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Influences of the invasive tamarisk leaf beetle (*Diorhabda carinulata*) on avian diets along the Dolores River in Southwestern Colorado USA

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Abstract The tamarisk leaf beetle (*Diorhabda carinulata*), introduced from Eurasia in 2001 as a biological control agent for the invasive plant *Tamarix ramosissima*, has spread widely throughout the western USA. With *D. carinulata* now very abundant, scientists and restoration managers have questioned what influence this introduced arthropod might have upon the avian component of riparian ecosystems. From 2009 through 2012 we studied the consequences

of biological invasions of the introduced tamarisk shrub and tamarisk leaf beetles on the diets of native birds along the Dolores River in southwestern Colorado, USA. We examined avian foraging behavior, sampled the arthropod community, documented bird diets and the use of invasive tamarisk shrubs and tamarisk leaf beetles by birds. We documented *D. carinulata* abundance, on what plants the beetles occurred, and to what degree they were consumed by birds as compared to other arthropods. We hypothesized that if *D. carinulata* is an important new avian food source, birds should consume beetles at least in proportion to their abundance. We also hypothesized that birds should forage more in tamarisk in the late summer when tamarisk leaf beetle larvae are more abundant than in early summer, and that birds should select beetle-damaged tamarisk shrubs. We found that *D. carinulata* composed 24.0 percent (\pm 19.9–27.4%) and 35.4% biomass of all collected arthropods. From the gut contents of 188 birds (25 passerine species), only four species ($n = 11$ birds) contained tamarisk leaf beetle parts. Although *D. carinulata* comprised one-quarter of total insect abundance, frequency of occurrence in bird gut contents was only 2.1% by abundance and 3.4% biomass. Birds used tamarisk shrubs for foraging in proportion to their availability, but foraging frequency did not increase during the late summer when more tamarisk leaf beetles were present and birds avoided beetle-damaged tamarisk shrubs. Despite *D. carinulata* being the most abundant

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arthropod in the environment, these invasive beetles were not frequently consumed by birds and seem not to provide a significant contribution to avian diets.

Keywords Invasive tamarisk · Bird foraging · Diet preferences · Arthropods biological control · Riparian habitat · Salt cedar · Passerine birds

Introduction

Narrow belts of riparian vegetation along streams and rivers in the Southwestern United States are important ecosystems in an otherwise arid region (Knopf et al. 1988). Although riparian vegetation contributes to only a small percentage of land cover, it is very important for maintaining high species diversity and densities of birds (Anderson and Omhart 1977; Krueper et al. 2003; Brand et al. 2010). Anthropogenic changes to western riverine systems have enhanced their susceptibility to invasion by introduced plant species (Baker 1986; Mack et al. 2000). As a result, the biological control of invasive plant species is commonly a priority for management in the restoration of riparian ecosystems. Biologic control agents, however, may have unexpected effects especially on native bird species (Simberloff and Stiling 1996). Therefore, monitoring restoration activities and the interactions between biologic control agents and native communities is essential so that the appropriateness of any control method, and its overall success, can be objectively evaluated (Blossey 1999; Bateman et al. 2014; Darrah and van Riper 2017).

Tamarisk (*Tamarix* spp.), an invasive deciduous shrub native to drier regions of Eurasia and Africa, was introduced into the United States in the mid-1800 s as an ornamental plant, to provide shade, and for erosion control (Shafroth et al. 2005; Vincent et al. 2009). Aided by its capacity to grow in saline soil, its prolific seed production, and a tolerance for drought conditions, the invasive tamarisk now occupies ~ 400,000 to 600,000 ha of habitat in the western United States (Neill 1985), and particularly in areas where natural flood regimes have been altered (Warren and Turner 1975; Cleverly et al. 1997). Establishment of tamarisk can culminate in substantial changes to the structure and function of riparian systems, including reduction in water quantity due to an increase in

evapotranspiration rates, degradation of habitat for some native plant and animal species, increase in the frequency and severity of fire, and displacement of native vegetation (Stromberg et al. 2007; Nagler and Glenn 2013). Several studies, however, have shown that the invasive tamarisk can provide important habitat features for birds (Hunter et al. 1988; Ellis 1995; van Riper et al. 2008; Sogge et al. 2013). Regardless, controlling invasive tamarisk is important to many agencies in their habitat restoration efforts, especially in light of the plant's expanding geographic distribution (Barz et al. 2009).

Traditional strategies in restoration efforts for controlling tamarisk include mechanical removal, fire, and herbicide application (Hultine et al. 2010). These techniques, each of which has its advantages and limitations, may affect growth of native vegetation in riparian communities. Release of the tamarisk leaf beetle (*Diorhabda carinulata*) as a biologic control agent has been a relatively new addition. Originally from Eurasia, this beetle was selected because of high host specificity, restricted geographic range, and presumed ability to adapt to conditions in the United States. Biologic control of tamarisk by the tamarisk leaf beetle, which was first implemented in 2001, has resulted in expanding beetle populations that have been established in the states of Arizona, Colorado, Nevada, New Mexico, Utah, and Wyoming (Bloodworth et al. 2016).

Following their release, tamarisk leaf beetles have spread rapidly and currently defoliate tamarisk plants over a broad geographic scale in southwestern North America (Hultine et al. 2010; Meng et al. 2012; Jamison et al. 2015). It has been suggested that the presence of *D. carinulata* in riparian systems might enhance habitat quality for birds by providing a superabundant food resource (DeLoach et al. 2004; Longland and Dudley 2008), and this idea has just started to be rigorously tested (Mahoney et al. 2017). In addition, the magnitude of this benefit would largely depend upon the degree that *D. carinulata* was consumed by birds. The palatability of arthropod prey can often be predictable on the basis of coloration, behavior, and the chemical properties of their host plants (Bowers and Farley 1990). Although little is known about the palatability of *D. carinulata* to vertebrate predators, it feeds exclusively on tamarisk, a plant genus known to be rich in noxious substances, including tannins (Levin 1976), germacrene D, and

benzyl benzoate (Arimura et al. 2004). As specialist herbivores are well-known to be adept at sequestering host plant compounds for their own defense (Bowers and Farley 1990), a specialist such as *D. carinulata* might be less palatable to birds than other arthropods.

To resolve these conflicting predictions about the introduced tamarisk leaf beetle, we test the hypothesis that *Diorhabda* beetles are beneficial food source to passerine birds by quantifying the extent of beetle consumption by passerines via gut content analysis. Additionally, if *Diorhabda* beetles are an important bird food source, we would hypothesize that: (1) passerine birds would select tamarisk leaf beetles as prey items relative to levels of beetle abundance; (2) passerine birds would regularly forage in tamarisk; (3) passerines should use tamarisk more in the late summer, when tamarisk leaf beetle larvae are present; and, (4) passerine birds should prefer beetle-affected tamarisk over healthy tamarisk.

