Chapter 2. A Naturalized Riparian Ecosystem: Consequences of Tamarisk Leaf Beetle (*Diorhabda* spp.) Biocontrol

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Introduction

Presence of the introduced genus *Tamarix* has been a perplexing problem for decades along rivers of the southwestern States. It is clearly an invasive species occurring along most perennial, ephemeral, and intermittent drainages of the Southwest including rivers, small streams, and normally dry washes. It seems to reach highest densities and form monocultures along waterways with altered flow regimes, but it can also invade unaltered streams and small springs, where it may become the dominant or exclusive woody species. Approximately 150 years after *Tamarix* was first introduced into the Southwest, it was being reviled as a notorious phreatophyte that was thought to measurably deplete ground and surface water at the expense of native riparian habitat (Chew 2013; Robinson 1952).

Over the past 60-plus years, much research and effort have gone into understanding *Tamarix* biology and the largely failed struggles to eradicate this nonnative shrub/tree's species (Chew 2009, 2013; El Waer et al. volume 1; Horton 1964, 1977; Sher and Quigley 2013; Zavaleta 2000, 2013). On the issue of water consumption by *Tamarix*, recent findings discourage generalizations as to excessive water use. Findings indicate that the species' complex is a stress-adapted group with a low to moderate water consumption that primarily replaces native vegetation when conditions within watersheds become unsuitable for native species colonization (Nagler and Glenn 2013; Nagler et al. 2012). Nagler and Glenn (2013) also demonstrated that from 1967 to 1982, water salvage projects by *Tamarix* removal did not achieve a sustainable recovery of water. Analysis of more recent water salvage/*Tamarix* removal literature concluded that increases in water yield after removal are only likely to occur when a *Tamarix* stand with high leaf area is replaced with low leaf area recolonizers (Shafroth et al. 2005).

It is also well documented that its two dominant species, *T. ramosissima* and *T. chinensis* and their hybrids, can become a naturalized part of the landscape in many areas and provide a unique *Tamarix*-dominated habitat type (Brown et al. 1987; Chew 2013; Johnson and Carothers 1987; Scott et al. volume 1). Although not all riparian birds find *Tamarix* to be suitable nesting habitat (i.e., woodpeckers, most cavity nesters, large raptors), studies over the past 30 years show that remarkably productive wildlife habitat is provided where *Tamarix* dominates and mixes with native riparian woody species (Bateman et al. 2013a; Brown et al. 1987; Brown and Trosset 1989; Darrah and van Riper 2017; Hunter et al. 1988; Johnson et al. 2012; Sogge et al. 2005, 2008, 2013; van Riper et al. 2008). In this chapter, we call this a "naturalized community," which is a unique vegetation assemblage or group of woody riparian plant species, largely dominated by the nonnative *Tamarix*, but intermixed with native species like mesquite (*Prosopis* spp.), cottonwood (*Populus* spp.), willow (*Salix* spp.), arrowweed (*Pluchea sericea*), seepwillow (*Baccharis* spp.), and others that are repeatedly found together within a riparian corridor.

The relatively brief reign of *Tamarix* appears to be coming to an end. In 1999, the Department of Agriculture through its division of Animal and Plant Health Inspection Service (APHIS) issued research permits for the release of *Diorhabda elongata*[1] (Coleoptera: Chrysomelidae), a species of nonnative tamarisk leaf feeding beetle, in secure field cages at 10 sites in six States. Based on the success of the field trial, in 2001 permits for the release of the beetle from field cages were issued by APHIS to the Agricultural Research Service, Bureau of Land Management, and Bureau of Reclamation. By August of 2005, the biocontrol program was officially underway. This was the culmination of a *Tamarix* biocontrol effort that had been in development for at least two decades (Bean et al. 2013; DeLoach et al. 2003; McLeod volume 1). These beetles of Asian origin rapidly spread throughout the West, beginning in limited areas of Colorado, Nevada, and Utah.

By 2015, the expanding beetle invasion and their repeated episodic defoliation of *Tamarix* eventually led to varying rates of dieback. This included significant levels of plant mortality in some riparian ecosystems throughout the West (Bloodworth et al. 2016; Hultine et al. 2015). The leaf-beetles have not only become more widespread than once predicted, they are also rapidly adapting their life cycles and behavior to facilitate penetration into areas where they were never expected (Hultine et al. 2015; Meinhardt and Ghering 2012). Thus, it finally appears as if the *Tamarix* invasion of wet places in aridland regions of North America has met its first serious challenge as a result of successful biocontrol.

Many biocontrol efforts have had unforeseen consequences (Howarth 1983, 1991; Louda et al. 2003; Simberloff and Stilling 1996; many others). We believe that one unforeseen consequence of the *Tamarix* biocontrol triumph has been the rapid alteration of the functional benefit of thousands of acres of riparian habitat as breeding, stop-over, and wintering habitat for many species of wildlife, especially birds, in areas where the beetle impacts have led to repeated defoliation and plant mortality (McLeod volume 1). Moreover, we are not as optimistic as biocontrol proponents that the long-term benefit of the *Tamarix* destruction will be unassisted native species habitat restoration. With limited exceptions (see discussion on Grand Canyon below), most available evidence to date indicates that without massive efforts at active habitat rehabilitation, once *Tamarix* is removed, it is most often replaced by a mixture of native and nonnative grasses and herbaceous cover, not the woody vegetation necessary to support riparian wildlife (Gonzales et al. 2017).

In the arid Southwest, the beetle biocontrol has had a significant adverse impact on riparian habitat and wildlife conservation. Contrary to the assurances of the original proponents of the biocontrol efforts (DeLoach and Tracy 1997), there is little evidence that reestablishment of native woody species will naturally occur in most areas where

[1] *Diorhabda elongata* was later reclassified as *D. carinulata* and after that species release, three additional species (*D. carinata, D. elongate,* and *D. sublineata*) were tested in cages between 2002 and 2009. All four species were eventually released at about 70 sites in Texas (see McLeod volume 1). Today, *D. carinulata* and *D. sublineata* are known to be established and are responsible for most *Tamarix* defoliation with the former occupying the Colorado River Basin and expanding in range south and east while the latter is moving north and west from its original release sites in Texas.

biocontrol has resulted in significant defoliation and mortality of *Tamarix*. No serious efforts at habitat restoration are currently planned in any reasonable timeframe.

In this chapter, we have three objectives: first, we document the value of nonnative *Tamarix* as summer habitat for birds compared to native riparian habitats of mesquite bosques and cottonwood/willow, and mixed deciduous gallery woodlands; second, we specifically focus on the unintended consequences to native avifauna of dam construction, *Tamarix* invasion, native vertebrate colonization of the *Tamarix*-dominated riparian habitat, and subsequent biocontrol along approximately 300 miles of the Colorado River in Grand and Glen Canyons; and, third, we briefly review current allelopathic studies on the potential long-term fate of native woody riparian vegetation when growing alongside *Tamarix*.

Importance of *Tamarix* to Riparian Birds

Tamarix has not always been appreciated for its importance as wildlife habitat. Beginning in the late 1950s, investigations into the avian use of *Tamarix*-dominated riparian areas consistently demonstrated that the loss of native riparian vegetation and invasion of *Tamarix* had a negative effect on the population sizes of riparian birds (Anderson and Ohmart 1977). However, as verification of the fact that ecological generalizations concerning *Tamarix* are elusive, there were exceptions. Rosenberg et al. (1991) reported 14 pairs of nesting white-winged doves per acre in *Tamarix*-screwbean mesquite (*Prosopis pubescens*) communities in the Lower Colorado River Valley. In the late 1950s, Shaw (1961) and Shaw and Jett (1959) reported nesting white-winged dove (*Zenaida asiatica*) populations as high as 60 nests per acre in the “saltcedar” thickets adjacent to declining mesquite bosques near the mouth of the Salt and Gila Rivers near Gillespie Dam in central Arizona.

Hunter et al. (1988) compared avian use on three river systems, the Lower Colorado, Rio Grande, and Pecos Rivers. They found that on the Pecos River in New Mexico, where riparian trees were mostly rare before the invasion of *Tamarix*, several species of obligate riparian birds expanded their range into the Pecos River Valley coincident with the arrival of *Tamarix*. The Hunter et al. (1988) findings were surprising as avian use of *Tamarix* on the Lower Colorado and Rio Grande was comparatively low. Brown et al. (1987) and Carothers and Brown (1991) also documented avian range and population increases along the Colorado River in Grand Canyon and linked those increases to the arrival of *Tamarix*. For both the Pecos River and Colorado River in Grand Canyon, quantitative estimates of native vegetation cover and bird species density prior to the invasion of *Tamarix* were mostly non-existent. In the Pecos River Basin, *Tamarix* is reported to have invaded in 1912 (Hildebrant and Ohmart 1982). In Grand Canyon, *Tamarix* was first reported as relatively rare with only isolated occurrences along the river corridor in 1938 (Clover and Jotter 1944); however, as early as 1936 a pair of southwestern willow flycatchers was found nesting in *Tamarix* below Glen Canyon at Lees Ferry (Woodbury and Russell 1945).

