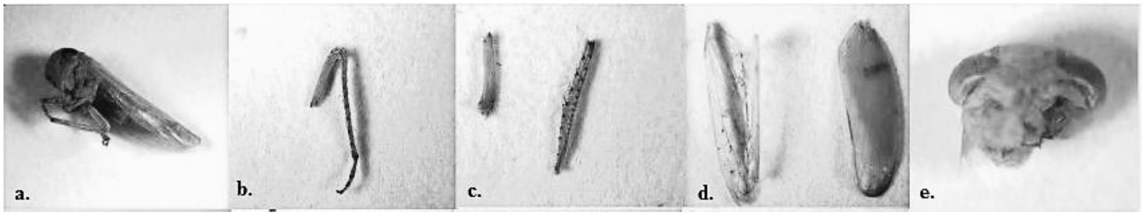


Figure 1. Study area in southwestern Colorado, showing locations of three representative study sites at river miles 47, 54, and 97 (Slick Rock, Crocker-Bedford Ranch, and Bedrock) along the Dolores River.


A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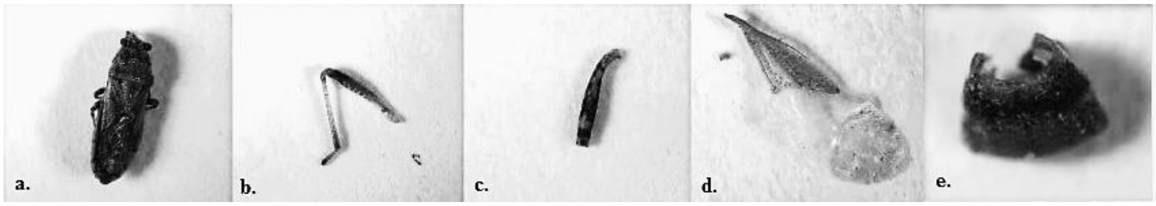
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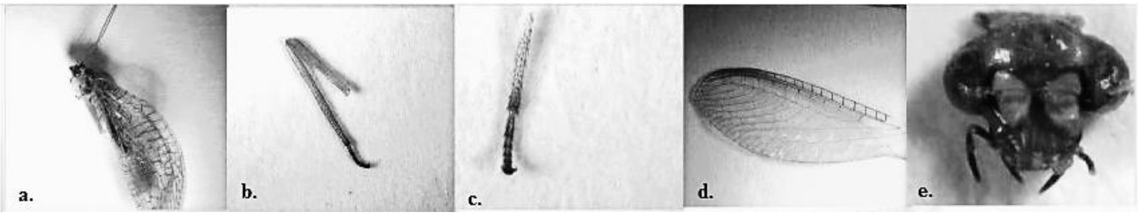
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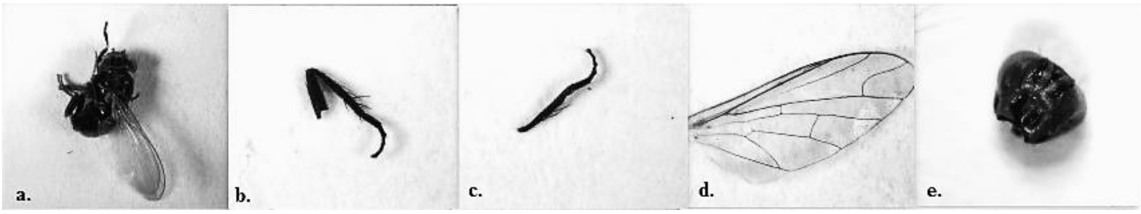
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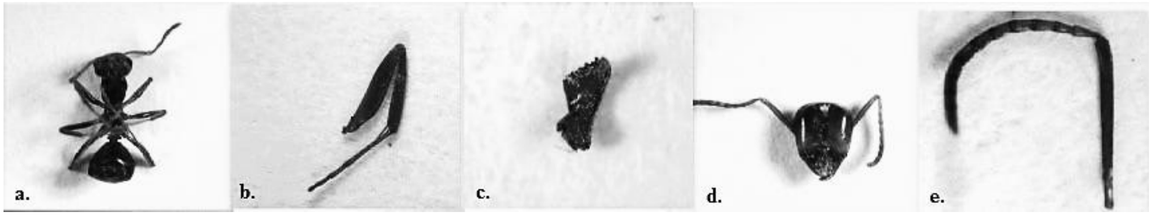
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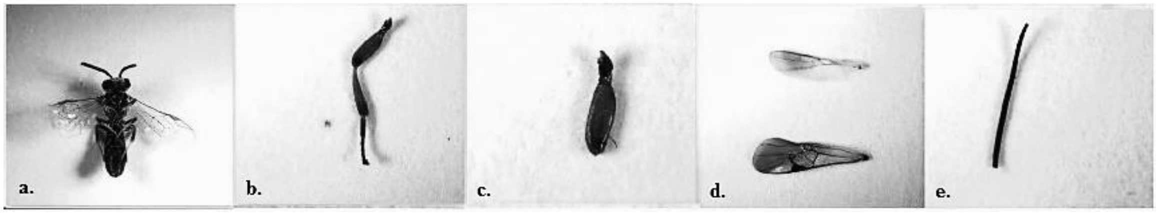
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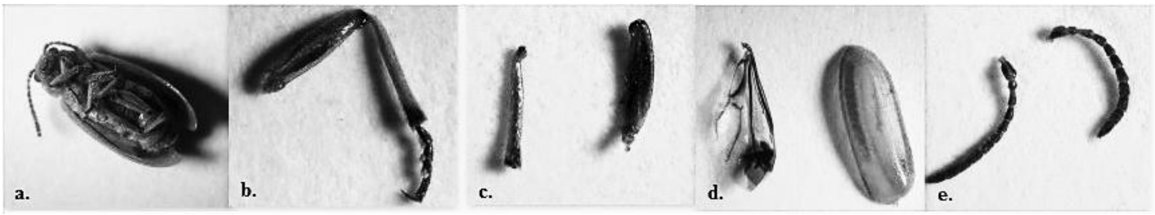

Figure 2. Arthropod structures commonly observed in regurgitated gizzard contents from birds. Fragments to the right of whole arthropods were derived from that taxon. *A*, Araneae, family Sparassidae. From left to right: (a.) whole (x16), (b.) whole leg (x25), (c.) tibia (x25), (d.) fang (x40), and (e.) chelicerae fang absent (x40). *B*, Hemiptera, family Cicadellidae. From left to right: (a.) whole (x20), (b.) whole leg (x25), (c.) fragments of femur or tibia (x25), (d.) hindwing and forewing (x25) and (e.) head fragment (x30). *C*, Hemiptera, family Lygaeidae. From left to right: (a.) whole (x16), (b.) whole leg (x16), (c.) femur (x20), (d.) forewing with associated clavus and corium (x20), and (e.) pronotum (x25). *D*, Neuroptera, family Hemerobiidae. From left to right: (a.) whole (x10), (b.) whole leg (x20), (c.) whole leg (x20), (d.) wing (x16), and (e.) head (x25). *E*, Diptera, family Anthomyiidae. From left to right: (a.) whole (x16), (b.) whole leg (x16), (c.) tibia and tarsus (x16), (d.) wing (x25), and (e.) head (x16). *F*, Hymenoptera, family Formicidae. From left to right: (a.) whole (x10), (b.) whole leg (x25), (c.) mandible (x40), (d.) head (x25), and (e.) antenna (x25). *G*, Hymenoptera, family Halictidae. From left to right: (a.) whole (x10), (b.) whole leg (x16), (c.) femur (x25), (d.) hindwing and forewing (x16), and (e.) antenna (x25). *H*, Coleoptera, family Chrysomelidae (*Diorhabda carinulata* spp.). From left to right: (a.) whole (x10), (b.) whole leg (x25), (c.) tibia and femur (x20), (d.) wing and elytra (x16), and (e.) antennae (x25).