Methods

Study area

The Dolores River, a tributary to the Colorado River, flows ~ 400 km through southwest Colorado and southeastern Utah. We established three study sites at river miles 47, 54, and 97 (Slick Rock, Crocker-Bedford Ranch, and Bedrock; Fig. 1). Annual precipitation averaged ~ 30 cm while summer temperatures ranged from 7 to 35 °C. Data were collected between June 2010 and August 2012, analyzed with SPSS and the R statistical packages, and all values are given with 95% confidence intervals.

Vegetation sampling

We sampled vegetation within 30 circular plots, 10 at each study area. Each circular plot was 0.04-ha (11.3-m radius) with centers ~ 25 m from the river bank, and at 100-m intervals parallel to the river after James and Shugart (1970). All trees (any woody species ≥ 7.5 cm in diameter at breast height [DBH]) were counted, measured to the nearest cm, and identified to species. To measure shrub species availability, 22.6-m transects were established perpendicular to the river across each of the 30 vegetation plots. All shrub woody stems ≤ 7.5 cm in diameter that made contact

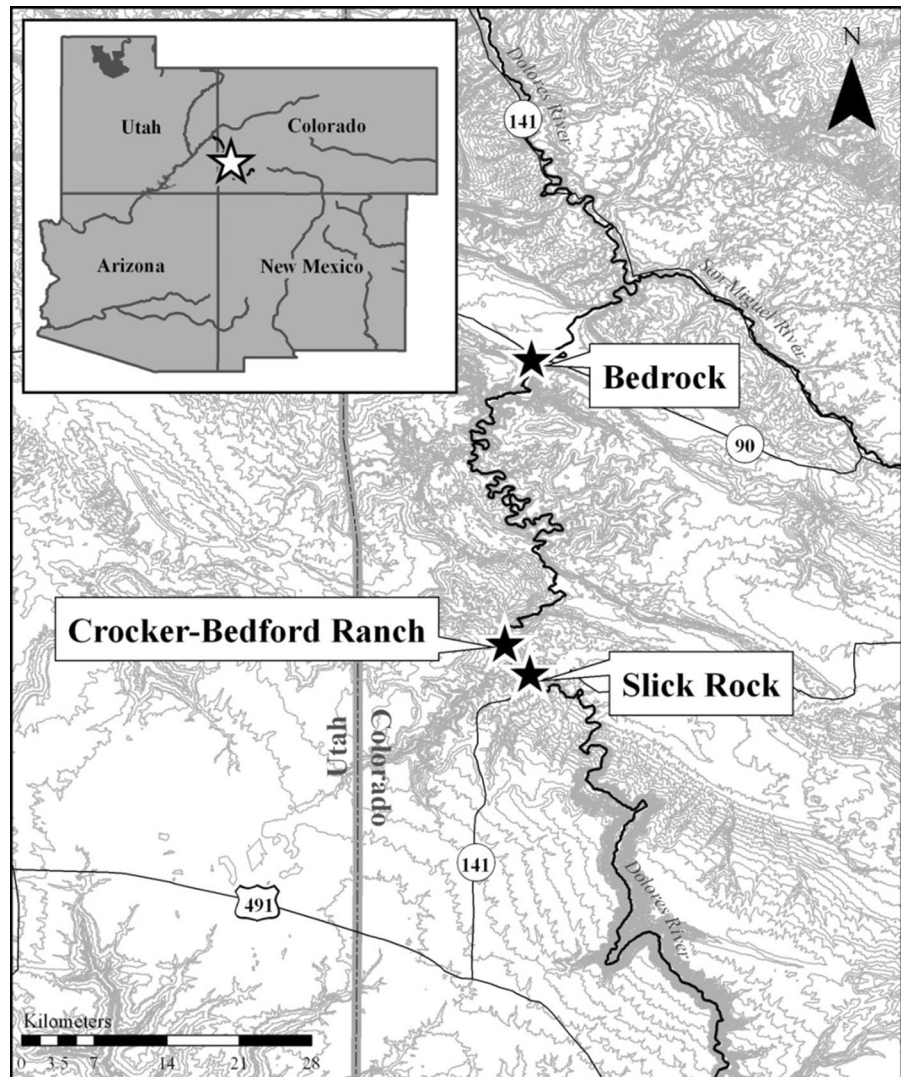
with a 2-m rod, held at breast height parallel to the ground, were counted. The percentage of coverage of woody stems per hectare was calculated for the seven dominant shrub species: coyote willow (*Salix exigua*), desert olive (*Foresteria pubescens*), sumac (*Rhus trilobata*), big sagebrush (*Artemisia tridentata*), rabbitbrush (*Ericameria nauseosa*), greasewood (*Sarcobatus vermiculatus*), and tamarisk (*Tamarix ramosissima*). Estimates of the availability of various shrub species were then compared with observations of avian foraging behavior to quantify plant substrate selection by birds.

Observers assessed the extent of tamarisk defoliation during each site visit using visual phenology assessments sensu van Riper (1980) and McGrath et al. (2009). Observers sampled 100 individual tamarisk trees along an established transect at each site, and for each tree, the observer visualized a full canopy and estimated the percent composed of green and brown (beetle damaged) foliage, with 100% green representing a full canopy of all green leaves. Observations from 100 individual trees were averaged for each visit to obtain estimates of current conditions (average % green leaf and % brown leaf). This visual estimation method produces similar results to more rigorous measures using a digital camera (McGrath and van Riper 2005).

Arthropod sampling

At 10 plots that contained mixed tamarisk we used sweep nets to collect arthropods, from the seven dominant plant species and grass, every month from June through August in 2010 and 2011. Arthropod sampling took place when tamarisk leaf beetle numbers were at relatively similar levels for all sampling periods (see Darrah and van Riper 2017). Plots were spaced 100 m apart along the same 1-km transects used for avian foraging observations and mist-net bird capture. Sampling consisted of 25 vertical sweeps per plant species at ground level to the top of the vegetation at 3 m, using a standard 38-cm-diameter canvas insect sweep net. Arthropod samples were collected from sunrise to 1000 h, during the same time period that we mist netted to sample bird diets. All collected arthropods were transferred to vials and preserved in 70 percent ethanol, then later identified to order and morphospecies. We utilized the definition of Cronquist (1978) for morphospecies, which allowed

Fig. 1 Study area in Southwestern Colorado, showing locations of three tamarisk leaf beetle study sites (Slick Rock, Crocker-Bedford Ranch, and Bedrock) at river miles 47, 54, and 97 along the Dolores River, Colorado, USA



us a finer level of resolution for each arthropod group. Body lengths were measured to the nearest 0.05 mm with an ocular micrometer fitted to a dissecting binocular microscope (Rogers et al. 1977). Voucher specimens were placed into a reference collection at the University of Arizona.