Quantitative estimates of bird life along the Pecos and Colorado Rivers are only available long after the respective *Tamarix* invasions. However, prior to the invasion of *Tamarix* along the Pecos River, Hildebrandt and Ohmart (1982) report, without citing the source for their conclusion, that there were few existing tall and mature stands of vegetation that could be used by riparian birds. In the Grand Canyon, *Tamarix* only proliferated significantly in the riparian zone after 1963, coincident with the construction and operation of Glen Canyon Dam and the significant reduction of annual scouring floods (see more below on Glen Canyon Dam river corridor impacts).

It was not until the surprising rate of spread and rapid and repeated defoliation and tree mortality caused by the *Diorhabda* became obvious that the value of *Tamarix* as wildlife habitat was quantified. Sogge et al. (2008) reviewed some available literature (see Corman and Wise-Gervais 2005) for nesting birds in Arizona and elsewhere and determined that 49 species used *Tamarix* as nesting habitat. Over 75 percent of low- and mid-elevation riparian birds in Arizona are known to build their nests in *Tamarix* (Bateman et al. 2013a; Corman and Wise-Gervais 2005; Sogge et al. 2008).

In this chapter, we have expanded the *Tamarix*-bird-use literature search to include: (1) over 50 publications spanning several decades; (2) more southwestern States than just Arizona; and (3) birds recorded as using *Tamarix* for foraging and roosting as well as for nesting. For reference, we compare bird use of *Tamarix* to that of riparian vegetation associations dominated by native species, including mesquite, cottonwood/willow, and mixed deciduous habitats (table 3). Of a total of 143 species of lowland birds in the southwestern United States normally found during the spring and summer months associated with breeding activities, 105 (73 percent) have been recorded in *Tamarix*, 98 (69 percent) in mesquite, 81 (57 percent) in cottonwood-willow, and 67 (47 percent) in mixed deciduous habitat types. While not all the species listed in table 3 necessarily build their nests in the specific tree types or associations, the lists do serve to emphasize the relative importance of the *Tamarix* shrub/tree species as a wildlife resource.

The value of *Tamarix* to riparian wildlife is especially evident where native riparian species have significantly declined over the past decades. It is also apparent in disturbed drainages where native vegetation species can no longer recruit and survive due to land conversion by urbanization, agriculture, and/or alteration of the natural hydrograph (Sogge et al. 2013). Where native riparian species are specifically precluded, *Tamarix* is a far superior habitat to no woody habitat at all. It provides structural diversity for riparian wildlife species that does not exist when there are no woody tree species and/or low-growing native and nonnative grasses and forbs. We believe increased use by birds of *Tamarix*-dominated habitats versus exclusively native species-dominated habitats is the result of increased general habitat structure provided by the increased foliage volume and foliage height diversity. A *Tamarix*-dominated understory is normally unavailable in the exclusively native stands. The *Tamarix* growth form provides vegetative cover and foraging areas from the ground up, while riparian habitat consisting of mostly native species normally has low-growing herbaceous plants under the gallery forest or mesquite bosque canopies (see Bateman et al. 2013a). In addition, *Tamarix*'s ability to rapidly establish after disturbance and its high stress tolerance compared to native vegetation has resulted in the rapid proliferation of vegetative cover. Thus wildlife habitat is quickly available where previously either low-growing, non-woody cover predominated, or only bare ground was present (Hultine and Dudley 2013).

Moreover, it has been demonstrated that invertebrate density and diversity can increase within the riparian ecosystem in some areas where *Tamarix* has invaded (Stevens 1976, 1985; Strudly and Dalin 2013). Within a little over two decades following the closing of the floodgates of Glen Canyon Dam, *Tamarix* supported a relatively low species richness of invertebrates compared with native species, but it supported

Table 3—A comparison of breeding birds recorded in lowland riparian habitats) of the southwestern United States.

Table Key

* Birds recorded from the Colorado River and its tributaries in Grand Canyon (Brown et al. 1987; Corman and Wise-Gervais 2005).

Riparian dependency at lower elevations:

F = facultative, occurring approximately equally in or out of riparian habitats;

O = obligate, occurring in riparian or similar wetland habitats >90 percent of the time;

P = preferential, occurring in riparian habitats < 90 percent of the time but more often than in nonriparian or other wetland habitats;

W = may occur in riparian habitats but often occurring in other wetland types, e.g., marshes, open water, or openings near water.

Although most species nest in the habitat in which they have been listed they may forage in or over the vegetation types listed below.

			-------------- Vegetation type --------------			
Common name	**Scientific name**[b]	**Riparian dependency code**	***Tamarix***[c]	**Mesquite**[d]	**Cottonwood-Willow**[e]	**Mixed-Deciduous**[f]
Abert's towhee	*Melozone aberti*	O	2,11,15	X	X	
Acorn woodpecker	*Melanerpes formicivorus*					X
American coot	*Fulica americana*	* W	6,13,16	X		
American dipper	*Cinclus mexicanus*	* O	12,17,21			
American kestrel	*Falco sparverius*	* P	4,18	X	X	X
American robin	*Turdus migratorius*	P			X	X
Anna's hummingbird	*Calypte anna*	P		X	X	X
Arizona woodpecker	*Picoides stricklandi*					X
Ash-throated flycatcher	*Myiarchus cinerascens*	* F	2,3,15,16	X	X	X
Bald eagle	*Haliaeetus leucocephalus*	O	6,13	X	X	
Barn owl	*Tyto alba*		2	X	X	X
Bell's vireo[k]	*Vireo bellii*	* P	1,11,15	X	X	X
Belted kingfisher	*Megaceryle alcyon*	O	12,17			
Bendire's thrasher	*Toxostoma bendirei*	F		X		
Bewick's wren	*Thryomanes bewickii*	*	2,10,11	X	X	X
Black phoebe	*Sayornis nigricans*	* O	6,12,15	X	X	X
Black rail	*Laterallus jamaicensis*	O W	21	X		
Black-caped gnatcatcher	*Polioptila nicriceps*	P		X	X	X
Black-chinned hummingbird	*Archilochus alexandri*	* P	1,2,17,18	X	X	X
Black-crowned night-heron	*Nycticorax nycticorax*	* O	1,12,13	X	X	
Black-headed grosbeak	*Pheucticus melanocephalus*					X
Black-tailed gnatcatcher	*Polioptila melanura*	* P	4,12,22	X	X	
Black-throated sparrow	*Amphispiza bilineata*			X		
Blue grosbeak	*Passerina caerulea*	* O	1,2,3,15	X		X
Blue-gray gnatcatcher	*Polioptila caerulea*	*	1,5	X	X	
Botteri's Sparrow	*Peucaea botterii*	F		X	X	X

Table 3—*Continued.*

Common name	Scientific name[b]	Riparian dependency code	Vegetation type: *Tamarix*[c]	Mesquite[d]	Cottonwood-Willow[e]	Mixed-Deciduous[f]
Bridled titmouse	*Baeolophus wollweberi*	O			X	X
Broad-billed hummingbird	*Cynanthus latirostris*	P		X	X	X
Bronzed cowbird	*Molothrus aeneus*	O		X	X	
Brown thrasher	*Toxostoma rufum*		12,17,20		X	
Brown-crested flycatcher	*Myiarchus tyrannulus*	P	12,18	X	X	X
Brown-headed cowbird	*Molothrus ater*	* F	1,2,3,16	X	X	X
Bullock's oriole	*Icterus bullockii*	* O	2,3,15,18	X	X	X
Cactus wren	*Campylorhynchus brunneicapillus*	*	3,12,15	X		
Canyon towhee	*Melozone fusca*	*	18	X		
Canyon wren	*Catherpes mexicanus*	* F		X		
Cassin's kingbird	*Tyrannus vociferans*	F	18		X	X
Cattle egret	*Bubulcus ibis*	P	17,20,21	X		
Chihuahuan raven	*Corvus cryptoleucus*		12,17,18	X	X	X
Clapper rail	*Rallus crepitans*	O W	21	X		
Clark's grebe	*Aechmophorus clarkii*	* W	5			
Cliff swallow[l]	*Petrochelidon pyrrhonota*	* O	4,12,17	X	X	X
Common black hawk	*Buteogallus anthracinus*	O		X	X	X
Common ground-dove	*Columbina passerina*	P	18,21	X		
Common moorhen	*Gallinula chloropus*	W	6,12,13	X		
Common poorwill	*Phalaenoptilus nuttallii*			X		
Common raven	*Corvus corax*	*	4,10,18	X	X	X
Common yellowthroat	*Geothlypis trichas*	* O W	11,12,15	X	X	X
Cooper's hawk	*Accipiter cooperii*	* O	18	X	X	X
Costa's hummingbird	*Calypte costae*	*	14	X		
Couch's kingbird	*Tyrannus couchii*				X	
Crissal thrasher	*Toxostoma crissale*	* P	3,9,12,15	X		
Curve-billed thrasher	*Toxostoma curvirostre*	F	7	X		
Double-crested Cormorant	*Phalacrocorax auritus*	* O	21	X	X	
Dusky-capped flycatcher	*Myiarchus tuberculifer*					X
Eastern bluebird	*Sialia sialis*				X	X
Elf owl	*Micrathene whitneyi*	P	12,20,17	X	X	X
European starling	*Sturnus vulgaris*	* P	4	X	X	X
Ferruginous pygmy-owl	*Glaucidium brasilianum*	P		X	X	
Gambel's quail[g]	*Callipepla gambelii*	* P	6,11,13	X	X	X
Gila woodpecker	*Melanerpes uropygialis*	P	4,15,18	X	X	X