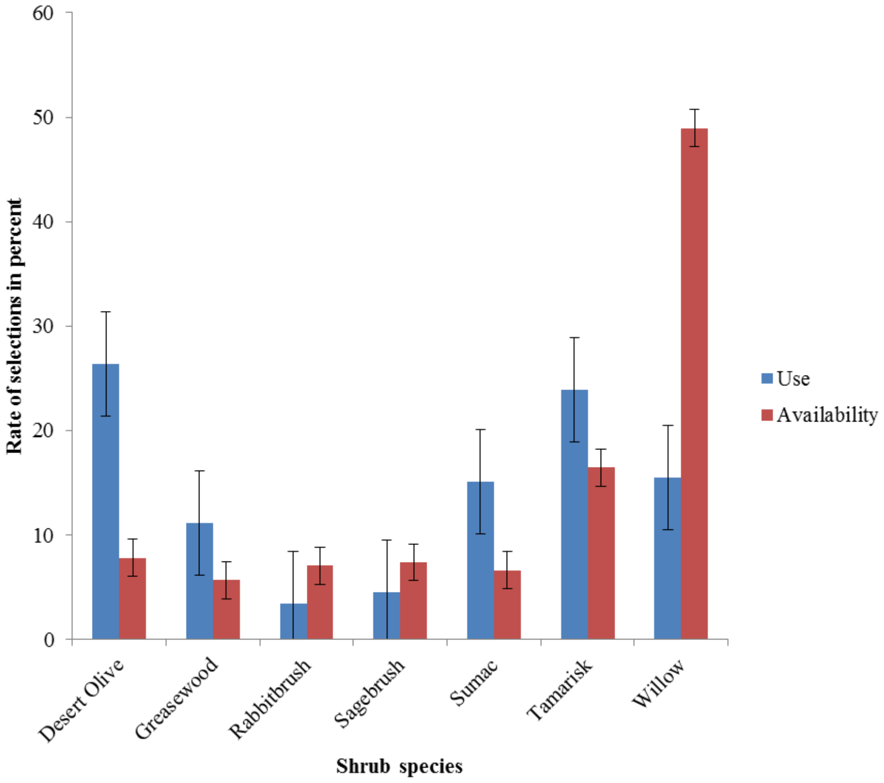

Figure 3. Percent availability of Shrub-species and percent selected by birds during 2010-12 on the Dolores River, Colorado. Observations of bird use from all years were combined. Birds foraged preferentially in desert olive over other species more than expected, given its availability. Birds foraged less in willow, given its availability.

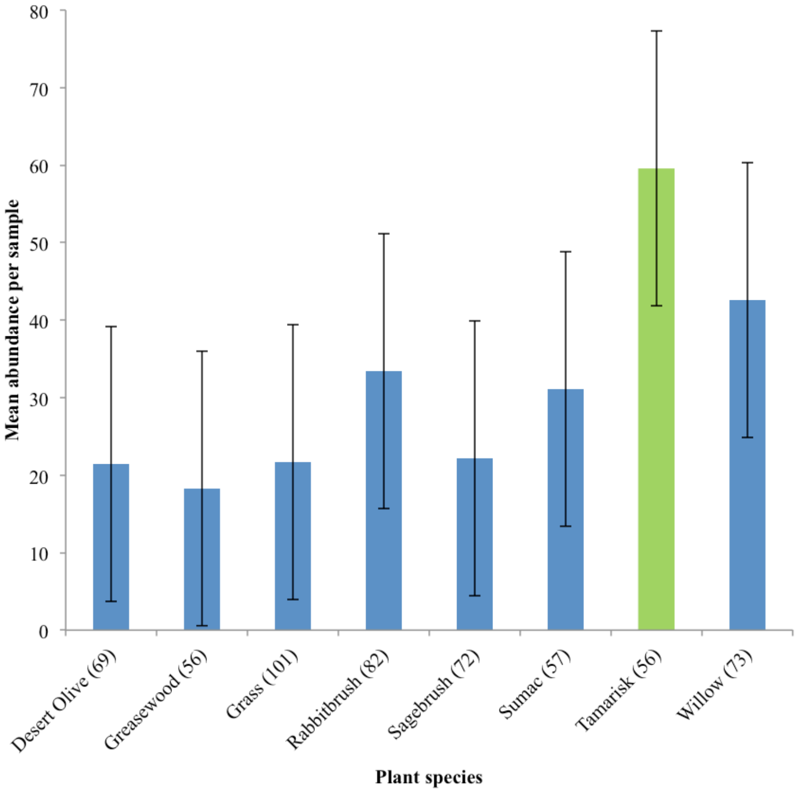

Figure 4. Mean total abundance of arthropods (number per 25 sweeps) in eight plant species along the Dolores River, southwestern Colorado, 2010-11 (see fig. 1 for location). Numbers in parenthesis are sample sizes; error bars depict 95-percent-confidence intervals.

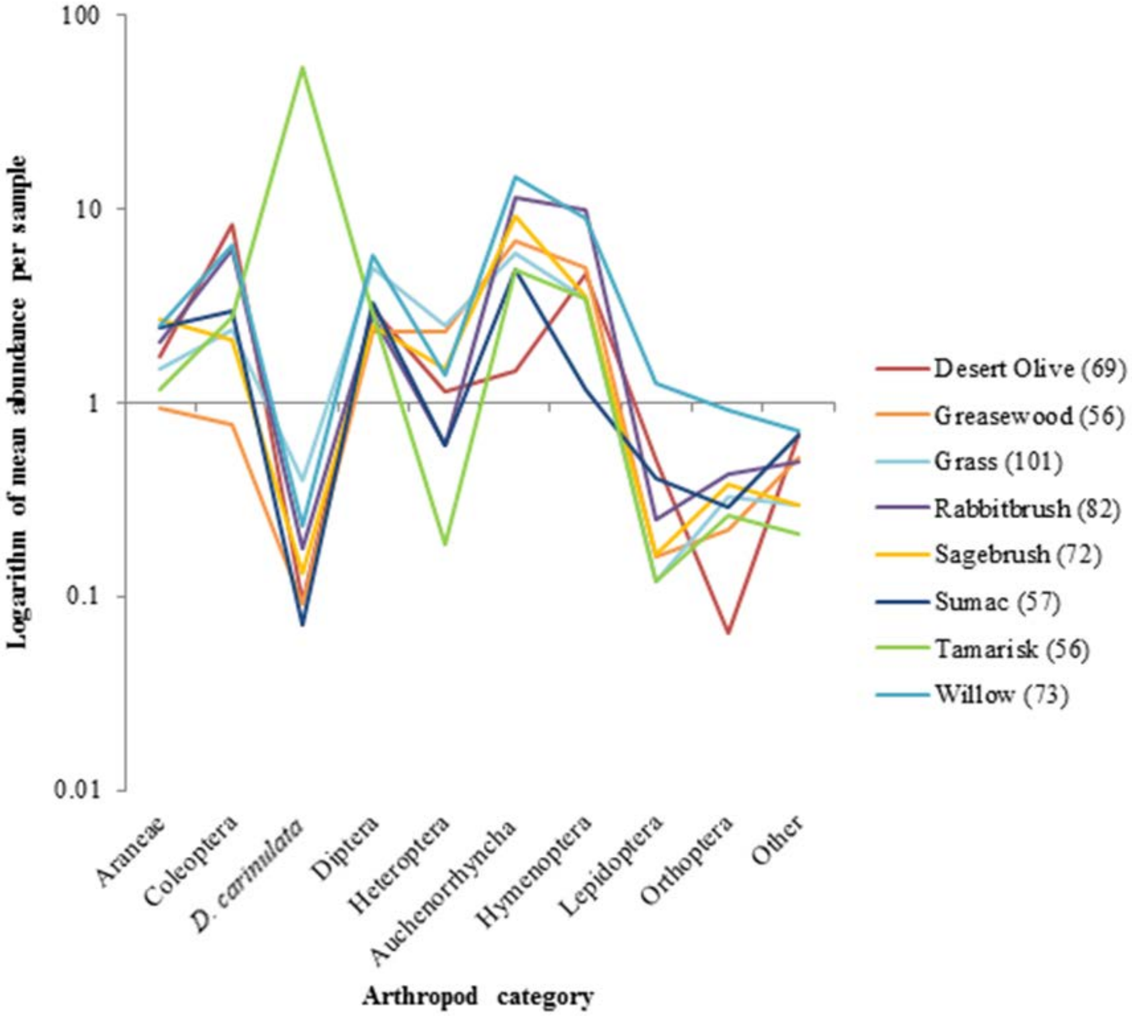

Figure 5. Mean abundance of arthropod categories (number per 25 sweeps) from eight dominant plant species along the Dolores River, southwestern Colorado, 2010-11 (see fig. 1 for location). Categories are *Diorhabda carinulata*, Araneae (spiders), Coleoptera (beetles), Diptera (flies), Heteroptera (true bugs), Auchenorrhyncha (leafhoppers), Hymenoptera (ants and wasps), Lepidoptera (largely caterpillars), Orthoptera (grasshoppers), and other (Acari, Isoptera, Mantidae, Neuroptera, Phasmatodea, Thysanoptera, Thysanura, and Trichoptera). Numbers in parenthesis are sample sizes.