The purpose of sweep sampling was to quantify arthropod abundance and biomass from each plant species and then to compare those relative measures with arthropod prey that we found in the upper portion of bird gastrointestinal tracts. We divided the arthropod community into 10 taxonomic categories: 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). *Diorhabda carinulata* was separated out as its own group from other Coleoptera. Additionally, we compared the arthropod community in tamarisk to the arthropod communities of other native riparian plant species, where abundance and biomass were recorded by dry weight (in grams) of arthropods and species richness as the number of detected morphospecies collected per 25 sweeps. Samples were averaged among plant species within each sampling period and study site.

To analyze arthropod data we used a generalized regression equation because it permits an estimate of

dry weight (in grams) based on length (in millimeters) to calculate biomass for each morphospecies group (Rogers et al. 1977). One-way analysis of variance was used to test for differences in mean abundance and biomass among arthropod categories. We then used Chi square and repeated-measures analysis of variance with Bonferroni adjustments 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 sampling: foraging and substrate selection

We conducted foraging observations on birds throughout the 2010–2012 breeding seasons, recording substrate use for each attack maneuver, defined as a directed movement toward a potential food item. We used the location of first attack maneuver, as opposed to the location of first detection, when analyzing observations of foraging behavior (McGrath et al. 2009). The use of the first attack maneuver reduces visual bias associated with foraging behavior (Bell et al. 1990). Observations of subsequent foraging maneuvers were excluded in the analysis of use versus availability, but those data were used to characterize the overall foraging behavior of avian families. Frequency of substrate use was calculated for nine insectivorous, foliage-gleaning bird species that use the Dolores riparian corridor during breeding or migration; Gray Vireo (*Vireo vicinior*), Warbling Vireo (*Vireo gilvus*), Blue-gray Gnatcatcher (*Poliophtila caerulea*), Orange-crowned Warbler (*Oreothlypis celata*), Virginia's Warbler (*Oreothlypis virginiae*), Common Yellowthroat (*Geothlypis trichas*), Yellow Warbler (*Setophaga petechia*), Black-throated Gray Warbler (*Setophaga nigrescens*), and Yellow-breasted Chat (*Icteria virens*).

To test the hypothesis that tamarisk shrubs are used by birds in proportion to availability, we compared shrub use and availability for all bird species combined using the rank comparison method described in Johnson (1980). We summed observations of substrate

use for each bird species across years, and restricted inferences to the eight predominant woody shrubs, which accounted for 81% of foraging observations and for which we had available data. For each bird species, we ranked the use of each shrub species from 1 (most frequent use) to 7 (least used), and compared the use rankings to availability rankings. We tested for an overall significant difference in use vs. availability rankings with the Hotelling *T* test, implemented via program R (R Core Team 2016) package “Hotelling” (Curran 2017).

To examine bird species-specific patterns of substrate use, we used Chi-squared (X^2) tests to compare the total frequency of substrate use by each species to expected use in the absence of substrate preference (calculated as proportion cover by each shrub species multiplied the number of foraging observations for each bird species). To assess preferences for substrates among four focal species (Blue-gray Gnatcatcher, Black-throated Gray Warbler, Yellow Warbler, and Yellow-breasted Chat), we calculated selection coefficients (Manly et al. 2002) for 8 shrub species from foraging observations, combining observations across sites and years. We restricted our analysis to the four bird species with at least 100 foraging observations: Blue-gray Gnatcatcher, Black-throated Gray Warbler, Yellow Warbler, and Yellow-breasted Chat. For the Blue-gray Gnatcatcher, we had sufficient observations in both May–June (“early”) and July–August (“late”) to compare relative substrate preference in the early versus late season, during the latter of which tamarisk leaf beetle larvae are most abundant. To test the prediction that birds should choose beetle-affected tamarisk over unaffected tamarisk if they are targeting *Diorhabda* beetles for consumption, we used logistic regression to compare the percent beetle-damage (brown leaf) of tamarisk selected by birds for foraging to percent brown leaf of tamarisk available at the site (measured while conducting tamarisk phenology transects).

Avian diet

We collected diet samples from 188 birds (25 species) within nine families of the order Passeriformes. Birds were captured using 6- and 12-m mist nets (30-mm mesh), with nets opened one hour after sunrise to ensure sufficient foraging time for birds prior to capture. Immediately upon bird removal, a modified

irrigation technique was used to acquire upper gut contents (Moody 1970; Laursen 1978; Ford et al. 1982; Rosenberg and Cooper 1990). A 3-cm³ syringe was filled with warm water, had a French feeding tube attached. The bird was then inverted to prevent water from entering the trachea, and water pushed into the upper digestive tract at a rate of 1 cm³/s. As fluid was forced into the crop, gut contents were flushed out and collected in a plastic dish (McGrath and van Riper 2005). Those contents were transferred to a vial and preserved with 70 percent ethanol. This protocol was approved by the University of Arizona Institutional Animal Care and Use Committee (protocol #11-273). Later, in the laboratory diet samples were sorted under a variable-power dissecting microscope to the lowest possible taxonomic level, after Tatner (1983), Ralph et al. (1985), and Moreby (1987).

The number of arthropods in each diet sample was estimated by counting paired body parts (Jenni et al. 1989; Rosenberg and Cooper 1990). A reference collection assembled from previous arthropod sampling was utilized for identifying fragmented arthropods. Abundance was defined as the number of individuals of a prey type found in diet samples, frequency of occurrence as percentage of times a prey species was found in gut samples relative to all prey, and biomass as the total number of prey items multiplied by the known weight of that prey species. We multiplied the numbers of prey items observed in the gut contents by known weights of whole collected insects to establish total volumes. This allowed us to calculate an indirect estimate of biomass (Tatner 1983). Consequently, the percentages by number of individuals (abundance) and by estimated biomass were used to describe the relative contributions of arthropod categories to avian diet.