Table 3—*Continued.*

Common name	Scientific name[b]	Riparian dependency code	Vegetation type			
			Tamarix[c]	Mesquite[d]	Cottonwood-Willow[e]	Mixed-Deciduous[f]
Gilded flicker	*Colaptes chrysoides*	F	4	X	X	
Golden-fronted woodpecker	*Melanerpes aurifrons*	P				
Gray hawk	*Buteo plagiatus*	O	18	X	X	X
Great blue heron	*Ardea herodias*	O	4,6	X	X	
Great egret	*Ardea alba*	O	21			
Great horned owl	*Bubo virginianus*	*	4	X	X	X
Great-tailed grackle	*Quiscalus mexicanus*	* O	11,15			
Greater roadrunner	*Geococcyx californianus*	* F	3,12,22	X	X	X
Green heron	*Butorides virescens*	O	6,13		X	
Harris hawk	*Parabuteo unicinctus*	P		X	X	
Hooded oriole	*Icterus cucullatus*	* P		X	X	X
House finch F	*Haemorhous mexicanus*	* F	11,14,15	X	X	X
House sparrow	*Passer domesticus*	*		X	X	
Hutton's vireo	*Vireo huttoni*	F				X
Indigo bunting	*Passerina cyanea*	* O	12,17	X	X	X
Killdeer	*Charadrius vociferus*	W P	6,14,16	X		
Ladder-backed woodpecker	*Picoides scalaris*	* P	2,3,15,16	X	X	X
Lazuli bunting	*Passerina amoena*	* O	12,17		X	X
Least bittern	*Ixobrychus exilis*	W	5,10	X	X	
Lesser goldfinch	*Spinus psaltria*	* P	11,15,18	X	X	X
Lesser nighthawk	*Chordeiles acutipennis*	*	4,6,13	X	X	X
Loggerhead shrike	*Lanius ludovicianus*		3,21	X		
Long-billed thrasher	*Toxostoma longirostre*			X		
Lucy's warbler	*Oreothlypis luciae*	* O	1,2,15,18	X	X	X
Marsh wren	*Cistothorus palustris*		4,5			
Meadowlark	*Sturnella* sp.		7			
Mexican jay	*Aphelocoma wollweberi*					X
Mississippi kite	*Ictinia mississippiensis*	O	19,21	X	X	
Montezuma quail	*Cyrtonyx montezumae*					X
Mourning dove	*Zenaida macroura*	* P	2, 6,11,13	X	X	X
Northern beardless-tyrannulet	*Camptostoma imberbe*	O	18	X	X	X
Northern cardinal	*Cardinalis cardinalis*	P	9,18	X	X	
Northern flicker	*Colaptes auratus*			X	X	X
Northern mockingbird	*Mimus polyglottos*	P	3,11,7,18	X	X	X

Table 3—*Continued.*

Common name	Scientific name[b]	Riparian dependency code	-------------- Vegetation type --------------			
			Tamarix[c]	Mesquite[d]	Cottonwood-Willow[e]	Mixed-Deciduous[f]
Northern rough-winged swallow	*Stelgidopteryx serripennis*	P	6,12,13	X	X	X
Orchard oriole	*Icterus spurius*	P		X	X	
Painted bunting	*Passerina ciris*		22			
Peregrine falcon[j]	*Falco peregrinus*	* P	5			
Phainopepla	*Phainopepla nitens*	* P	4,14,18	X	X	X
Pied-billed grebe	*Podilymbus podiceps*	W	5,6,10			
Prairie falcon	*Falco mexicanus*	*				
Purple martin	*Progne subis*			X		
Pyrrhuloxia	*Cardinalis sinuatus*	P	3,12,22	X		
Red-tailed hawk	*Buteo jamaicensis*	*	14,21	X	X	X
Red-winged blackbird	*Agelaius phoeniceus*	* W P	2,8,14,16	X		
Ring-necked pheasant	*Phasianus colchicus*		7			
Rose-throated becard	*Pachyramphus aglaiae*	O			X	X
Ruddy duck	*Oxyura jamaicensis*	W	5,13			
Rufous-winged sparrow	*Peucaea carpalis*	P		X		
Say's phoebe	*Sayornis saya*		14,15,16			
Snowy egret	*Egretta thula*	O	21			
Song sparrow	*Melospiza melodia*	* O W	2,6,10,15	X	X	X
Sora	*Porzana carolina*	O W	5	X		
Spotted sandpiper	*Actitis macularius*	* W	1,21		X	
Spotted towhee	*Pipilo maculatus*		7			
Sulphur-bellied flycatcher	*Myiodynastes luteiventris*	O				X
Summer tanager	*Piranga rubra*	* O	2,9,12,17	X	X	X
Swainson's hawk	*Buteo swainsoni*		21	X		
Thick-billed kingbird	*Tyrannus crassirostris*	P	21			
Tricolored blackbird	*Agelaius tricolor*	W P	12,17,20			
Tropical kingbird	*Tyrannus melancholicus*	P	9	X	X	
Turkey vulture	*Cathartes aura*	*	4	X	X	X
Varied bunting	*Passerina versicolor*	F	18	X		
Verdin	*Auriparus flaviceps*	P	2,14,15	X		
Vermilion flycatcher	*Pyrocephalus rubinus*		2,18	X	X	X
Violet-green swallow	*Tachycineta thalassina*	*				X
Virginia rail	*Rallus limicola*	O W	5	X		
Western grebe[h]	*Aechmophorus occidentalis*	* W	5			

Table 3—*Continued.*

Common name	Scientific name[b]	Riparian dependency code	-------------- Vegetation type -------------- *Tamarix*[c]	Mesquite[d]	Cottonwood-Willow[e]	Mixed-Deciduous[f]
Western kingbird	*Tyrannus verticalis*	* F	3,15,18	X	X	X
Western meadowlark	*Sturnella neglecta*		4			
Western screech-owl	*Megascops kennicottii*	* P	2	X	X	X
Western wood-pewee	*Contopus sordidulus*	O		X	X	X
White-breasted nuthatch	*Sitta carolinensis*					X
White-faced ibis	*Plegadis chihi*	W	12,20,17			
White-throated swift	*Aeronautes saxatalis*	*	5			
White-winged dove	*Zenaida asiatica*	P	2,6,8,13	X	X	X
Willow flycatcher	*Empidonax traillii*	* O	9,17		X	
Yellow warbler	*Setophaga petechia*	* O	1,2,15,18	X	X	X
Yellow-billed cuckoo[i]	*Coccyzus americanus*	* O	2,3,7,17	X	X	X
Yellow-breasted chat	*Icteria virens*	* O	1,13,15	X	X	
Yellow-headed blackbird	*Xanthocephalus xanthocephalus*	O W	4,5,12,17			
Zone-tailed hawk	*Buteo albonotatus*	P		X	X	X
*58 Grand Canyon	Total species: 143		105	98	81	67
			Total	Total	Total	Total

[a] After Johnson et al. (1977, 1987) with modifications from information gathered since those publications. Several species of cavity nesters are obligate or preferential riparian nesters except for using saguaros (*Carnegiea gigantea*), e.g., western screech-owl, elf owl, Gila woodpecker, gilded flicker, and American kestrel.

[b] Common and scientific names after the 2017 checklist of North and Middle American birds by the North American Classification Committee (NACC) of the American Ornithologists' Union.

[c] Tamarisk or saltcedar; after 3 or 4 references are listed for a given species additional references are not cited.

[d] Velvet (*Prosopis velutina*), honey (*P. glandulosa*), or screwbean mesquites (*P. pubscens*).

[e] Fremont (*Populus fremontii*) and plains cottonwoods (*P. deltoides*), and Goodding willow (*Salix gooddingii*).

[f] Largely Arizona (*Platanus wrightii*) and California sycamores (*P. racemosa*); ash (*Fraxinus* spp.), and walnut (*Juglans* spp.).

[g] Although numerous historic records of Gambel's quail the species was extirpated by the mid-1900s.

[h] Western and Clark's grebes have been recently separated so there is confusion about which occurs (one or both?) on upper Lake Mead at the lower end of Grand Canyon.