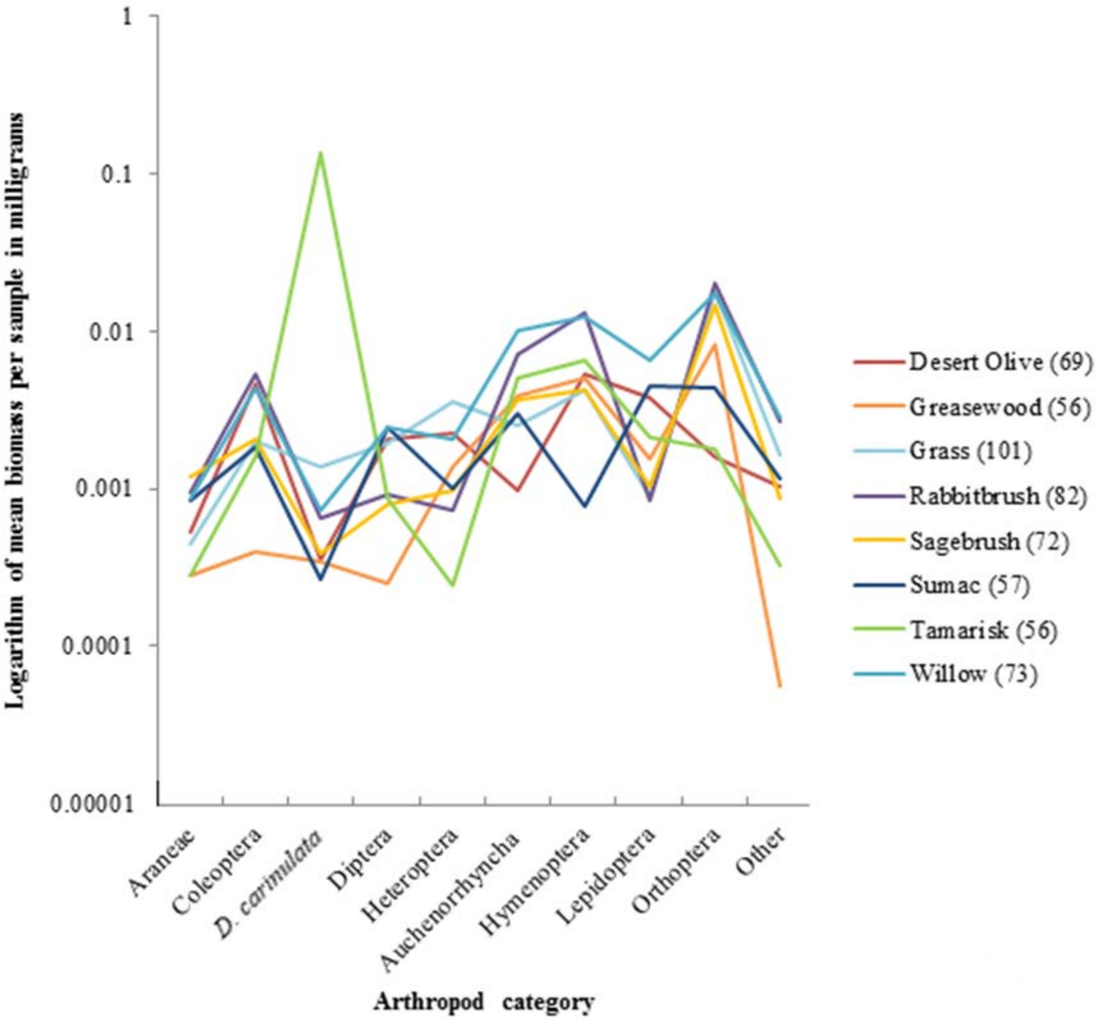

Figure 6. Mean biomass of arthropod categories (milligrams per 25 sweeps) in eight dominant plant species along the Dolores River, southwestern Colorado, 2010-11 (see fig. 1 for location). Categories are *Diorhabda carinulata*, Araneae (spiders), Coleoptera (beetles), Diptera (flies), Heteroptera (true bugs), Auchenorrhyncha (leafhoppers), Hymenoptera (ants and wasps), Lepidoptera (largely caterpillars), Orthoptera (grasshoppers), and other (Acari, Isoptera, Mantidae, Neuroptera, Phasmatodea, Thysanoptera, Thysanura, and Trichoptera). Numbers in parenthesis are sample sizes.

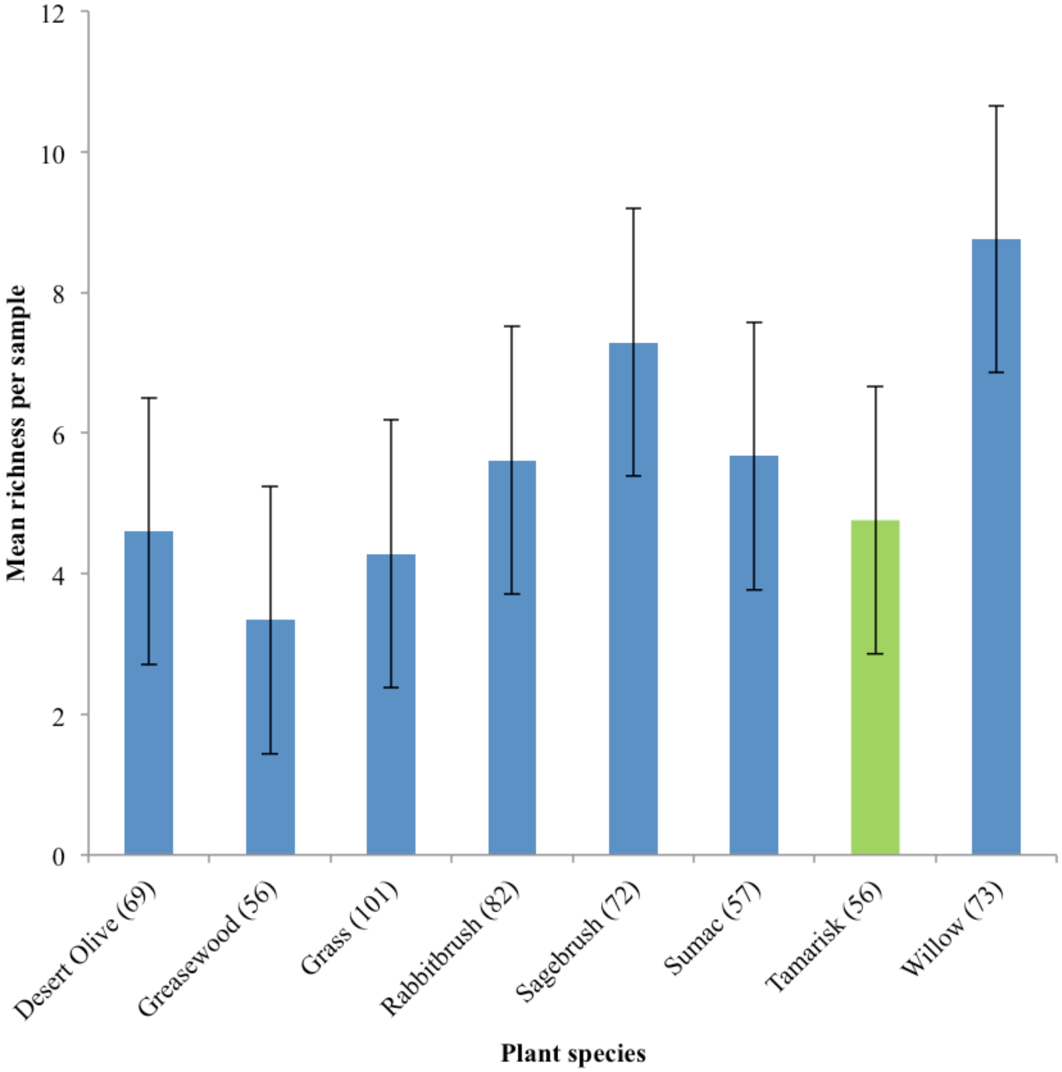

Figure 7. Mean species richness (number of morphospecies per 25 sweeps) of arthropods in eight dominant plant species along the Dolores River, southwestern Colorado, 2010-11 (see fig. 1 for location). Numbers in parenthesis are sample sizes; error bars depict 95-percent-confidence intervals.