Percentages of food item abundance and biomass in gut contents within each avian family were pooled and calculated for 11 food-item categories: Araneae (spiders), Coleoptera (beetles), *D. carinulata*, Diptera (flies), Hemiptera and 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). *Diorhabda carinulata* were separated out from other Coleoptera and analyzed as a separate group. We defined “preferred prey” as all insect species that we detected in gut contents. 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. Arthropod prey observed in bird diets was analyzed by using repeated-measures analysis of variance, with date as the repeated measure. Between-subject effects were arthropod category, arthropod source (total and preferred), and date. To further test for diet preferences, we calculated selection coefficients (Manly et al. 2002; Mahoney et al. 2017) separately for six time periods to account for temporal changes in the relative abundances of different available insect taxa. To ensure robust calculation of selection coefficients, we lumped any insect taxa into an “Other” category if there were < 5 insects of that category in the diet samples for that time period.

Results

Vegetation

Vegetation at each study site was dominated by coyote willow and tamarisk, with the other shrub species each comprising of < 10% available woody plants (Table 1). Other less common plants included four-wing saltbush (*Atriplex canescens*), boxelder (*Acer negundo*), Gambel oak (*Quercus gambelii*), Siberian elm (*Ulmus pumila*), and mulefat (*Baccharis salicifolia*). Cottonwood (*Populus* spp.) was rare at all sites,

Table 1 Total canopy coverage and mean height of dominant shrub species within 40 m of the riverbank along the Dolores River in SW Colorado, USA

	Cover (% total shrub cover)		Height (m)	
	Mean	SE	Mean	SE
Tamarisk	14.0	9.9	2.8	0.3
Willow	55.0	10.3	2.2	0.1
Desert olive	8.5	2.9	2.2	0.2
Rabbitbrush	6.0	1.2	1.3	0.1
Sumac	5.7	3.3	1.4	0.1
Greasewood	4.7	3.5	1.6	0.1
Sagebrush	6.1	1.4	1.4	0.1

Data were collected during June–August, 2010–2011. (SE standard error, *m* meters; see Fig. 1 for locations)

and pinyon (*Pinus edulis*) and juniper (*Juniperus* spp.) dominated scree along the canyon slopes. Large gallery trees were largely absent from our study areas, so tamarisk was the tallest vegetation, followed by willow and desert olive (Table 1).

Arthropod availability

A total of 18,855 arthropods representing 141 morphospecies in 17 orders was collected in 503 samples from eight plant species (Table 2). Tamarisk leaf beetles were the most commonly collected arthropod (24.0 percent; 95% CI 19.9–27.4), sometimes occurring at more than two orders of magnitude greater numbers than other insect groups. Other collected arthropod groups, in decreasing order of abundance were Auchenorrhyncha, Hymenoptera, other beetles (Coleoptera), Diptera, Araneae, Heteroptera, Lepidoptera, and Orthoptera. Additionally, *D. carinulata* contributed the most to total arthropod biomass (35.4 percent; 95% CI 32.4–45.1) followed by Orthoptera, Hymenoptera, Auchenorrhyncha, Coleoptera, Lepidoptera, Heteroptera, other, Diptera, and Araneae (Table 2). There was a significant difference in the mean abundance of arthropod species among study areas ($F_{9, 1110} = 13.40$, two-sided p value < 0.01 from ANOVA F -test), but at our three study locations tamarisk leaf beetles were always the most abundant arthropod.

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) and abundance of arthropods was

significantly different among plant species ($F_{63, 297.72} = 6.89$; two-sided p value < 0.01 ; Supplement Fig. S1). Total arthropod abundance in tamarisk was higher than in all other plant species (due largely to the tamarisk leaf beetle *D. carinulata*), while 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 the other five plant species ($F_{76, 931} = 3.47$; two-sided p value, < 0.01 from a repeated-measures-ANOVA F -test; Fig. 2; Supplemental Fig. S2). In tamarisk, *D. carinulata* was more abundant than any other arthropod category ($F_{9, 130} = 20.56$; two-sided p value < 0.01). On average, *D. carinulata* composed 73.6 percent (95% CI 66.8–80.3) of the arthropod abundance in tamarisk, and we rarely collected *D. carinulata* from any plant other than tamarisk.

Biomass of arthropods was also affected by plant species ($F_{118, 891} = 6.90$; two-sided p value, < 0.01 , repeated-measures-ANOVA F -test; Fig. 2; Supplement Fig. S3). 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 from analyses, arthropod biomass in tamarisk was lower than that in willow and rabbitbrush but comparable to that in other plant species ($F_{116, 891} = 4.46$; two-sided p value, < 0.01 , repeated-measures-ANOVA F -test).

Similarly, biomass within each arthropod category was affected by plant species ($F_{63, 309.84} = 5.31$; two-sided p value, < 0.01 from a repeated-measures-

Table 2 Mean total abundance (number per 25 sweeps) and biomass (milligrams per 25 sweeps) of arthropods collected per sample ($n = 503$) among all plant species in the study areas along the Dolores River, CO, USA from 2010 to 2011 (note that *Diorhabda carinulata* has been separated out from other Coleoptera)

Arthropod category	Abundance			Biomass		
	Mean	SE	Percent	Mean	SE	Percent
Auchenorrhyncha	7.7	1.9	23.5	0.0116	0.0019	22.8
Hymenoptera	5.1	1.6	15.6	0.0063	0.0015	12.4
Coleoptera	4.1	1.5	12.7	0.0044	0.0013	8.6
<i>Diorhabda carinulata</i>	7.8	1.9	24.0	0.0180	0.0021	35.4
Diptera	3.3	1.3	10.2	0.0029	0.0010	5.7
Araneae	2.0	1.1	6.1	0.0027	0.0010	5.3
Heteroptera	1.3	0.9	4.1	0.0016	0.0008	3.1
Other	0.5	0.6	1.6	0.0014	0.0007	2.8
Lepidoptera	0.4	0.5	1.1	0.0013	0.0007	2.6
Orthoptera	0.4	0.5	1.1	0.0007	0.0005	1.4