[i] Formerly the Yellow-billed cuckoo was a rare summer resident in the Canyon but last recorded in 1971 (Brown et al. 1987).

[j] Peregrines commonly nest on cliffs close to water from where they hunt for birds on and over water.

[k] Bell's vireo has progressed steadily upstream in *Tamarix* thickets since the construction of upstream Glen Canyon Dam; one of the most noticeable species because of its persistent song (Brown et al. 1983).

[l] The cliff swallow was formerly a common breeding species along the Colorado River in Grand Canyon but by the mid-1970s it was extirpated, apparently due to sediment being entrapped by upstream Glen Canyon Dam, thus a lack of mud for nest-building (Brown et al. 1987).

[m] The overall period covered was from 1978 to 2012 with the states of CA, AZ, NM, TX, and NV all represented and although the same locations were sometimes sampled more than once each sampling listed different species.

[n] van Riper et al. (2008) does not list how species use riparian habitat or differentiate between use of *Tamarix* and other riparian vegetation for each species.

[o] https://birdsna.org/Species-Account/bna/species/

Table 3—*Continued.*

I. Tamarix citations[m]	**Rivers and states**
1. Brown et al. (1987)	Colorado R. in Grand Canyon, AZ
2. Rosenberg et al. (1991)	Lower Colorado R. Valley, AZ & CA
3. Hunter et al. (1988)	Pecos, Rio Grande, lower Colorado rivers, TX, AZ & CA
4. Anderson (2017)	Lower Colorado R. Valley, AZ & CA
5. R. Roy Johnson (Pers. observ.),	unpublished Various, SW U.S.
6. Johnson and Simpson (MS b)	Salt R., AZ
7. Livingston and Schemnitz (1996).	Pecos R., NM
8. Rea (2007).	Gila R., AZ
9. Hunter et al. (1987)	Colorado, Gila, Pecos, Rio Grande, Salt, San Pedro, Santa Cruz, Verde rivers, TX, AZ & CA
10. Johnson et al. (2000)	Lower Salt River, AZ
11. Engel-Wilson and Ohmart (1979)	Rio Grande, TX
12. Sogge et al. (2008)	Various, SW U.S.
13. Johnson and Simpson (MS a)	Gila, Salt, Verde rivers, AZ
14. Cardiff et al. (1978a)	Mojave R., CA
15. van Riper et al. (2008)[n]	Lower Colorado R., AZ & CA
16. Cardiff et al. (1978b)	Mojave R., CA
17. Paxton et al. (2011)	Southwestern U.S.
18. Brand et al. (2008)	San Pedro R., AZ
19. Glinski and Ohmart (1983)	San Pedro R., AZ
20. Birds of North America accounts[o]	Various, SW U.S.
21. Corman and Wise-Gevais (2005)	Arizona rivers, AZ
22. Hunter et al. (1985)	Colorado, Pecos, Rio Grande rivers, SW U.S.

II. Mesquite citations: (Arnold 1940; Bendire 1872, 1892; Brandt 1951; Brown 1987; Brown et al. 1984; Carothers and Brown 1991; Carothers and Sharber 1976; Carothers et al. 1976; Corman and Wise-Gervais 2005; Dawson 1921; Gavin and Sowles 1975; Glinski and Ohmart 1983; Huels et al. 2013; Hunter et al. 1987; Johnson and Simpson Ms A, Ms B; Johnson et al. 2000; Monson and Phillips 1981; Ohmart et al. 1988; Phillips et al. 1964; Rea 1983, 2007; Rosenberg et al. 1991; Stamp 1978; Webb et al. 2014; Willson and Carothers 1979).

III. Cottonwood-willow citations: (Brandt 1951; Carothers and Johnson 1976; Carothers et al. 1974; Corman and Wise-Gervais 2005; Engel-Wilson and Ohmart 1979; Glinski and Ohmart 1983; Hunter et al. 1987; Johnson and Simpson Ms A, Ms B; Johnson et al. 2000; Monson and Phillips 1981; Ohmart et al. 1988; Phillips et al. 1964; Rea 1983, 2007; Rosenberg et al. 1991; Stamp 1978; Webb et al. 2014).

IV. Mixed deciduous citations: (Bock and Bock 1984; Carothers et al. 1974; Monson and Phillips 1981; Phillips et al. 1964).

a 10-fold higher biomass of invertebrates compared with the co-occurring native willow (*Salix exigua*) (Stevens 1985). Most of the invertebrate biomass increase found in *Tamarix* reported by Stevens (1985) was due to high density of the *Tamarix* host-specific, nonnative leaf hopper (*Opsius stactogalus*)—a species that Grand Canyon birds commonly feed upon during the breeding season (Yard et al. 2004). In addition, *Tamarix* is a rapid invader and fast to grow in conditions otherwise marginal for most native riparian species. These conditions include inflows and outflows to reservoirs like Lakes Mead and Powell, where annual tailwater flows are severely reduced from pre-dam flows, and where receding reservoirs expose bare ground.

The unintended and unexpected consequence of a major reduction in wildlife habitat caused by the rapid and widespread loss of *Tamarix*-dominated habitat in many areas has now been well documented (Bateman et al. 2015, 2013b; Darrah and van Riper 2017; McLeod volume 1; Paxton et al. 2011; Sogge et al. 2008, 2013; van Riper et al. 2008; Yard et al. 2004). Sogge et al. (2008) also determined that there were no negative effects from breeding in *Tamarix* habitats expressed in several studies on the southwestern willow flycatcher (*Empidonax traillii extimis*). This finding contradicted the conventional wisdom that birds that nested in *Tamarix* had lower reproductive fitness as measured in nest and fledgling survival (see Brand et al. 2008; DeLoach et al. 2000). In Grand Canyon, the earliest southwestern willow flycatcher breeding record (1936) reported by Woodbury and Russell (1945) in the Lees Ferry area was in *Tamarix*, and every nest found along the Colorado River in Grand Canyon by Brown (1988) was also in *Tamarix* (table 4)[2]. Sogge et al. (2008) warned that the overall ecological costs and benefits of *Tamarix* control were difficult to predict and that restoration projects that resulted in removal of *Tamarix* without replacement with high quality habitat had the potential to reduce net riparian habitat value for local and/or regional bird populations. Their predictions were prophetic.

Darrah and van Riper (2017) proposed that the impacts to riparian bird species resulting from *Diorhabda* biocontrol will continue until regrowth of native vegetation is established. Whereas they recognized that active restoration may be necessary in some areas, they did not discuss the challenges that will be faced by private, State, and Federal organizations in providing human and financial resources necessary for active habitat restoration[3] on thousands of acres of *Tamarix* habitat destroyed by the beetle. One estimate for comprehensive eradication and restoration of *Tamarix*-dominated habitat prior to biocontrol concluded that, although costs per acre are difficult to average depending on local site conditions and other factors, they normally reach thousands of dollars per acre (Zavaleta 2000).

An early review of the potential for habitat restoration following anticipated successful biocontrol questioned whether the habitat that occurs following *Tamarix* control and revegetation was any better for wildlife than the original habitat (Shafroth et al. 2005). Indeed, in their review, Shafroth et al. (2005) observed that following *Tamarix* control efforts, failure to plan and implement restoration efforts could result in recolonization of a site by other exotic species. This prediction has been largely verified by Gonzales et al. (2017) in their study of 244 sites where *Tamarix* was removed or disadvantaged by one means or another. In another study of a restoration project on Las Vegas Wash in Nevada where *Tamarix* was removed from several sites, replaced by native trees and shrubs, and then monitored for avian use, benefits to birds were not as evident as predicted (Shanahan et al. 2011). However, the apparent lack of wildlife benefits in *Tamarix* removal projects reviewed to date may be partially a consequence of the assessments being too early after control impacts. There may have been insufficient time for revegetation following the defoliation and mortality of the exotic species.

[2] Nesting records for the endangered southwestern willow flycatcher are important not only because of the rarity of the species but because of its nesting in *Tamarix* in Grand Canyon rather than in willows or other native species. The flycatcher had formerly occurred throughout much of the state (Phillips et al. 1964) but had largely disappeared by the 1970s. For example, 34 nests were collected along the Colorado River in the Yuma area in 1902 by Herbert Brown (Unitt 1987) but the species was later extirpated as a breeding bird for that region (Rosenberg et al. 1991). Monson and Phillips (1981) wrote, "No nests found [in Arizona] since 1970," obviously unaware of our nesting records (table 2) and those published by Carothers and Johnson (1975). Thus, the southwestern willow flycatchers nesting in Grand Canyon during the 1970s and into the 1980s represented the only known breeding population for the state at that time.

[3] We are distinguishing between *passive* restoration and *active* restoration as defined by Shafroth et al. 2013; i.e.: "Passive restoration refers to facilitating the return of desirable system dynamics and species composition by removing one or more underlying stressor(s). Active restoration approaches include manipulating a site to prepare it for restoration; revegetating the site by introducing seeds, transplant stock, or cuttings; or irrigating or otherwise manipulating the site to enhance recovery" (Shafroth et al. 2013, p. 411).