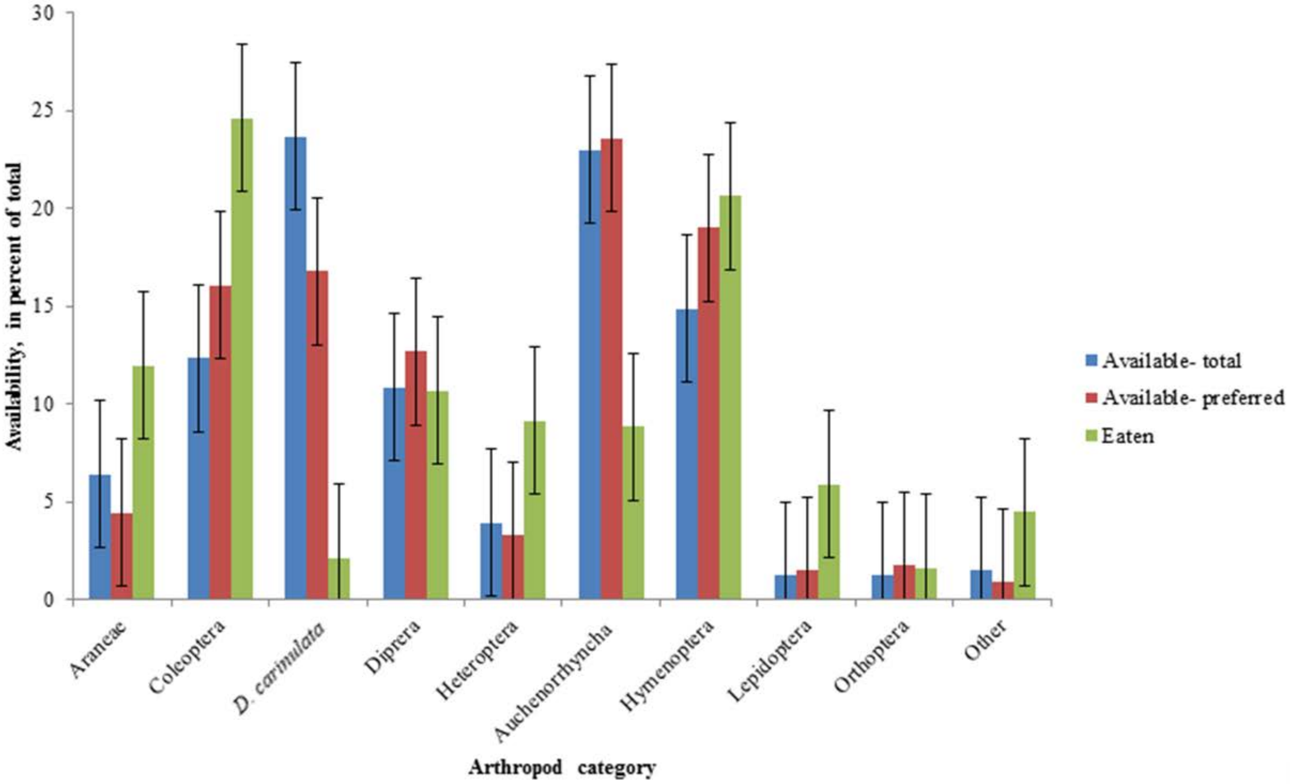

Figure 8. Availability of total and preferred arthropods versus abundance of arthropods in diets of all birds along the Dolores River, southwestern Colorado, 2010-11 (see fig. 1 for location). Error bars depict 95-percent-confidence intervals.

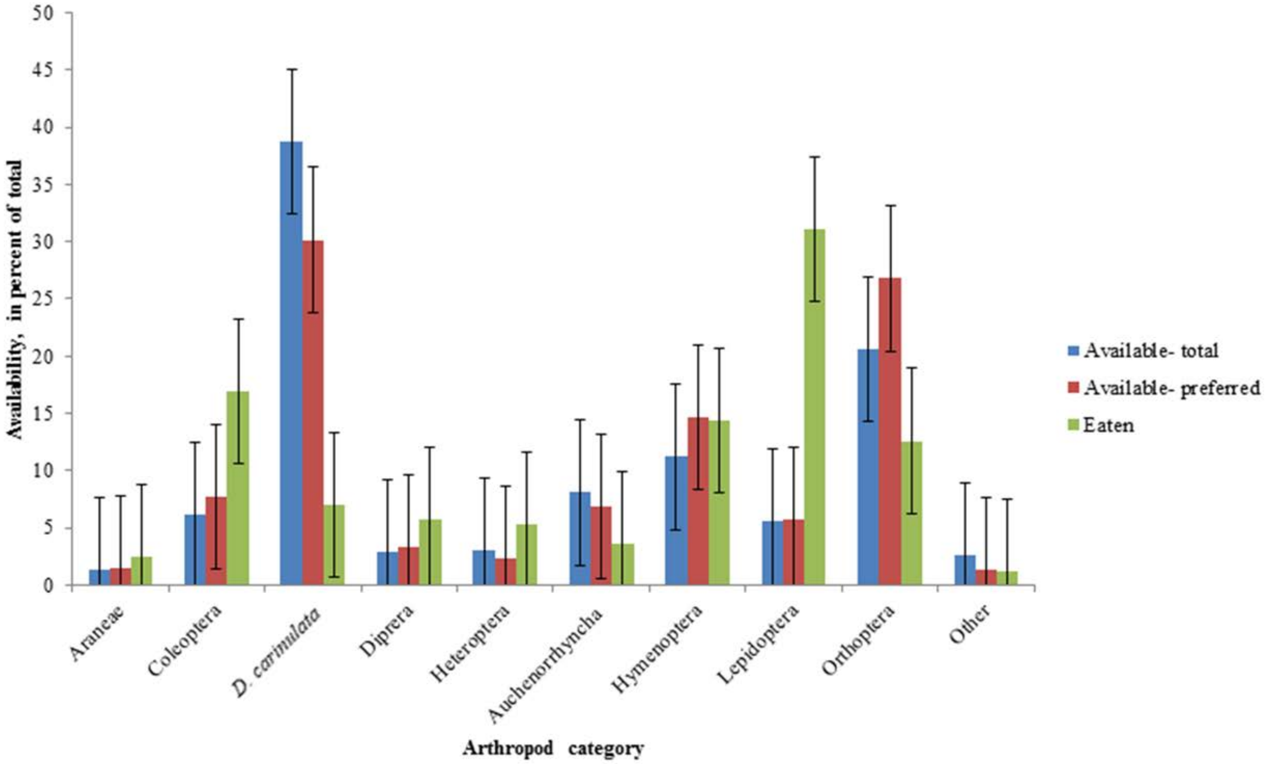

Figure 9. Availability of total and preferred arthropods versus biomass (in milligrams), of arthropods in diets of all birds along the Dolores River, southwestern Colorado, 2010-11 (see fig. 1 for location). Error bars depict 95-percent-confidence intervals.

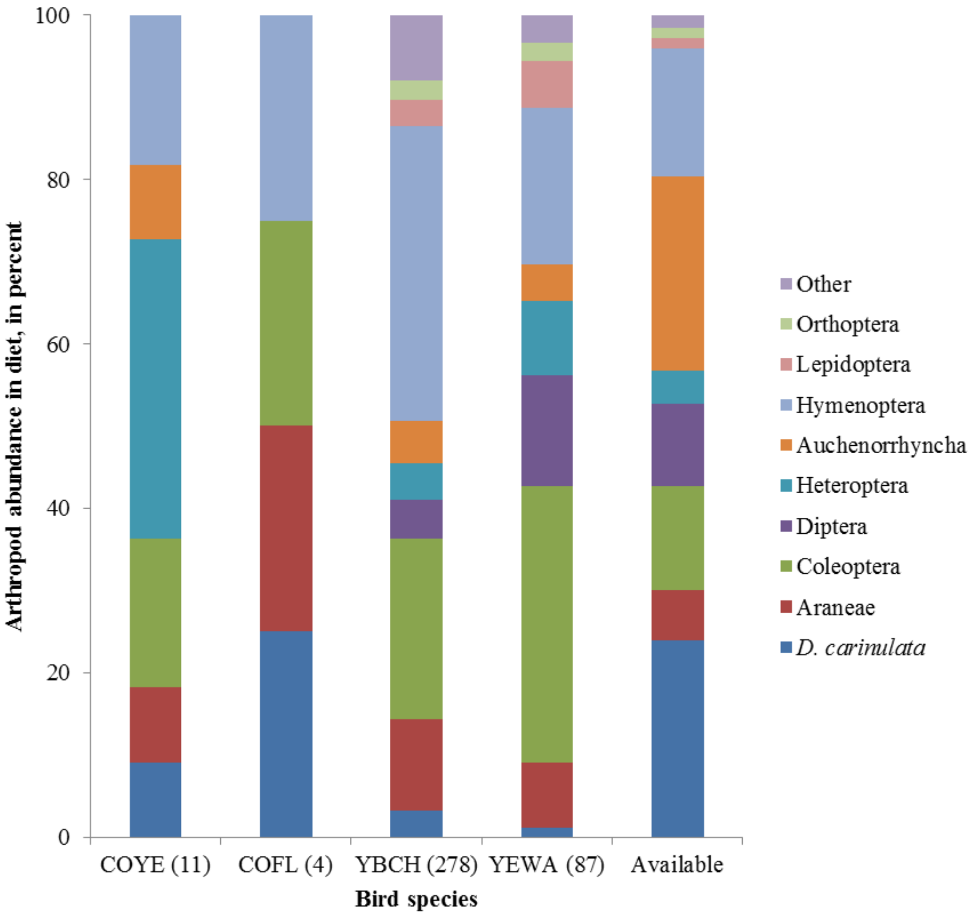

Figure 10. Percentage, by abundance, of *Diorhabda carinulata* in diets of four bird species whose gizzards contained fragmented remains of tamarisk leaf beetles. Numbers in parenthesis are number of individual arthropods detected in gizzards of these species, pooled.