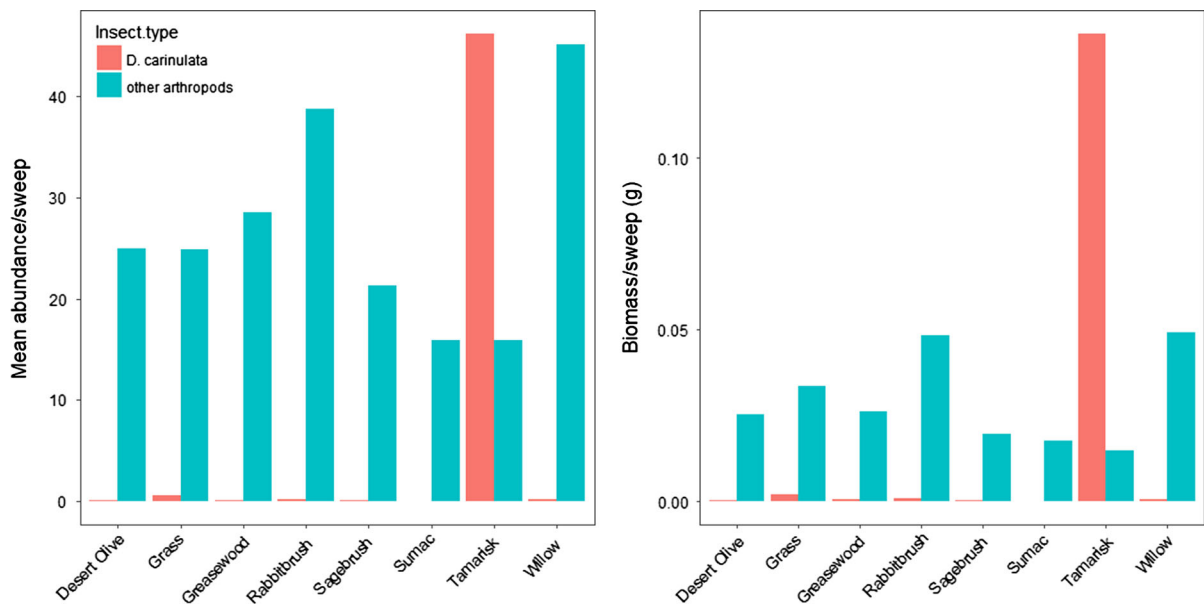


Fig. 2 Abundance and biomass comparisons of tamarisk leaf beetles (*Diorhabda carinulata*—represented with orange bars), with all other arthropods (blue bars) collected during insect sweeps during 2010–11, on the eight dominant plant species along the Dolores River, southwestern Colorado, USA, (see Fig. 1 for locations). The other arthropods include 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), and specific mean abundance and biomass levels can be seen in Supplement Fig. S2 and Fig. S3, respectively

ANOVA F -test). 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, < 0.01 , one-way-ANOVA F -test). On average, the biomass of *D. carinulata* composed 87.7 percent (95% CI 66.8–80.3) of the total arthropod biomass in tamarisk. No significant difference was detected in the abundance or biomass of the other arthropod categories in tamarisk.

Mean richness of arthropod morphospecies was also significantly different among plant species ($F_{7, 24.31} = 3.57$; two-sided p value, 0.009 from a repeated-measures-ANOVA F -test). Arthropod richness in tamarisk was lower than that in willow and sagebrush, but higher than that in greasewood (Supplement Fig. S4). On average, samples from tamarisk contained 4.0 fewer arthropod morphospecies than those from willow (two-sided p value = 0.007), 2.5 fewer morphospecies than those from sagebrush (two-sided p value 0.009), and 1.4 more than greasewood (two-sided p value 0.04).

Bird foraging behavior and substrate selection

From 916 avian recorded foraging observations, we found that birds foraged most often in tamarisk (37% of observations), followed by native desert olive, greasewood, willow, sumac, rabbit brush, and big sage (Fig. 3). With all nine foliage-gleaning insectivores combined, substrate use did not differ from availability (Hotelling t -test $F = 2.44$, $df = 8, 10$, $p = 0.09$), although there was a tendency toward selection of sumac, big sagebrush, and desert olive. However, individual bird species varied in their relative use of the different shrub species. Blue-gray Gnatcatchers preferred tamarisk and greasewood and avoided willow ($X^2 = 82.69$, $df = 6$, $p < 0.001$). Black-throated Gray Warbler preferred desert olive and avoided big sagebrush, willow, and rabbitbrush ($X^2 = 123.65$, $df = 6$, $p < 0.001$). Yellow-breasted Chat preferred desert olive, sumac, and tamarisk ($X^2 = 61.687$, $df = 6$, $p < 0.001$). Yellow Warbler preferred desert olive, sumac, and tamarisk, and did not use big sagebrush or rabbitbrush ($X^2 = 52, 121$,

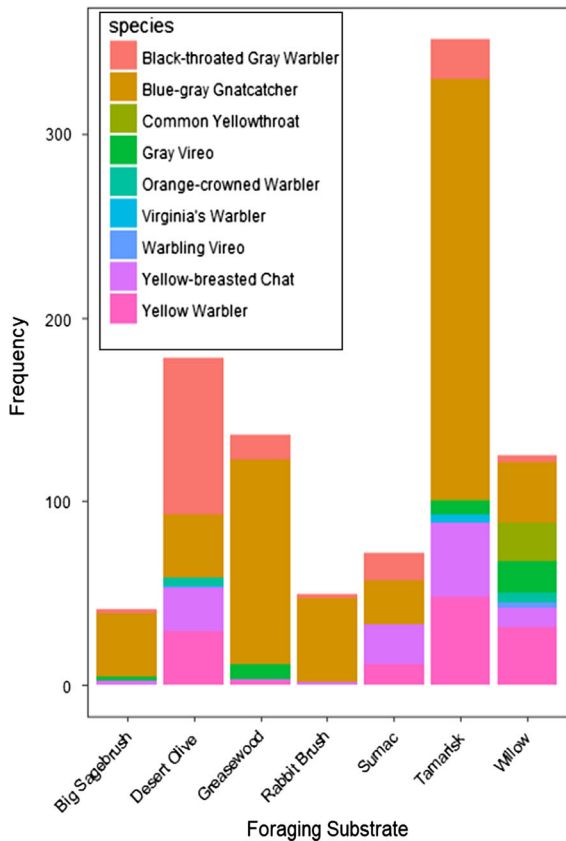


Fig. 3 Frequencies of avian foraging use from 2010–2012, on the seven predominant woody shrub species at three study areas along the Dolores River in southwestern Colorado, USA. Data represent 916 independent foraging observations of the nine most common passerine bird species

$df = 6, p < 0.001$). When foraging in tamarisk, birds avoided defoliated and shrubs with brown leaves ($\beta = -0.15, SE 0.02, p < 0.001$; Fig. 4).

To further assess preferences for substrates among our four focal species (Blue-gray Gnatcatcher, Black-throated Gray Warbler, Yellow Warbler, and Yellow-breasted Chat), we combined observations for 8 shrub species across sites and years calculating selection coefficients with Manly et al. (2002). Two species (Blue-gray Gnatcatcher and Yellow-breasted Chat) selected tamarisk as a foraging substrate. Sumac was preferred by all four species, with selection coefficients for sumac an order of magnitude greater than for any other preferred substrates (Table 3). All species avoided Big Sage, and three species avoided Rabbit Brush. Desert Olive was selected by Black-throated Gray Warbler and Yellow-breasted Chat. Greasewood

was preferred by Blue-gray Gnatcatcher but avoided by Yellow-breasted Chat and Yellow Warbler. Black-throated Gray Warbler avoided Willow but other species had neutral selection coefficients (Table 3). The Blue-gray Gnatcatcher did not significantly change relative substrate use between early and late seasons ($X^2 = 0.53, df = 7, p = 0.99$).