Table 4—Summer records of the endangered southwestern willow flycatcher (*Empidonax traillii extimus*) from the Colorado River in Grand Canyon prior to 1989; see especially Brown (1988).

Date	Location	Observation	Observer and reference
June 7, 1933	RM 2[1]	Female collected	Woodbury and Russell (1945)
August 18, 1936	Near Lees Ferry	Nest collected from *Tamarix*	Woodbury and Russell (1945)
June 16, 1953	Lees Ferry	Specimen collected	R.W. Dickerman; Monson (1953)
June 17, 1953	Mouth of Little Colorado River	Specimen collected	R.W. Dickerman; Monson (1953)
July 12, 1971	Cardenas Marsh	Nest with eggs in Goodding willow	Johnson; Carothers and Johnson (1975)
July 27, 1971	Cardenas Marsh	1 pair	Carothers; Carothers and Johnson (1975)
May 20, 1974	Cardenas Marsh	1 pair	Johnson; Carothers and Johnson (1975)
1974-1976	225 mi of Colorado R.	1 known pair	Carothers et al. 1976; Carothers and Sharber (1976)
1974-1976	225 mi of Colorado R.	1 known pair	Carothers et al. 1976; Carothers and Sharber (1976)
1982	Saddle Can. to Nankoweap Crk.	1 singing male	Brown (1988)
1982	Cardenas Marsh	1 singing male	Brown (1988)
1983	Saddle Can. to Nankoweap Crk.	4 singing males	Brown (1988)
1984	Saddle Can. to Nankoweap Crk.	3 singing males, 2 nests* In *Tamarix*	Brown (1988)
1984	Cardenas Marsh	1 singing male	Brown (1988)
1985	Saddle Can. to Nankoweap Crk.	7 singing males, 4 nests* In *Tamarix*	Brown (1988)
1985	Cardenas Marsh	1 singing male	Brown (1988)
1986	Saddle Can. to Nankoweap Crk.	8 singing males 2 nests* In *Tamarix*	Brown (1988)
1986	Nankoweap Crk. to Kwagunt Crk.	1 singing male	Brown (1988)
1986	Cardenas Marsh	2 singing males	Brown (1988)
1987	Saddle Can. to Nankoweap Crk.	4 singing males 2 nests* In *Tamarix*	Brown (1988)
1987	Cardenas Marsh	3 singing males	Brown (1988)

[1] River Miles downstream from Lees Ferry.

*Exact location of nests not given by Brown (1988).

Whereas biocontrol appears to be satisfying the long-desired eradication of this invasive species much more quickly than expected, there is little evidence at this time that native riparian vegetation will, without active restoration, eventually colonize most areas as originally assumed (DeLoach and Tracy 1997). Beetle-release proponents admitted early in the development of the biocontrol that evidence for native vegetation species to replace *Tamarix* was circumstantial and not well supported (see McLeod volume 1) and clearly underestimated the value of the *Tamarix* to native riparian wildlife species. Recent revegetation efforts attempted along the Colorado River in Glen Canyon indicate that once *Tamarix* is gone, reestablishment of native woody vegetation can be rapid and effective, but only coincident with labor intensive planting, fencing, and watering (Stevens et al. 2015).

However, in other areas where active restoration has not been implemented after *Tamarix* removal, passive revegetation is almost exclusively limited to recolonization by a mixture of native and nonnative grasses and herbaceous cover with the conspicuous absence of woody species (González et al. 2017; Sher et al. 2018). In a study in Grand Canyon tributaries, Belote et al. (2010) found that 1 to 3 years after mechanical removal of *Tamarix*, there was no recruitment or increase in the number of native species; however, there was approximately a 50 percent decline in precipitation between pre- and post-restoration periods that could have prevented a greater success in restoration of native species.

Tamarix-Dominated Riparian Habitat In Grand Canyon: A New Wildlife Resource

Prior to the closing of the flood gates of Glen Canyon Dam in 1963 and creation of Lake Powell, annual flood scour in the river channel precluded riparian growth in all but a narrow margin at the edge of the high water line. Composed of honey mesquite (*Prosopis glandulosa*), netleaf hackberry (*Celtis reticulata*), four species of Baccharis, and western redbud (*Cercis occidentalis*), this narrow band of vegetation constituted the extent of riparian habitat in the river corridor. Below this narrow band of high water line vegetation, the annual scour zone was largely devoid of woody vegetation and composed of annual forbs and grasses that could establish between flood flows. After the dam began to hold back annual highwater and annual scouring floods were largely controlled, a *Tamarix*-dominated vegetation zone became established in the river corridor. This included *Tamarix* (*T. chinensis/ramosissima*) intermixed with native species, arrowweed (*Pluchea sericea*), *Baccharis* spp., coyote willow (*Salix exigua*), and Goodding's willow (*Salix gooddingii*) where previously only forbs and grasses occurred. Figures 1 and 2 provide a graphic representation of the riparian vegetation condition of the river corridor in Grand Canyon before and after the Dam. Scott et al. (volume 1) demonstrate these vegetation changes with photographic comparisons.

By the time Glen Canyon Dam had been in place for 20 years (1963-1983), natural resources studies below the Dam were focused on attempting to quantify changes that dam-controlled flow had on aquatic and terrestrial ecosystems within Grand Canyon National Park. At that time, approximately 300 miles of river corridor from the dam to Lake Mead were under control and management of the National Park Service, but dam releases were under control of the Bureau of Reclamation and fluctuated according to power needs by cities. Also, during this time, researchers first recognized that the terrestrial *Tamarix*-dominated habitat was becoming increasingly more utilized by river corridor wildlife in Grand Canyon. The New High Water Zone (NHWZ; see fig. 2) habitat was recognized as a boon to native wildlife species.

Within only two decades of the closing of the flood gates at Glen Canyon Dam in 1963, *Tamarix*-dominated habitat below the dam became remarkably productive for native vertebrates and invertebrates and some nonnative invertebrates as well (Brown et al. 1987; Stevens 1985; Yard et al. 2004). The NHWZ vegetation introduced an extensive "new" river margin zone of vegetation along the river corridor from Glen Canyon Dam to the inflow of Lake Mead. Moreover, studies soon demonstrated that the NHWZ not only increased the overall density of canyon birds, but also contributed to the range expansions of several avian species that invaded from the south where native habitats and some avian species were in rapid decline (Brown et al. 1987; Rosenberg et al. 1991). Table 5 presents a list of the birds and mammals that have colonized or experienced range extensions into *Tamarix*-dominated habitat along the Colorado River in Grand Canyon since the closing of Glen Canyon Dam floodgates.

Remarkably, it soon became obvious that NHWZ was expanding rapidly and that it was significantly more productive and robust in vegetative growth and in carrying capacity for riparian birds and other vertebrates and invertebrates than the native mesquite-dominated Old High Water Zone (OHWZ; fig. 1) (Brown and Trosset 1989; Carothers and Brown 1991; Holmes et al. 2005; Ruffner et al. 1978; Stevens 1995; Yard et al. 2004). Studies targeted specifically on OHWZ tree/shrub species indicated that plants in this zone were slowly senescing, presumably due to the absence of flows no longer reaching the OHWZ habitats \(Anderson and Ruffner 1987, 1988).

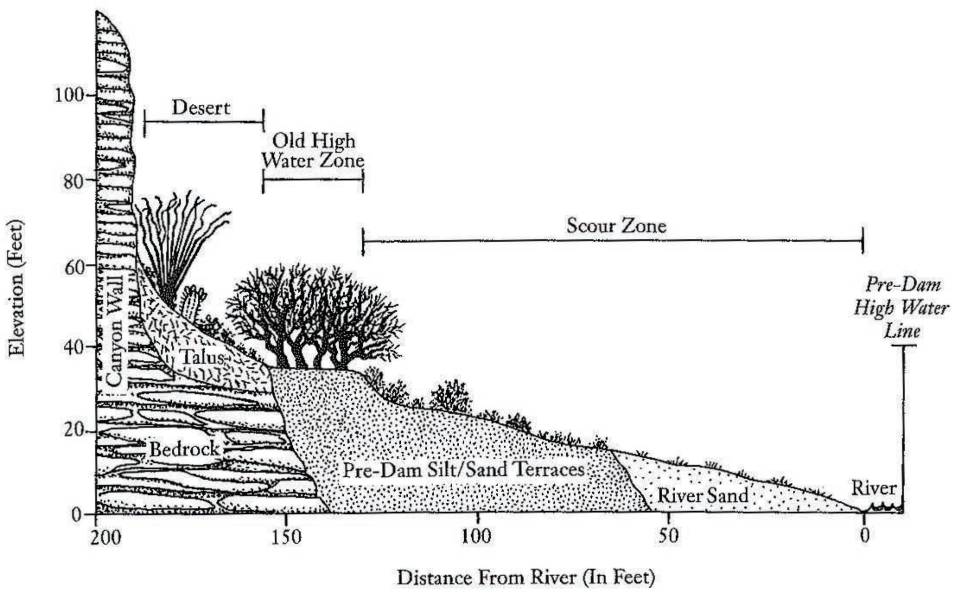

Figure 1—Pre-dam floods normally scoured the lower-lying river terraces of all woody vegetation, allowing only a few annual grasses and herbs to develop in the pre-dam flood zone. From *Grand Canyon Birds* by Bryan T. Brown, Steven W. Carothers, and R. Roy Johnson, © 1987 The Arizona Board of Regents. Reprinted by permission of the University of Arizona Press.