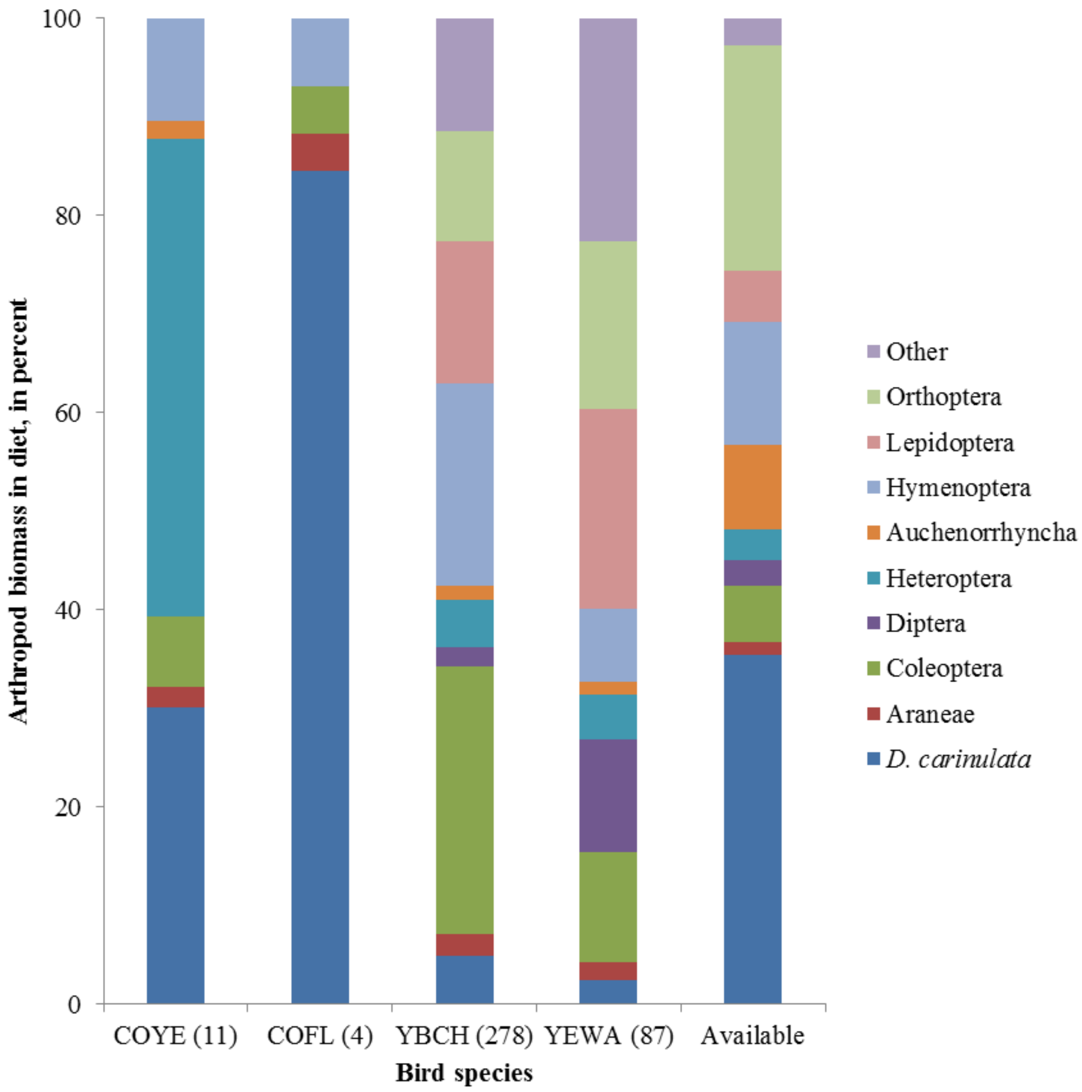

Figure 11. Percentage, by biomass (in milligrams), of *Diorhabda carinulata* in diets of four bird species whose gizzards contained fragmented remains of tamarisk leaf beetles. Numbers in parenthesis are combined number of individual arthropods detected in gizzards of these species.

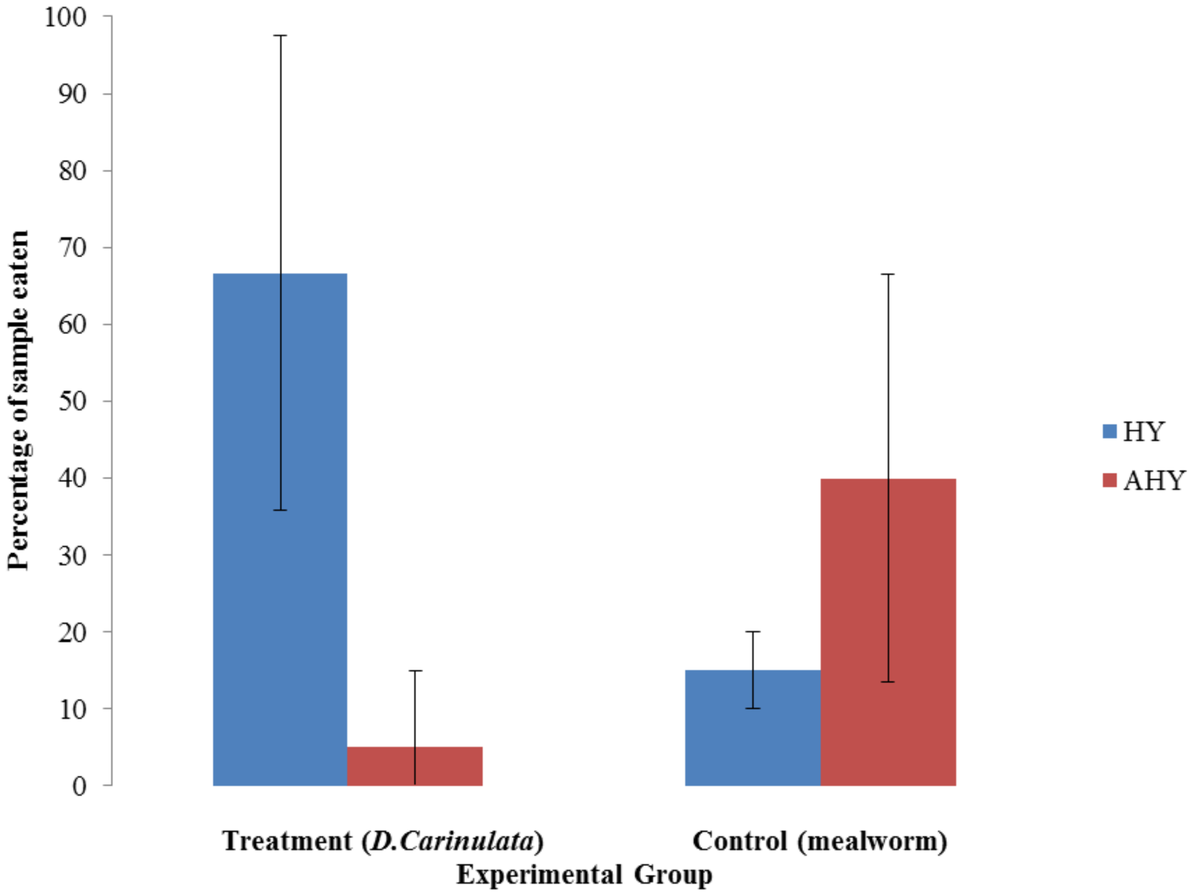

Figure 12. Average percentage of food items eaten by wild yellow-breasted chats over the course of a 2-hour food-choice experiment. Treatments consisted of 20 live tamarisk leaf beetles or mealworm prey items. Age classes: AHY, after hatch-year; HY, hatch-year.

Figure 13. Three life-stages of the tamarisk leaf beetle (*Diorhabda carinulata*). *a.* First instar larva. *b.* Third instar larvae. *c.* Adult beetle

Table 1. Phytochemical constituents of *Tamarix gallica.*

Compound	Percent	Characteristics
Tannin	49.4	Widely distributed in many species of plants; may protect against herbivory (Levin, 1976; Coley, 1986)
Hexadecanoic acid	18.1	Most common fatty acid in animals and plants
Docosane	13.3	Alkanes
Germacrene D	7.7	Produced by several plant species for their antimicrobial and insecticidal properties (Arimura and others, 2004)
Frenchyl acetate	7.3	A common building block for biosynthesis
Benzyl benzoate	4.1	As a topical solution, can be used as an antiparasitic insecticide (Landegren and others, 1979)

Table 2. Coverage and mean height of dominant shrub species in the study area.

[See figure 1 for locations. Data collected within 40 m of the riverbank. SE, standard error]

	Slick Rock	Crocker-Bedford Ranch	Bedrock	Cover (percent)		Height (m)	
				Mean	SE	Mean	SE
Tamarisk	4.6	2.5	33.3	13.5	9.9	2.8	0.3
Willow	51.8	73.1	37.5	54.2	10.3	2.2	0.1
Desert olive	12.2	10.2	2.7	8.3	2.9	2.2	0.2
Rabbitbrush	7.8	3.7	6.3	5.9	1.2	1.3	0.1
Sumac	11.8	4.6	0.6	5.7	3.3	1.4	0.1
Greasewood	2.6	0.0	11.6	4.7	3.5	1.6	0.1
Sagebrush	7.8	3.4	7.1	6.1	1.4	1.4	0.1

Table 3. Avian species and sample sizes in the study area.