Avian diets

Stomach contents of 188 birds, from 25 species within nine Passeriformes families were analyzed in this study. We identified 520 arthropod prey items from diet samples, representing 76 morphospecies within 10 arthropod orders (Fig. 5). The frequency of occurrence by abundance of food-item categories in bird diets varied significantly among avian families ($F_{10, 144} = 4.04$; two-sided p value, < 0.01 from a one-way-ANOVA F -test). Overall, seed (17.0 percent), Coleoptera (14.4 percent), and Hymenoptera (13.0 percent) were the most abundant detected prey items. Seeds were detected in the diets of four avian families and contributed significantly to the diets of Cardinalidae (51.7 percent, $F_{10, 143} = 2.10$; two-sided p value, 0.02), Emberizidae (61.1 percent, $F_{10, 143} = 3.08$; two-sided p value, 0.01), and Fringillidae (96.7 percent, $F_{10, 143} = 2.57$; two-sided p value, 0.01). 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 < 0.01). No difference was detected in the frequency of occurrence of food items in Icteridae, Mimidae, Polioptilidae, Tyrannidae, or Vireonidae (Supplement Table S1).

By biomass, birds ate significantly more Lepidoptera (29.0 percent) than any other food-item category ($F_{10, 1375} = 3.07$; two-sided p value, 0.01; ANOVA F -test). Fringillidae preferred seed (98.2%, $F_{10, 143} = 2.58$; two-sided p value 0.01), whereas Parulidae ate more Coleoptera (24.5 percent) ($F_{10, 143} = 2.91$; two-sided p value = 0.01). No preferential use of food items was detected in Cardinalidae, Emberizidae, Icteridae, Mimidae, Polioptilidae, Tyrannidae, or Vireonidae (Fig. 6; Supplement Table S1).

When seed was excluded, the interaction between arthropod category and availability by abundance (total and preferred) affected the frequency of occurrence of arthropod categories in bird diets

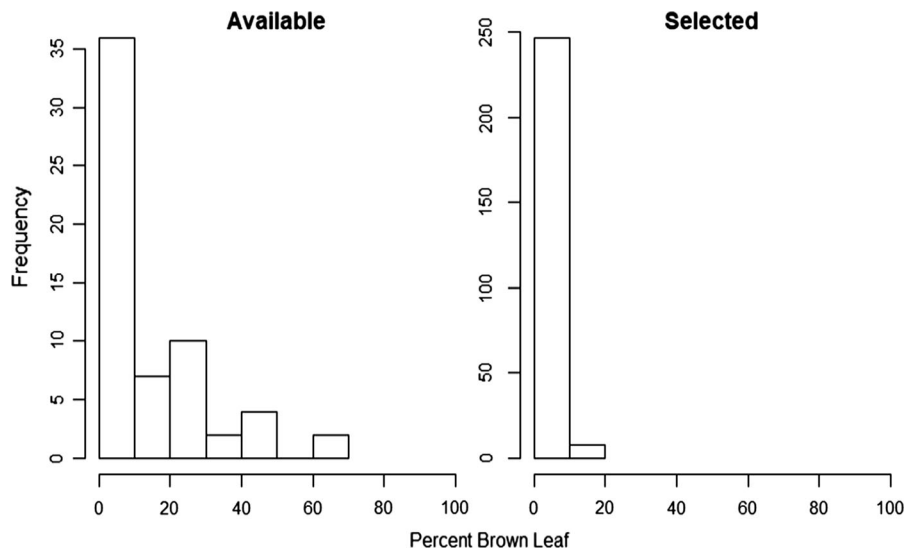


Fig. 4 Frequencies of beetle-damaged (% of canopy in brown leaf) tamarisk shrubs available, and those selected from 2010–2012 by foliage-gleaning insectivorous bird species at three study sites along the Dolores River in southwestern Colorado, USA

Table 3 Selection coefficients (means, followed by Bonferroni-corrected confidence intervals) bird selected prey for 8 insect taxa across 6 sampling periods during 2010–2014

Arthropod Taxa	7–30 Jun 2010		1–16 Jul 2010		17 Jul–10 Aug 2010		14–30 Jun 2011		1–16 Jul 2011		17 Jul–10 Aug 2011	
	N = 27		N = 57		N = 33		N = 31		N = 25		N = 62	
	Mean	CI	Mean	CI	Mean	CI	Mean	CI	Mean	CI	Mean	CI
Araneae			2.39	0.75, 4.03							1.08	- 0.16, 2.34
Tamarisk Beetle	3.43	- 1.41, 8.27	0.05	- 0.09, 0.19	0.03	- 0.05 , 0.12	0.09	- 0.14, 0.33			0.19	- 0.16 , 0.54
Coleoptera—other	0.43	0.11 , 0.74	1.43	0.38, 1.43	0.67	0.16, 1.17	0.89	0.25, 1.54	1.32	0.02, 2.62	5.86	3.26 , 8.47
Diptera			0.85	0.21, 1.50			0.62	0.04, 1.20			0.46	- 0.02, 0.93
Hemiptera			1.51	0.43, 2.59					4.93	1.78, 8.10	2.22	0.10, 4.36
Hymenoptera	0.87	0.27, 1.47	0.97	0.43, 1.51	0.35	0.05 , 0.65					0.96	0.49, 1.42
Lepidoptera			10.55	2.26 , 18.84			3.84	- 0.43, 8.11				
Other	1.43	1.10 , 1.75	1.02	0.62, 1.41	1.76	1.60 , 1.91	1.26	1.02 , 1.51	0.71	0.48 , 0.93	0.67	0.25, 1.06

Diet samples were obtained from crop irrigation of 188 passerine birds (25 species) at 3 study sites along the Dolores River in Southwestern Colorado, US. The means and CI that are bold, and with an * denote statistical significance, in either a positive or negative direction

($F_{18, 155.14} = 2.47$; two-sided p value < 0.01 from a repeated-measures-analysis-of-variance F -test). Birds ate fewer Auchenorrhyncha than expected, and more

Coleoptera, Heteroptera, and Araneae, given their availability. Finally, fewer *D. carinulata* were eaten by birds (2.1 ± 1.3 – 2.9 percent) than expected, given

Fig. 5 Availability of 10 arthropod groups collected during insect sweeps during 2010–11, compared to numbers of preferred arthropods and numbers consumed, as found in diets of 188 birds along the Dolores River, southwestern Colorado, USA (Note that the tamarisk beetle has been separated out from the other Coleoptera). Error bars depict 95-percent-confidence intervals