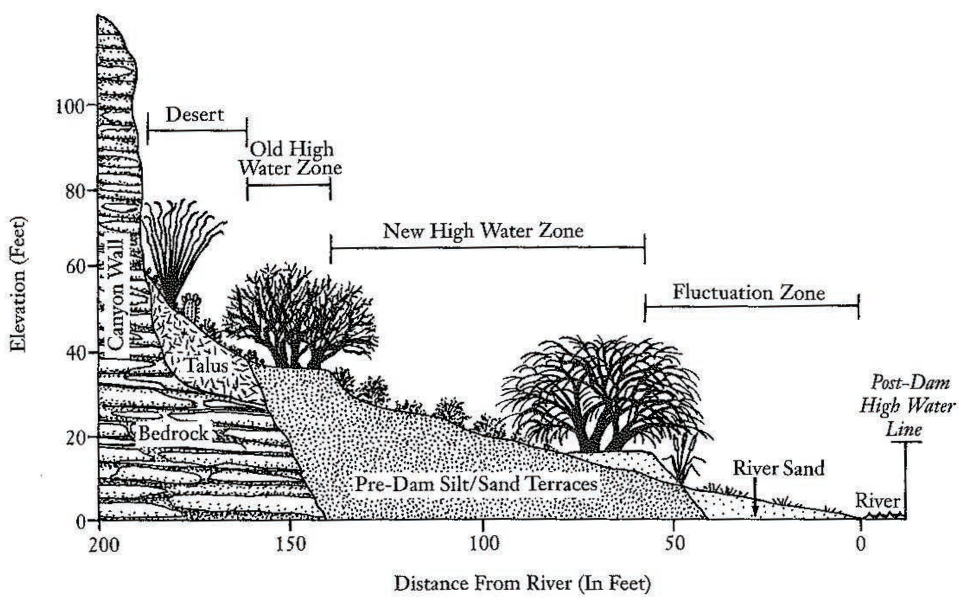

Figure 2—Beginning in 1963, Glen Canyon Dam prevented the annual scouring floods. A new zone of riparian vegetation, dominated by the exotic *Tamarix*, developed in the pre-dam flood zone and was quickly colonized by riparian breeding birds and other native vertebrates. From *Grand Canyon Birds* by Bryan T. Brown, Steven W. Carothers, and R. Roy Johnson, © 1987 The Arizona Board of Regents. Reprinted by permission of the University of Arizona Press.

Table 5—Birds and mammals that have colonized (newly arrived species) or experienced range extensions (moved upriver from downstream breeding locations) into *Tamarix*-dominated habitat along the Colorado River in Grand Canyon since the closing of Glen Canyon Dam floodgates in 1963 (modified from Johnson and Carothers 1987).

Common name	Scientific name	Status and notes
	Birds	
Western grebe[a]	*Aechmophorus occidentalis*	Colonized, nesting in dead *Tamarix* at upper Lake Mead
Clark's grebe[a]	*A. clarkii*	Colonized, nesting in dead *Tamarix* at upper Lake Mead
Black-chinned hummingbird	*Archilochus alexandri*	Colonized
Green heron	*Butorides virescens*	Nonbreeding
Black-crowned night-heron	*Nycticorax nycticorax*	Colonized, nesting in dead *Tamarix* at upper Lake Mead
Willow flycatcher	*Empidonax traillii*	Colonized, endangered species
Vermilion flycatcher	*Pyrocephalus rubinus*	Range expansion
Bell's vireo	*Vireo bellii*	Range expansion
Lesser goldfinch	*Spinus psaltria*	Colonized
Yellow-breasted chat	*Icteria virens*	Colonized
Hooded oriole	*Icterus cucullatus*	Range expansion
Bullock's oriole	*I. bullockii*	Colonized
Red-winged blackbird	*Agelaius phoeniceus*	Colonized
Brown-headed cowbird	*Molothrus ater*	Colonized
Great-tailed grackle	*Quiscalus mexicanus*	Range expansion
Lucy's warbler	*Oreothlypis luciae*	Colonized
Common yellowthroat	*Geothlypis trichas*	Colonized
Yellow warbler	*Setophaga petchia*	Colonized
Summer tanager	*Piranga rubra*	Range expansion
Blue grosbeak	*Passerina caerulea*	Colonized
Lazuli bunting	*P. amoena*	Colonized
Indigo bunting	*P. cyanea*	Range expansion
	Mammals	
Beaver	*Castor canadensis*	Colonized
Brush mouse	*Peromyscus boylei*	Colonized
Deer mouse	*P. maniculatus*	Colonized

[a]The western grebe was recently split into two species and it is not known if only one or both are nesting here.

Table 6—Comparison of species richness and population densities for spring and summer breeding birds showing preferences for *Tamarix*-dominated habitat relative to mesquite-dominated habitat along the Colorado River in Grand Canyon; after Brown (1987) and Brown and Trosett (1989).

Type of study plot and year	Total species	Species/site	Average species/site	Population (densities/site pairs/40 ha)	Average (density/ site pairs/40 ha)
Tamarix 1984	21	1-15	7.9	200-1,200	611
Tamarix 1985	23	1-16	8.0	100-1,200	565
Prosopis 1984	20	2-14	8.6	182-986	449
Prosopis 1985	20	3-17	8.0	73-943	379
Prosopis 1985	20	3-17	8.0	73-943	379

[1] River Miles downstream from Lees Ferry.

*Exact location of nests not given by Brown (1988).

Table 6 provides a summary of the number of species and relative density of birds found in both the *Tamarix*- and mesquite-dominated habitats (NHWZ vs. OHWZ, respectively). While species richness was similar in both habitats with 20-23 nesting species, surprisingly, and against all conventional wisdom at the time, avian density in the *Tamarix*-dominated habitat was significantly greater than in the mesquite-dominated habitats with similar cover and height attributes (Brown 1987; Willson and Carothers 1979). Additionally, most species demonstrated a preference for *Tamarix* as nesting habitat. For example, black-chinned hummingbird (*Archilochus alexandri*), blue-gray gnatcatcher (*Polioptila caerulea*), Lucy's warbler (*Oreothlypis luciae*), yellow warbler (*Setophaga petechia*), and common yellowthroat (*Geothlypis trichas*) occurred most consistently in the *Tamarix*-dominated NHWZ, with these five species comprising 51.5 percent of the total density and 31 percent of the breeding species in 1985 at the inner canyon study sites.

Lucy's warbler and black-chinned hummingbird were the most abundant and widespread species in *Tamarix*-dominated habitats during 1984 and 1985 and remarkably, of 24 Lucy's warbler nests found during that time, 15 (62.5 percent) were in *Tamarix*. What is most remarkable about the Lucy's warbler nests in *Tamarix* is the fact that the warbler is primarily a cavity-nesting species and *Tamarix* is not known for an abundance of cavities. The warblers were all found forming a cavity nest (pseudo-cavity) within the clumps of leaf litter debris caught in the forks of upper canopy branches (Johnson et al. 1997). In addition, all 12 nests of the southwestern willow flycatcher in the Grand Canyon were in *Tamarix* (Brown 1988).

The overriding preference for birds nesting in *Tamarix* in the Grand Canyon led Brown and Trosset (1989) to conclude that *Tamarix*-dominated habitats can be the ecological equivalent of native communities that are required habitat of some obligate riparian nesting birds. This is especially true in a situation like Grand Canyon where the NHWZ vegetation community did not displace a community composed of native plants but became established where previously there was no nesting habitat.

While the impact of Glen Canyon Dam on terrestrial habitats of the river corridor clearly had created habitat for native species where previously habitat did not exist, dam-related changes to the aquatic ecosystem were not as favorable to the native aquatic species, especially the native fish. The river had been dramatically changed from an aquatic ecosystem driven by an annual hydrograph with seasonal flow periodicity, sediment laden flows, and dramatically fluctuating water temperatures to a relatively steady flow, sediment starved, perpetually cold system that was largely incapable of nurturing the native aquatic species (Carothers and Brown 1991; Gloss et al. 2005; Johnson and Carothers 1987). Within the National Park, the post-dam environment bore no semblance to the pre-dam river. One of the major findings from research on changes to the aquatic and terrestrial ecosystems of the riparian corridor below Glen Canyon Dam concluded that the exotic *Tamarix* species had become a wildlife-valuable "naturalized" element of the land-based ecosystem. This *Tamarix*-based ecosystem has been termed a naturalized ecosystem, supporting high densities of native vertebrates, while the aquatic ecosystem was termed an exotic ecosystem due to the loss of indigenous species and addition of numerous exotics (Johnson and Carothers 1987).