[See figure 1 for locations. Species codes used for labels in all tables are based on common names, according to nomenclature of the American Ornithological Union. Columns denote sample sizes for point count surveys, mist netting, foraging observations, and diet sampling. Data pooled for 2010-12]

Family	Scientific name	Common name	Code	Survey	Net	Forage	Diet
Ardeidae	*Ardea herodias*	Great blue heron	GBHE	2	−	−	−
Cathartidae	*Cathartes aura*	Turkey vulture	TUVU	1	−	−	−
Accipitridae	*Accipiter cooperii*	Cooper's hawk	COHA	1	−	−	−
	Buteo jamaicensis	Red-tailed hawk	RTHA	6	−	−	−
Falconidae	*Falco sparverius*	American kestrel	AMKE	1	−	−	−
Charadriidae	*Charadrius vociferus*	Killdeer	KILL	2	−	−	−
Scolopacidae	*Actitis macularia*	Spotted sandpiper	SPSA	7	−	−	−
Columbidae	*Zenaida macroura*	Mourning dove	MODO	78	7	−	−
	Steptopelia decaocto	Eurasian collared dove	EUCD	2	−	−	−
Apodidae	*Aeronautes saxatalis*	White-throated swift	WTSW	40	−	−	−
Trochilidae	*Calypte anna*	Anna's hummingbird	ANHU	4	−	1	−
	Archilochus alexandri	Black-chinned hummingbird	BCHU	22	1	1	−
	Selasphorus platycercus	Broad-tailed hummingbird	BTAH	4	2	6	−
	Selasphorus rufus	Rufous hummingbird	RUHU	21	−	2	−
Picidae	*Colaptes auratus*	Northern flicker	NOFL	8	−	−	−
Tyranidae	*Myiarchus cinerascens*	Ash-throated flycatcher	ATFL	96	11	25	7
	Sayornis nigricans	Black phoebe	BLPH	−	−	3	−
	Tyrannus vociferans	Cassin's kingbird	CAKI	3	−	2	−
	Empidonax occidentalis	Cordilleran flycatcher	COFL	2	3	1	1
	Sayornis saya	Say's phoebe	SAPH	37	−	24	−
	Tyrannus verticalis	Western kingbird	WEKI	60	3	14	1
	Contopus sordidulus	Western wood-pewee	WEWP	8	3	8	3
Vireonidae	*Vireo vicinior*	Gray vireo	GRVI	34	6	9	3
	Vireo plumbeus	Plumbeous vireo	PLVI	9	−	1	−
Corvidae	*Gymnorhinus cyanocephalus*	Pinyon jay	PIJA	29	−	2	−
	Aphelocoma californica	Western scrub-jay	WESJ	112	2	14	2
Corvidae	*Corvus corax*	Common raven	CORO	12	−	−	−
	Pica hudsonia	Black-billed magpie	BBMA	3	−	−	−
Hirundinidae	*Petrochelidon pyrrhonota*	Cliff swallow	CLSW	61	1	−	−
	Hirundo rustica	Barn swallow	BARS	3	−	−	−
	Tachycineta thalassina	Violet-green swallow	VGSW	25	−	−	−
Paridae	*Baeolophus ridgwayi*	Juniper titmouse	JUTI	4	−	2	−
Aegithalidae	*Psaltriparus minimus*	Bushtit	BUSH	20	10	14	−
Troglodytidae	*Catherpes mexicanus*	Canyon wren	CANW	22	−	1	−
	Troglodytes aedon	House wren	HOWR	−	−	1	−
	Salpinctes obsoletus	Rock wren	ROWR	80	−	11	−

Family	Scientific name	Common name	Code	Survey	Net	Forage	Diet
Regulidae	*Regulus calendula*	Ruby-crowned kinglet	RCKI	1	−	−	−
Polioptilidae	*Polioptila caerulea*	Blue-gray gnatcatcher	BGGN	195	8	83	5
Turdidae	*Turdus migratorius*	American robin	AMRO	38	1	11	−
	Sialia mexicana	Western bluebird	WEBL	7	−	−	−
Mimidae	*Mimus polyglottos*	Northern mockingbird	NOMO	32	7	15	3
	Dumetella carolinensis	Gray catbird	GRCA	−	1	−	1
Parulidae	*Icteria virens*	Yellow-breasted chat	YBCH	496	69	35	53
	Dendroica petechia	Yellow warbler	YEWA	120	25	19	22
	Dendroica caerulescens	Black-throated gray warbler	BTYW	15	14	17	10
	Geothlypis trichas	Common yellowthroat	COYE	66	7	4	4
	Vermivora celata	Orange-crowned warbler	OCWA	3	4	5	1
	Oreothlypis virginiae	Virginia's warbler	VIWA	3	4	1	4
Thraupidae	*Piranga ludoviciana*	Western tanager	WETA	8	−	3	−
Cardinalidae	*Passerina amoena*	Lazuli bunting	LAZB	19	1	1	1
	Pheucticus melanocephalus	Black-headed grosbeak	BHGR	44	13	20	7
	Passerina caerulea	Blue grosbeak	BLGR	191	14	29	6
Emberizidae	*Melospiza melodia*	Song sparrow	SOSP	13	2	3	2
	Pipilo maculatus	Spotted towhee	SPTO	408	22	19	12
	Pipilo chlorurus	Green-tailed towhee	GTTO	−	1	−	1
	Chondestes grammacus	Lark sparrow	LASP	80	50	29	17
	Spizella passerina	Chipping sparrow	CHSP	23	1	1	−
	Spizella breweri	Brewer's sparrow	BRSP	10	−	4	−
	Melospiza lincolnii	Lincoln's sparrow	LISP	−	1	−	−
	Passerella iliaca	Fox sparrow	FOSP	−	1	−	−
	Amphispiza bilineata	Black-throated sparrow	BTSP	96	11	16	3
	Zonotrichia leucophrys	White-crowned sparrow	WCSP	48	−	4	−
Icteridae	*Icterus bullockii*	Bullock's oriole	BUOR	10	6	6	3
	Agelaius phoeniceus	Red-winged blackbird	RWBL	−	2	−	−
	Molothrus ater	Brown-headed cowbird	BHCO	21	5	−	3
Fringillidae	*Carduelis psaltria*	Lesser goldfinch	LEGO	27	1	4	−
	Carpodacus mexicanus	House finch	HOFI	245	26	30	12

Table 4. Arthropod fragments used as indicators of prey taken by passerine birds in the study area.

[See figure 1 for locations. Partly reproduced from Ralph and others (1985)]

Group	Structure	Description
		Arachnids
Araneae (spiders)	Fang (*fig. 2D*)	Sharp and curved. Sometimes resembles tarsal claws, but this structure is more symmetrical.
	Chelicera (*fig. 2E*)	Distinguishable by slightly asymmetrical, but conical, shape.
	Leg (*fig. 2B*)	Segments tend to be straight-sided, whereas those of insects tend to taper at the joint. Commonly hairy; simple tarsus with two claws is diagnostic.
		Insects
Hemiptera (true bugs)		
Auchenorrhyncha	Tibia (*fig. 3C*)	Has rows of prominent spines.
Heteroptera	Tibia (*fig. 4B*)	Tibia has two long rows of small, dark spines.
	Hemelytra (*fig. 4D*)	Basal part of forewing is thickened and leathery, whereas apical part is membranous.
	Clavus, corium	Hardened sections of forewing, recognizable even when membrane is unattached.
Neuroptera (lacewings)	Wing (*fig. 5D*)	---
	Mandible	Smooth, slightly rounded, sickle-shaped.
Lepidoptera (butterflies/ moths)	Wing scales	Numerous small scales on wing.
Diptera (flies)	Wing (*fig. 6D*)	Leading edge commonly has small, curved bristles.
	Leg (*figs. 7A, 7B*)	Bristles common on leg.
	Bristles (setae)	Strong, black, slightly curved, and tapered, some still attached to leg.
	Antenna	Apical segment is acorn shaped.
Hymenoptera (ants/ wasps)	Leg (*fig. 7B, 8B*)	Drumstick-shaped femur and slender tibia.
	Wing (*fig. 8D*)	Pterostigma, a dark pigmented spot on leading edge of wing, sometimes on the forewing
	Mandible (*fig. 7C*)	Has two apical teeth.
	Head (*fig. 7D*)	Hard, with a distinct round foramen where it connects with thorax.
Coleoptera (beetles)	Antennae (fig. 9e)	Form varies greatly within Coleoptera.
	Head	Usually heavily sclerotized; may be found intact for smaller beetles
	Leg (fig. 9b)	
	Tibia (fig. 9c)	
	Femur (fig. 9c)	Enlarged, oval shaped femur found on some species
	Elytra (fig. 9d)	Almost flat and square in shape with curled edge
	Hind wing (fig. 9d)	Venation is reduced and modified

Table 5. Numbers of observations and mean heights of foraging events for all bird species combined in the study area, 2010-12.

[See figure 1 for locations. SE, standard error]

Substrate	N	Mean height (m)	SE
Air	64	2.35	0.26
Desert olive	81	1.69	0.11
Ground	52	0.00	0.00
Greasewood	33	0.91	0.09
Grass	42	0.38	0.06
Rabbitbrush	11	0.68	0.08
Sagebrush	17	0.88	0.13
Sumac	35	1.69	0.16
Willow	43	1.27	0.13
Tamarisk	77	2.97	0.20

Table 6. Bird family, sample size, number of foraging observations, and number of foraging events for all substrates in the study area, 2010-12.