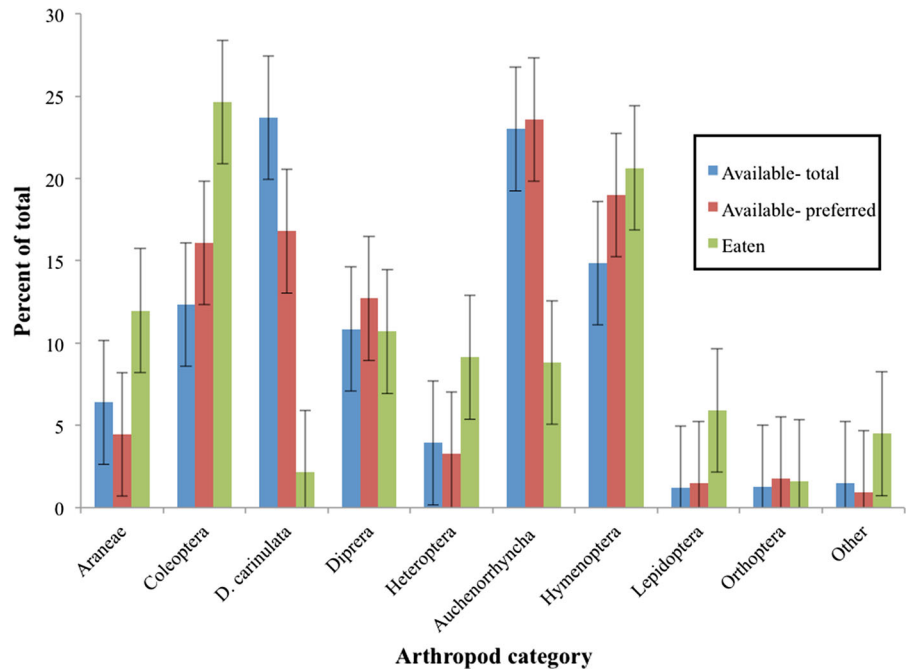
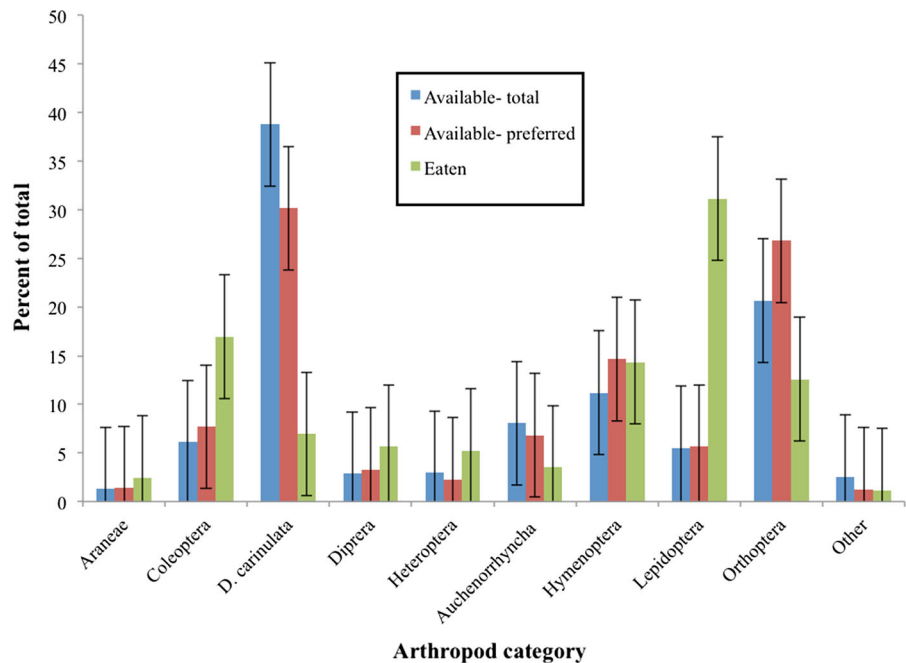


Fig. 6 Biomass (in dry-weight grams) of 10 arthropod groups collected during insect sweeps during 2010–11, compared to biomass of preferred and consumed biomass from the irrigated crops of 188 birds, along the Dolores River in southwestern Colorado, USA (Note that the tamarisk beetle has been separated out from the other Coleoptera). Error bars depict 95-percent-confidence intervals



its availability in both the total (24.0% ± 19.9–27.4) and preferred (16.8% ± 13.0–20.6) arthropod communities (Fig. 5).

The percentage by biomass of arthropod categories in the diets of birds was affected by availability ($F_{10, 155.14} = 2.47$; two-sided p value, 0.01 from a

repeated-measures-ANOVA; Fig. 6; Supplement Table S1). Orthoptera were eaten less than expected, whereas Coleoptera (with the exception of the tamarisk leaf beetle) and Lepidoptera were eaten more than expected, given their availability in the total and preferred arthropod communities. Again, the

Table 4 Substrate selection coefficients (means, with Bonferroni-corrected confidence intervals = CI) during foraging of four avian passerine species at two sites along the Dolores River in Colorado, US

Shrub species	Blue-gray Gnatcatcher		Black-throated Gray Warbler		Yellow Warbler		Yellow-breasted Chat	
	N = 515		N = 143		N = 238		N = 104	
	Mean	CI	Mean	CI	Mean	CI	Mean	CI
Salt Bush	0.03	– 0.04, 0.10*					0.39	– 0.22, 1.00
Desert Olive	0.77	0.42, 1.11	6.71	5.44, 7.98*	1.38	0.72, 2.03	2.61	1.33, 3.88*
Greasewood	3.4	2.62, 4.18*	1.42	0.39, 2.45	0.13	– 0.12, 0.38*	0.15	– 0.26, 0.56*
Rabbit Brush	1.09	0.67, 1.51	0.17	0.16, 0.50*			0.11	– 0.20, 0.44*
Sumac	31.51	14.36, 48.66*	70.93	23.63, 118.23*	31.25	6.13, 56.4*	143.04	69.11, 216.96*
Willow	0.87	0.47, 1.27	0.38	– 1.13, 0.89*	1.76	0.95, 2.57	1.43	0.32, 2.55
Tamarisk	3.00	2.60, 3.41*	1.04	0.48, 1.60	1.36	0.88, 1.84	2.6	1.72, 3.48*
Big Sage	0.15	0.08, 0.21*	0.02	– 0.03, 0.09*			0.04	– 0.03, 0.12*

Foraging data were collected on 8 shrub species from May–August of 2010–2014. The means and CI that are bold, and with an * denote statistical significance, in either a positive or negative direction

biomass of *D. carinulata* eaten by birds ($3.4\% \pm 2.6\text{--}4.2$) was less than expected, given its availability in the total ($35.4\% \pm 32.4\text{--}45.1$) and preferred ($30.1\% \pm 23.8\text{--}36.5$) arthropod communities. Selection coefficients (Manly et al. 2002) revealed that preferred food items taken by birds varied throughout the study period, with food preferences changing from other Coleoptera in Jun 2010 and in late July through August of 2011, to Lepidoptera from 1 to 16 July 2010, and then to Hymenoptera in late July through August of 2010 (Table 4).