Management of *Tamarix* in Grand Canyon: A Dilemma

Describing the dilemma of resource management in a National Park, where intense efforts are normally expended to eliminate all nonnative plants and animals, Johnson and Carothers (1987) opined on the futility of attempting to remove *Tamarix* from Grand Canyon. They argued for accepting and managing the relatively new and wildlife-supporting *Tamarix*-dominated riparian habitat as a "naturalized" community. Johnson and Carothers (1987) described the dam-influenced habitat as follows:

"… a naturalized ecosystem contains biotic communities with both indigenous and exotic plants and/or animals. In these communities, dominance or predominance is not a function of species origin (that is, native or nonnative), and the indigenous biota is not threatened either in species richness or population sizes by exotic species. In naturalized ecosystems biotic and abiotic processes have either reached or are evolving toward an equilibrium in which exotics do not restrict or interfere with native organisms or ecological processes, rather than evolving toward the destruction of components and processes of the original, natural ecosystem. If native species are extirpated or their populations are greatly reduced, the ecosystem cannot be considered naturalized. In Grand Canyon new post-dam riparian vegetation has led to larger populations of native species and generally has been beneficial to wildlife as well as recreationists."

In Grand Canyon, the "new" habitat became so productive for wildlife, especially birds, small mammals, reptiles, and amphibians that the National Park Service (NPS) eventually recognized the new vegetation zone as a naturalized ecosystem that would never be returned to its natural state as long as Glen Canyon Dam controlled the river (Sharrow 1990). As such, the NPS recognized the new riparian habitat as a wildlife resource and made no efforts to remove or attempt to control *Tamarix* in the dam-influenced river corridor.

The *Tamarix*-dominated riparian zone in the Grand Canyon is an unusual situation compared to most areas that are invaded by the exotic plant. In general, conditions allowing colonization by and proliferation of *Tamarix* are varied. Contrary to popular opinion, *Tamarix* is a weak competitor compared with native riparian species in systems where the stream hydrograph is largely unaltered (Sher et al. 2000; Stromberg et al. 2007). Rarely does *Tamarix* have an opportunity to colonize when perennial stream systems are in their native state (hydroriparian ecosystems), except where portions of a stream are naturally intermittent (Johnson et al. 1984).

Sometimes even minor changes in groundwater levels, stream flow and extended periods of stream intermittency can tip the scales away from native species dominance to conditions that favor the nonnative plant (Stromberg et al. 2007). However, in highly altered rivers—like the Lower Colorado River, where dams, channelization, groundwater pumping, and other factors leave no semblance of a natural hydrograph—*Tamarix* reaches its highest density and is often found in monotypic stands (Anderson 2017; Ohmart et al. 1988). Normally, in moderately altered systems that still maintain natural seasonal periodicity—but where flood control structures preclude large floods—*Tamarix* is typically intermixed with native woody vegetation (Nagler et al. 2011).

The Invasion of Tamarisk Leaf Beetles in Grand Canyon

The first arrival of *Tamarix* beetles in Grand Canyon after their release in 2001 is unknown, but by 2009 they were commonly seen, and the effects of year-after-year defoliation, although unquantified until 2015, were becoming more evident. By 2015, the

Tamarix along the river corridor was dying in many areas, with the mortality increasing with each passing year (L.E. Stevens, personal communication to S.W. Carothers). To quantify the rate and levels of defoliation of *Tamarix*, Flesh and Stevens (unpublished data, see fig. 3) visually estimated the percent defoliation by randomly selecting 266 points in the 240 miles between Glen Canyon Dam and Diamond Creek. Where it occurred, defoliation on individual trees was conspicuously evident as the once luxuriant foliage was reduced to dead branches and twigs showing no living leaves over most of the plant. The results of the 2015 defoliation estimate showed varying rates of plant mortality depending on location within the 240-mile reach (fig. 3). Mortality reached very high levels in the Glen Canyon reach down to about river-mile 50 where 70 to 80 percent of *Tamarix* was dead or dying. Below river-mile 50 to river-mile 225 defoliation was less, but mostly ranging from 10 to 50 percent.

Below river-mile 225 to river-mile 280 high levels of defoliation were like those above Lees Ferry in Glen Canyon (S.W. Carothers 2005-2018, personal observations, and fig. 4). The relatively low levels of defoliation found sporadically on some beaches in the canyon represent areas where *Tamarix* density is either relatively low, or limited areas where the leaf beetle has not yet invaded. It is expected that within the next few years, all the *Tamarix* in Glen and Grand Canyon will be defoliated and either dead or dying and no longer a significant wildlife habitat resource. It is important to clarify that some once dense and widespread stands of *Tamarix* on upper terraces of Lake Mead sediments have been completely dead for the last decade or more as the lake has reached all-time low levels. The water table has dropped so rapidly that even fast-growing and drought-hardy *Tamarix* has not been able to survive.

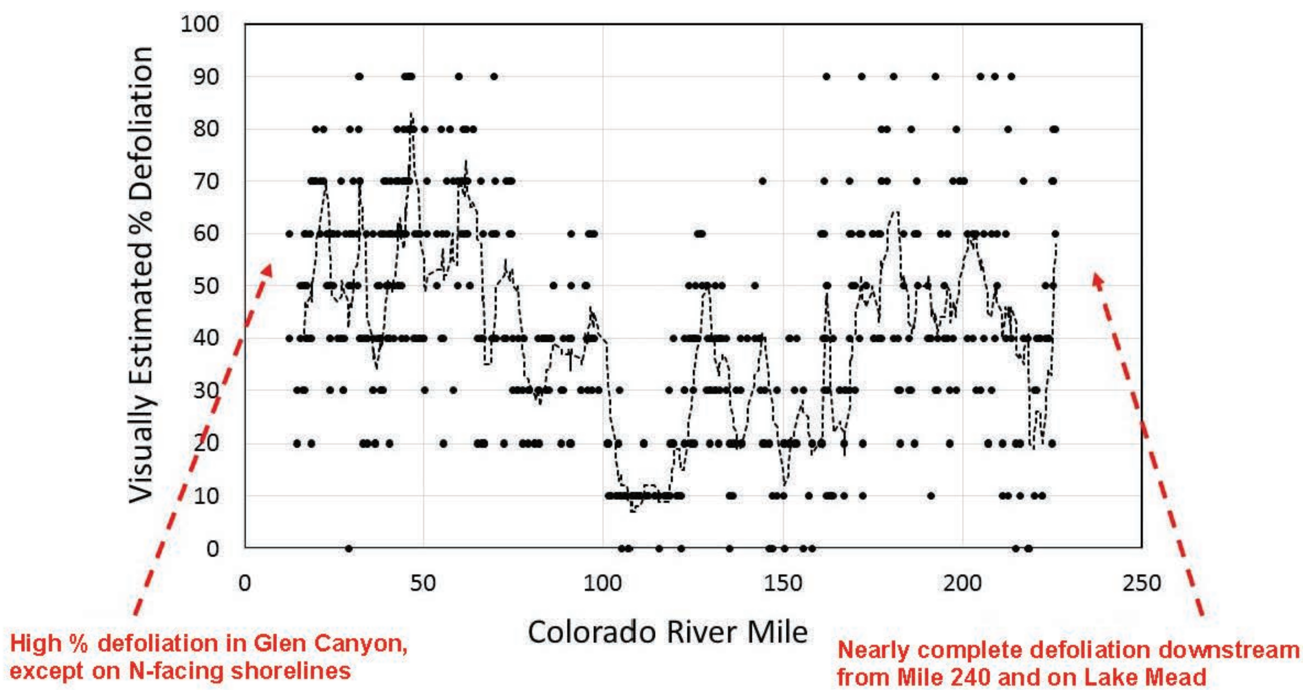

Figure 3—Percent defoliation of *Tamarix* by *Diorhabda* beetles along the Colorado River from below Glen Canyon Dam to the upper reaches of Lake Mead as determined by visual estimates in 2015. Defoliation was most extreme in the first 50-70 miles below the dam on south facing beaches in the upper river areas and high in the upper reaches of Lake Mead. Defoliation was less in the interior reaches of Grand Canyon. Data after Flesh and Stevens (unpublished manuscript 2015). Figure by Lawrence E. Stevens.

Figure 4—A comparison of the effects of tamarisk leaf beetle defoliation. Top photo 2005, before leaf beetle defoliation, photo by Steven W. Carothers. Bottom 2017, after defoliation, photo by Robb Irwin Eidemiller. Colorado River mile 7.5; Glen Canyon National Recreation Area, Arizona.