[See figure 1 for locations. *n*, mean; ±, standard error]

Foraging substrate	Aegithalidae (*n* = 14)	Cardinalidae (*n* = 50)	Corvidae (*n* = 16)	Emberizidae (*n* = 76)	Fringillidae (*n* = 34)	Icteridae (*n* = 6)	Mimidae (*n* = 15)
Air	0	2 (4 ± 0)	3 (19 ± 2)	0	1 (3 ± 0)	0	0
Desert olive	2 (14 ± 2)	8 (16 ± 1)	0	6 (8 ± 0)	16 (47 ± 1)	4 (67 ± 8)	7 (47 ± 3)
Grass	2 (14 ± 2)	3 (6 ± 0)	1 (6 ± 2)	15 (20 ± 1)	1 (3 ± 0)	0	0
Greasewood	6 (43 ± 4)	2 (4 ± 0)	1 (6 ± 2)	4 (5 ± 0)	1 (3 ± 0)	0	0
Ground	0	1 (2 ± 0)	1 (6 ± 2)	27 (36 ± 1)	9 (26 ± 1)	0	3 (20 ± 3)
Other[1]	0	8 (16 ± 1)	8 (50 ± 3)	3 (4 ± 0)	1 (3 ± 0)	0	1 (7 ± 2)
Rabbitbrush	0	2 (4 ± 0)	0	0	1 (3 ± 0)	0	0
Sagebrush	2 (14 ± 2)	1 (2 ± 0)	0	2 (3 ± 0)	0	0	0
Sumac	0	8 (16 ± 1)	1 (6 ± 2)	5 (7 ± 0)	0	0	0
Tamarisk	2 (14 ± 2)	7 (14 ± 1)	1 (6 ± 2)	11 (14 ± 0)	2 (6 ± 1)	0	4 (27 ± 3)
Willow	0	8 (16 ± 1)	0	3 (4 ± 0)	2 (6 ± 1)	2 (33 ± 8)	0

Foraging substrate	Parulidae (*n* = 81)	Polioptilidae (*n* = 83)	Thraupidae (*n* = 3)	Troglodytidae (*n* = 13)	Turdidae (*n* = 11)	Tyrannidae (*n* = 77)	Vireonidae (*n* = 10)
Air	2 (2 ± 0)	5 (6 ± 0)	0	1 (8 ± 2)	0	44 (57 ± 1)	0
Desert olive	19 (23 ± 1)	5 (6 ± 0)	1 (33 ± 16)	0	7 (64 ± 4)	4 (5 ± 0)	0
Grass	5 (6 ± 0)	5 (6 ± 0)	0	0	0	6 (8 ± 0)	0
Greasewood	3 (4 ± 0)	13 (16 ± 0)	0	0	0	2 (3 ± 0)	1 (10 ± 3)
Ground	0	0	0	8 (62 ± 4)	1 (9 ± 3)	1 (1 ± 0)	0
Other[1]	10 (12 ± 0)	7 (8 ± 0)	0	1 (8 ± 2)	0	8 (10 ± 0)	5 (50 ± 5)
Rabbitbrush	1 (1 ± 0)	4 (5 ± 0)	0	0	0	2 (3 ± 0)	0
Sagebrush	3 (4 ± 0)	8 (10 ± 0)	0	0	0	1 (1 ± 0)	0
Sumac	5 (6 ± 0)	8 (10 ± 0)	2 (67 ± 16)	0	2 (18 ± 4)	2 (3 ± 0)	0
Tamarisk	14 (17 ± 0)	23 (28 ± 1)	0	3 (23 ± 3)	1 (9 ± 3)	6 (8 ± 0)	2 (20 ± 4)
Willow	19 (23 ± 1)	5 (6 ± 0)	0	0	0	1 (1 ± 0)	2 (20 ± 4)

[1] Includes fourwing saltbush, mulefat, boxelder, pinyon, juniper, Gambel oak, and Siberian elm.

Table 7. Use and availability of dominant shrub species in the study area, 2010-12.

[See figure 1 for location. SE, standard error]

	Use		Available	
Foraging substrate	Percent	SE	Percent	SE
Aegithalidae (n = 12)				
Desert olive	16.7	3.1	8.3	2.9
Greasewood	50.0	4.2	4.7	3.5
Rabbitbrush	0.0	0.0	5.9	1.2
Sagebrush	16.7	3.1	6.1	1.4
Sumac	0.0	0.0	5.7	3.3
Tamarisk	16.7	3.1	13.5	9.9
Willow	0.0	0.0	37.5	10.3
Cardinalidae (*n* = 36)				
Desert olive	22.2	1.2	8.3	2.9
Greasewood	5.6	0.6	4.7	3.5
Rabbitbrush	5.6	0.6	5.9	1.2
Sagebrush	2.8	0.5	6.1	1.4
Sumac	22.2	1.2	5.7	3.3
Tamarisk	19.4	1.1	13.5	9.9
Willow	22.2	1.2	37.5	10.3
Corvidae (*n* = 3)				
Desert olive	0.0	0.0	8.3	2.9
Greasewood	33.3	15.7	4.7	3.5
Rabbitbrush	0.0	0.0	5.9	1.2
Sagebrush	0.0	0.0	6.1	1.4
Sumac	33.3	15.7	5.7	3.3
Tamarisk	33.3	15.7	13.5	9.9
Willow	0.0	0.0	37.5	10.3
Emberizidae (*n* = 31)				
Desert olive	19.4	1.3	8.3	2.9
Greasewood	12.9	1.1	4.7	3.5
Rabbitbrush	0.0	0.0	5.9	1.2
Sagebrush	6.5	0.8	6.1	1.4
Sumac	16.1	1.2	5.7	3.3
Tamarisk	35.5	1.5	13.5	9.9
Fringillidae (*n* = 22)				
Desert olive	72.7	2.0	8.3	2.9
Greasewood	4.5	0.9	4.7	3.5
Rabbitbrush	4.5	0.9	5.9	1.2
Sagebrush	0.0	0.0	6.1	1.4
Sumac	0.0	0.0	5.7	3.3
Tamarisk	9.1	1.3	13.5	9.9
Willow	9.1	1.3	37.5	10.3

	Use		Available	
Foraging substrate	Percent	SE	Percent	SE
Icteridae (*n* = 6)				
Desert olive	66.7	7.9	8.3	2.9
Greasewood	0.0	0.0	4.7	3.5
Rabbitbrush	0.0	0.0	5.9	1.2
Sagebrush	0.0	0.0	6.1	1.4
Sumac	0.0	0.0	5.7	3.3
Tamarisk	0.0	0.0	13.5	9.9
Willow	33.3	7.9	37.5	10.3
Mimidae (*n* = 11)				
Desert olive	63.6	4.4	8.3	2.9
Greasewood	0.0	0.0	4.7	3.5
Rabbitbrush	0.0	0.0	5.9	1.2
Sagebrush	0.0	0.0	6.1	1.4
Sumac	0.0	0.0	5.7	3.3
Tamarisk	36.4	4.4	13.5	9.9
Willow	0.0	0.0	37.5	10.3
Parulidae (*n* = 64)				
Desert olive	29.7	0.7	8.3	2.9
Greasewood	4.7	0.3	4.7	3.5
Rabbitbrush	1.6	0.2	5.9	1.2
Sagebrush	4.7	0.3	6.1	1.4
Sumac	7.8	0.4	5.7	3.3
Tamarisk	21.9	0.6	13.5	9.9
Willow	29.7	0.7	37.5	10.3
Polioptilidae (*n* = 66)				
Desert olive	7.6	0.4	8.3	2.9
Greasewood	19.7	0.6	4.7	3.5
Rabbitbrush	6.1	0.4	5.9	1.2
Sagebrush	12.1	0.5	6.1	1.4
Sumac	12.1	0.5	5.7	3.3
Tamarisk	34.8	0.7	13.5	9.9
Willow	7.6	0.4	37.5	10.3
Thraupidae (*n* = 3)				
Desert olive	33.3	15.7	8.3	2.9
Greasewood	0.0	0.0	4.7	3.5
Rabbitbrush	0.0	0.0	5.9	1.2
Sagebrush	0.0	0.0	6.1	1.4
Sumac	66.7	15.7	5.7	3.3
Tamarisk	0.0	0.0	13.5	9.9
Willow	0.0	0.0	37.5	10.3

Foraging substrate	Use		Available	
	Percent	SE	Percent	SE
Troglodytidae ($n = 3$)				
Desert olive	0.0	0.0	8.3	2.9
Greasewood	0.0	0.0	4.7	3.5
Rabbitbrush	0.0	0.0	5.9	1.2
Sagebrush	0.0	0.0	6.1	1.4
Sumac	0.0	0.0	5.7	3.3
Tamarisk	100.0	0.0	13.5	9.9
Willow	0.0	0.0	37.5	10.3
Turdidae ($n = 10$)				
Desert olive	70.0	4.6	8.3	2.9
Greasewood	0.0	0.0	4.7	3.5
Rabbitbrush	0.0	0.0	5.9	1.2
Sagebrush	0.0	0.0	6.1	1.4
Sumac	20.0	4.0	5.7	3.3
Tamarisk	10.0	3.0	13.5	9.9
Willow	0.0	0.0	37.5	10.3
Tyrannidae ($n = 18$)				
Desert olive	22.2	2.3	8.3	2.9
Greasewood	11.1	1.7	4.7	3.5
Rabbitbrush	11.1	1.7	5.9	1.2
Sagebrush	5.6	1.3	6.1	1.4
Sumac	11.1	1.7	5.7	3.3
Tamarisk	33.3	2.6	13.5	9.9
Willow	5.6	1.3	37.5	10.3
Vireonidae ($n = 5$)				
Desert olive	0.0	0.0	8.3	2.9
Greasewood	20.0	8.0	4.7	3.5
Rabbitbrush	0.0	0.0	5.9	1.2
Sagebrush	0.0	0.0	6.1	1.4
Sumac	0.0	0.0	5.7	3.3
Tamarisk	40.0	9.8	13.5	9.9
Willow	40.0	9.8	37.5	10.3

Table 8. Mean total abundance (number per 25 sweeps) of arthropod categories collected per sample (*n* = 503) among all plant species in the study area, 2010-11.