D. carinulata was observed in 11 of 188 bird gut contents. Four bird species, the Yellow-breasted Chat, Yellow Warbler (*Setophaga petechial*), Common Yellowthroat (*Geothlypis trichas*), and Cordilleran Flycatcher (*Empidonax occidentalis*) consumed *D. carinulata*. The frequency of tamarisk leaf beetle occurrence in bird gastrointestinal tracts was 2.1 percent (95% CI 1.5–2.7) by abundance and 3.4 percent (95% CI 2.6–4.2) by biomass. Most *D. carinulata* (8/11) eaten by birds were consumed by Yellow-breasted Chats (72.7%). However, the frequency of occurrence of *D. carinulata* in all sampled Yellow-breasted Chat diets was only 3.3 percent by abundance and 5.6 percent biomass. Birds exhibited neutral to negative selection of tamarisk leaf beetles, with avoidance occurring during the second half of the breeding season in both years. Only adult tamarisk leaf beetles were observed in the diet samples that we

collected from birds. Even though we found numerous Lepidoptera larvae parts in bird gut contents, no *D. carinulata* larvae were detected in any of our bird gut samples.

Discussion

The results of diet and foraging analyses show little support for our first hypothesis, that birds consume tamarisk leaf beetles relative to abundance in the environment, and in fact *Diorhabda* beetles did not constitute a significant food resource for any passerine bird species using the riparian corridor of the Dolores River in Colorado. We found that only 2.1% of the avian guts contained *Diorhabda carinulata*, when compared to the beetle's relative abundance of over 25% in the environment. Mahoney et al. (2017) found a similar situation on the Virgin River in Utah and Arizona, where two warbler species had a negative selection for adult tamarisk leaf beetles and their larvae. While we found that most bird species foraged in tamarisk shrubs in proportion to its availability, there was no significant difference between tamarisk use in the first half of the season (when beetle larvae are absent) compared to the second half of the season (when beetle larvae are abundant in tamarisk), again suggesting that this potential food resource is not of sufficient quality to attract birds away from seeking

prey in native riparian vegetation. Furthermore, when birds did select tamarisk, they tended to avoid tamarisk shrubs that were browning in response to beetle herbivory (Fig. 4).

Use of tamarisk leaf beetles as a food resource by birds has implications for avian communities in areas where biologic control with *Diorhabda carinulata* is occurring. Information related to the diets of birds is an important aspect of any insect biological control effort, and such data are vital to land managers when evaluating the role of birds as potential consumers of arthropod prey (Brower et al. 1968; Ford et al. 1982). In many places where avian populations have increased after the arrival of biologic control agents, this increase has been attributed to an abundance of newly introduced insects as prey, and sometimes due to environmental changes from defoliation (Paxton et al. 2011). *D. carinulata* can potentially affect native birds positively or negatively through changes in abundance, but we found no evidence of a positive effect of the beetle on birds in our study. We found that *Diorhabda carinulata* was taken in very low quantities when compared to the beetle's relative abundance, and that only insectivorous birds ate tamarisk leaf beetles. *Diorhabda carinulata* was completely avoided by avian species that tend toward more frugivorous and granivorous diets (for example, Cardinalidae, Emberizidae, Fringillidae, Turdidae).

Similar to the situation with the tamarisk leaf beetle, the introduced gypsy moth (*Lymantria dispar*) is a prolific invasive arthropod whose populations are capable of massive increases in numbers. Gypsy moths exploit a wide range of deciduous and coniferous host trees in eastern North America (Liebhold et al. 1992). Several bird species of warblers feed readily on early and late instars of larvae, but given a simultaneous choice between gypsy-moth larvae and alternative prey, birds showed a preference for other prey (Whelan et al. 1989). We found a similar situation where only 11 of 188 bird stomachs contained tamarisk leaf beetle parts, and with most birds preferring native arthropod species as prey. However, there are other tamarisk specialist insects in the system and they could have positive effects for native insectivore diets. Yard et al. (2004) found that tamarisk leafhoppers were being used by a number of native birds, Durst et al. (2008) found Willow Flycatchers also used tamarisk leafhoppers, and Mahoney et al. (2017) found that tamarisk weevils

were selected for by Lucy's and Yellow warblers. Each of these insects add to the complexity of non-native riparian vegetation systems, and should be taken into account especially when biocontrol is being used.

Although the addition of tamarisk leaf beetles to arthropod communities in the southwestern US contributes to a superabundance of potential prey items, any benefit to wildlife depends upon palatability of that prey. Tamarisk leaf beetles are monophagous and feed exclusively on *Tamarix*, and many members of the family Chrysomelidae produce secondary chemicals distasteful to birds (Hilker and Kopf 1994). Sequestration of the noxious compounds produced by this plant as a defense against herbivory may provide tamarisk leaf beetles with some defense against predation. From a field experiment, Puckett and van Riper (2014) found that Yellow-breasted Chats will eat tamarisk leaf beetles in captivity when no other food resource is available, but hatch-year birds ate significantly more tamarisk leaf beetles than did adults (66.7 vs. 5.0%, respectively), suggesting possibly learned avoidance. 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. On the Virgin River in southern Utah, Mahoney et al. (2017) found that two warbler species showed negative selection for tamarisk leaf beetles and their larvae, even when those insects were 10–100 times more abundant than other insects. Thus, the tamarisk leaf beetle may be to some degree unpalatable, and birds learn as they encounter this food item while foraging, but this needs to be further tested.

In summary, we found that *Diorhabda carinulata* contributed little to the diets of birds along the Dolores River riparian corridor in southwestern Colorado, despite high numbers of this arthropod in the environment. Thus, *D. carinulata* are less useful as an avian food source than initially predicted by advocates of their release (Deloach et al. 2004). Low rates of predation on beetles and their larvae by birds certainly facilitate population growth of this biologic control agent. 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 an avian food resource, and that restoration management will be a key to recovery of riparian habitat in defoliated tamarisk zones.

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