[See figure 1 for location. SE, standard error]

Arthropod category	Mean	SE	Percent
Diorhabda carinulata	7.8	1.9	24.0
Auchenorrhyncha	7.7	1.9	23.5
Hymenoptera	5.1	1.6	15.6
Coleoptera	4.1	1.5	12.7
Diptera	3.3	1.3	10.2
Araneae	2.0	1.1	6.1
Heteroptera	1.3	0.9	4.1
Other	0.5	0.6	1.6
Lepidoptera	0.4	0.5	1.1
Orthoptera	0.4	0.5	1.1

Table 9. Mean total biomass (in milligrams per 25 sweeps) of arthropod categories collected per sample (*n* = 503) among all plant species in the study area, 2010-11.

[See figure 1 for location. SE, standard error]

Arthropod category	Mean	SE	Percent
Diorhabda carinulata	0.0180	0.0021	35.4
Orthoptera	0.0116	0.0019	22.8
Hymenoptera	0.0063	0.0015	12.4
Auchenorrhyncha	0.0044	0.0013	8.6
Coleoptera	0.0029	0.0010	5.7
Lepidoptera	0.0027	0.0010	5.3
Heteroptera	0.0016	0.0008	3.1
Other	0.0014	0.0007	2.8
Diptera	0.0013	0.0007	2.6
Araneae	0.0007	0.0005	1.4

Table 10. Bird family, sample size, number of food items, and mean use of food items in diet samples (*n* = 188) of birds along the Dolores River, Colo., 2010-11.

[See figure 1 for locations]

Food-item category	Cardinalidae (*n* = 14)	Emberizidae (*n* = 36)	Fringillidae (*n* = 12)	Icteridae (*n* = 7)	Mimidae (*n* = 5)	Parulidae (*n* = 94)	Polioptilidae (*n* = 5)	Tyrannidae (*n* = 12)	Vireonidae (*n* = 3)
Araneae	3 (11 ± 6)	9 (7 ± 2)	0	0	0	36 (9 ± 1)	3 (23 ± 12)	13 (27 ± 6)	0
Coleoptera	3 (11 ± 6)	19 (15 ± 3)	1 (1 ± 1)	2 (20 ± 13)	1 (17 ± 15)	96 (23 ±2)	1 (8 ± 7)	4 (8 ± 4)	2 (22 ±14)
Diorhabda carinulata	0	0	0	0	0	10 (2 ± 1)	0	1 (2 ± 2)	0
Diptera	1 (4 ± 4)	3 (2 ± 1)	0	0	0	30 (7 ± 1)	2 (15 ± 10)	11 (23 ± 6)	2 (22 ±14)
Heteroptera	2 (7 ± 5)	5 (4 ± 2)	0	3 (30 ± 15)	1 (17 ± 15)	31 (8 ± 1)	1 (8 ± 7)	3 (6 ± 3)	2 (22 ±14)
Auchenorrhyncha	2 (7 ± 5)	4 (3 ± 2)	1 (1 ± 1)	1 (10 ± 9)	0	20 (5 ± 1)	3 (23 ± 12)	3 (6 ± 3)	0
Hymenoptera	1 (4 ± 4)	7 (5 ± 2)	1 (1 ± 1)	0	3 (50 ± 20)	109 (28 ± 2)	0	9 (18 ± 6)	0
Lepidoptera	1 (4 ± 4)	3 (2 ± 1)	0	3 (30 ± 15)	1 (17 ± 15)	14 (4 ± 1)	2 (15 ± 10)	5 (10 ± 4)	1 (12 ± 1)
Orthoptera	0	1 (1 ± 1)	0	0	0	8 (2 ± 1)	0	0	0
Other	0	0	0	1 (10 ± 9)	0	16 (4 ± 1)	1 (8 ± 7)	0	2 (22 ±14)
Seed	14 (52 ± 10)	79 (61 ± 4)	91 (97 ± 2)	0	0	33 (8 ± 1)	0	0	0

Table 11. Bird family, sample size, biomass of food items, and mean biomass of food items in diet samples (*n* = 188) of birds along the Dolores River, Colo., 2010-11.

[See figure 1 for location. All values in milligrams, with means in parentheses; dashed, no data]

Food-item category	Cardinalidae (*n* = 14)	Emberizidae (*n* = 36)	Fringillidae (*n* = 12)	Icteridae (*n* = 7)	Mimidae (*n* = 5)	Parulidae (*n* = 94)	Polioptilidae (*n* = 5)	Tyrannidae (*n* = 12)	Vireonidae (*n* = 3)
Araneae	1.3 x 10^{-3} (4 ± 3)	3.5 x 10^{-3} (1 ± 1)	0 ---	0 ---	0 ---	1.6 x 10^{-2} (2 ± 1)	3.0 x 10^{-3} (13 ± 9)	4.7 x 10^{-3} (2 ± 2)	0 ---
Coleoptera	3.4 x 10^{-3} (10 ± 6)	1.7 x 10^{-2} (5 ± 2)	7.0 x 10^{-4} (1 ± 1)	8.9 x 10^{-4} (7 ± 8)	5.7 x 10^{-4} (3 ± 6)	1.8 x 10^{-1} (24 ± 2)	5.7 x 10^{-4} (2 ± 4)	3.3 x 10^{-3} (1 ± 2)	2.9 x 10^{-3} (16 ± 12)
Diorhabda carinulata	0 ---	0 ---	0 ---	0 ---	0 ---	3.8 x 10^{-2} (5 ± 1)	0 ---	3.8 x 10^{-3} (2 ± 2)	0 ---
Diptera	1.3 x 10^{-3} (4 ± 3)	4.2 x 10^{-3} (1 ± 1)	0 ---	0 ---	0 ---	3.1 x 10^{-2} (4 ± 1)	1.1 x 10^{-3} (5 ± 6)	4.7 x 10^{-2} (20 ± 6)	4.7 x 10^{-4} (3 ± 5)
Heteroptera	1.4 x 10^{-3} (5 ± 3)	3.0 x 10^{-3} (1 ± 1)	0 ---	1.7 x 10^{-3} (13 ± 10)	5.8 x 10^{-4} (3 ± 6)	4.6 x 10^{-2} (6 ± 1)	4.3 x 10^{-3} (18 ± 10)	1.4 x 10^{-3} (1 ± 1)	2.1 x 10^{-3} (11 ± 10)
Auchenorrhyncha	2.4 x 10^{-3} (7 ± 5)	1.7 x 10^{-3} (1 ± 1)	2.3 x 10^{-4} (0.5 ± 0.5)	1.3 x 10^{-3} (10 ± 9)	0 ---	1.1 x 10^{-2} (2 ± 1)	6.9 x 10^{-4} (2 ± 5)	2.9 x 10^{-3} (1 ± 2)	0 ---
Hymenoptera	1.1 x 10^{-2} (34 ± 9)	8.4 x 10^{-3} (2 ± 1)	1.5 x 10^{-4} (0.5 ± 0.5)	0 -	6.0 x 10^{-3} (30 ± 18)	1.4 x 10^{-1} (18 ± 2)	0 ---	1.6 x 10^{-2} (7 ± 4)	0 ---
Lepidoptera	2.4 x 10^{-3} (7 ± 5)	9.8 x 10^{-2} (28 ± 4)	0 ---	7. x 10^{-3} (57 ± 16)	1.2 x 10^{-2} (64 ± 20)	1.3 x 10^{-1} (17 ± 2)	1.4 x 10^{-2} (57 ± 14)	1.5 x 10^{-1} (67 ± 7)	1.3 x 10^{-2} (69 ± 15)
Orthoptera	0 ---	1.1 x 10^{-1} (32 ± 4)	0 ---	0 ---	0 ---	9.4 x 10^{-2} (13 ± 2)	0 ---	0 ---	0 ---
Other	0 ---	0 ---	0 ---	1.7 x 10^{-3} (13 ± 10)	0 ---	1.4 x 10^{-2} (2 ± 1)	7.5 x 10^{-4} (3 ± 5)	0 ---	3.1 x 10^{-5} (1 ± 1)
Seed	9.9 x 10^{-3} (29 ± 9)	9.9 x 10^{-2} (29 ± 4)	16.2 x 10^{-2} (98 ± 1)	0 ---	0 ---	5.1 x 10^{-2} (7 ± 1)	0 ---	0 ---	0 ---