While it is too early to estimate the ground cover of the future in these canyon areas, OHWZ species are slowly moving downslope into the NHWZ and these species are expected to continue to increase in both size and area occupied (Holmes et al. 2005). In addition, the area occupied by and the structural robustness of the native shrub arrowweed, typically a NHWZ species, is steadily increasing in the shadow of declining *Tamarix*. Arrowweed is not generally recognized as nesting habitat for birds, but that may change as more of the moisture and soil nutrients previously consumed by *Tamarix* become available and arrowweed takes on a more robust growth form.

Tamarix Disruption of Mycorrhizal Fungal Communities of Cottonwood Trees

The iconic riparian gallery forest species of southwestern riparian habitats is the cottonwood tree. Though riparian ecologists often refer to the cottonwood-willow gallery forest community, the overriding foliage of the community is almost always provided by the cottonwood tree. It is the cottonwood tree, rather than the willow, that provides most canopy cover and root systems; and it is this species that accounts for unusually high wildlife productivity of the gallery forest (Johnson and Jones 1977). Willow trees require more water than cottonwoods and are usually found in a narrow band, one or two trees deep adjacent to the sides of a river or stream. Cottonwood trees can often be found throughout the entire floodplain where the water table is sufficient. In a recent estimate of the relative frequency of cottonwood versus willow trees within the gallery forest of the Upper San Pedro River, Carothers (2016) estimated that cottonwood trees contributed up to 90 percent of the riparian woodland, with willow only accounting for 5 to 10 percent. Thus, if cottonwood trees are disadvantaged or cannot recruit, the entire forest ecosystem is compromised. Cottonwood recruitment largely depends on natural river flow regimes (Stromberg 1993).

Recent studies have firmly established that healthy plant communities include a wide variety of interacting and interdependent species at many taxonomic levels, some of them cryptic and poorly understood (Corenblit et al. 2014; Franklin et al. 2016). Mycorrhizae and fungal endophytes, as well as a host of microbes, appear to be important participants in healthy plant communities. The contribution of mycorrhizal and other soil fungi to establishment, growth, and survival of cottonwood and other trees is becoming somewhat better understood as a result of recent and current research.

Conventional mycorrhizal fungi include the arbuscular endomycorrhizal (AM) fungi, which have been found in upward of 80 percent of terrestrial plant species, and ectomycorrhizal fungi (EM), which are found in about 2 percent of species (Smith and Read 2010). Cottonwood trees apparently have both, with probably many other associated microbes and fungi. The relationship is mutualistic. In this symbiotic relationship, fungi gain energy and carbon from tree photosynthesis while providing the tree with enhanced nutrient and water gathering capabilities from soil (Buckling et al. 2012). The trees depend on fungi for growth (Ghering et al. 2006; Meinhardt and Ghering 2012, 2013). Other biotic components of the rhizosphere and rhizoplane are only beginning to be understood, and knowledge of their roles in establishment and growth of native riparian plants is very limited. A few endophytic components are beginning to be understood (Lau et al. 2013), as are the complex interactions between species and individuals in establishment and maintenance of riparian communities (Corenblit et al. 2014).

Studies on the influence of *Tamarix* on beneficial mycorrhizal fungal communities of native cottonwood trees reveal one of the more insidious capabilities that this invasive tree/shrub employs to gain a competitive advantage over native riparian woody species. For example, when cottonwood trees are found in close association with *Tamarix*, the mycorrhizal relationship is disrupted by the invasive species' ability to alter soil chemistry by concentrating chemical compounds like salts, nitrogen, and phosphorus in leaf litter (Hultine et al. 2015; Meinhardt and Ghering 2012, 2013). Researchers have demonstrated that cottonwood trees growing in association with even low-density of *Tamarix* have two-fold reduced mycorrhizal colonization compared to native trees that do not have the invasive tree/shrub as a neighbor (Meinhardt and Ghering 2012). The impact of *Tamarix* on the other gallery forest species is not as well studied, but both willow (Beauchamp et al. 2006) and mesquite (Titus et al. 2003) are known to benefit from mycorrhizae and both are likely negatively impacted when in association with *Tamarix*.

Whereas studies on complex mycorrhizal interactions within the soil and roots of cottonwood trees in association with *Tamarix* are still in their infancy, it appears that the long-term survival of the mixed native/nonnative *Tamarix*-dominated riparian habitat was uncertain even before the *Tamarix* leaf-eating beetle was released. As Hultine et al. (2015) emphasized, the combination of climate change and the ability of *Tamarix* to disrupt the integrity of mycorrhizal relationships in the native gallery forest foundation species is a harbinger of long-term deterioration of native riparian habitats when growing in the presence of *Tamarix*. Thus, as the *Tamarix* declines because of the biocontrol efforts, the possibility of long-term native species recolonization of suitable habitat may eventually be enhanced.

However, the length of time and suite of conditions needed to remove or sufficiently attenuate the disruptive effects of *Tamarix* on mutualistic rhizosphere and rhizoplane species are not well studied. Therefore, the potential for reasonably complete restoration of native riparian communities is still largely unknown. Wildlife ecologists in the past several decades have promoted the benefits of the *Tamarix*-dominated riparian habitats, measured as increases in range and density of many vertebrate and invertebrate species. While we promoted the wildlife benefits, the *Tamarix* has apparently been altering the soil around and below the remaining native plant species. Hultine et al. (2015) suggest that the combination of mycorrhizal disruption by *Tamarix* and the vagaries of climate change constitute threats to riparian habitats that we had not previously anticipated.

These recent findings have clear implications on the future restoration and survival of the cottonwood forest type that is already considered one of the most threatened vegetation communities in the United States (Stromberg 1993; Webb et al. 2007). Dixon et al. (2009) reviewed the most up-to-date model predictions on climate change and found that the drier, hotter southwestern climate of the future would result in decreases in cottonwood-willow forests within the Upper San Pedro River by two-thirds. The additional mycorrhizal impacts to the gallery forest ecosystem when *Tamarix* is present are yet another threat to the declining riparian habitat throughout the southwestern United States.

Conclusions

The human life span is short, and the attention span of researchers is even shorter compared to the time needed for ecological change. The reign of *Tamarix* spp. as a dominant or co-dominating invasive species in western riparian areas has also been short. Longer-term consequences of this invasion are unknown. Along some rivers, especially those with drastically altered flow regimes, *Tamarix* has created a unique ecosystem that has been exploited by many wildlife species, including some that have lost habitat in the period since human activities started to have a significant impact on the earth's geology and ecosystems (the Anthropocene, see Kingsley, this volume). Currently (2019) we are witnessing major changes in the *Tamarix*-dominated ecosystem because of the very successful biocontrol effort. We have documented potential riparian wildlife impacts associated with the removal of *Tamarix* and cited studies documenting that the *Tamarix*-dominated native/nonnative riparian community can support more avian species than native species-dominated habitats of cottonwood-willow, mesquite, and mixed deciduous woodlands. It is now apparent that the biocontrol program was pursued with the removal or disadvantaging of *Tamarix* as a major goal without a clear understanding of revegetation dynamics post-biocontrol.

It appears so far that in the absence of active restoration efforts, recolonization of the post-biocontrol *Tamarix*-dominated habitat is almost exclusively limited to a mixture of native and nonnative grasses and often weedy, herbaceous cover with the conspicuous absence of woody species. Thus, at least in the short term, the biocontrol effort has resulted in the loss of important wildlife-producing habitat without replacement. In most areas where *Tamarix* has proliferated, both human-caused alteration of natural flow regimes and *Tamarix*-caused alteration of soils are complicating or prohibiting the establishment of native riparian woody plants.

In the specific case of the Grand Canyon, an unprecedented naturalized riparian community became established after construction of upstream Glen Canyon Dam. The ultimate disposition of that community is largely unknown at present; however, short- and long-term changes in riparian vegetation along the river corridor are the subject of regular inventory and monitoring (Palmquist et al. 2018) and we are assured that the answer to what comes after *Tamarix* will eventually be known.

What we do know now however, is that the *Tamarix*-dominated riparian community developed since Glen Canyon Dam became operational is now dramatically changing. It is possible, in time, that the OHWZ species (principally the mesquite and acacia) will continue to move downslope, as they have done for decades, and eventually replace *Tamarix* as it is reduced or eliminated. With the native OHWZ mesquites and acacias available to continue moving into the NHWZ, the Colorado River corridor in Glen and Grand Canyons may eventually be composed of mostly native species. They may provide an example, albeit rare so far, of the biocontrol effort realizing the potential that was originally anticipated by APHIS. At present, however, the decline of the *Tamarix* in Glen and Grand Canyons represents a loss of this unique naturalized habitat. Hence, we create a requiem to that declining community and the suite of wildlife species that were a part of it. Future research will document the development and replacement of an evolving community of vegetation and wildlife and hopefully the riparian habitat of the river corridor of the future is likely to be more dominated by native riparian vegetation species than it has been since Glen Canyon Dam altered the hydrograph.

Thus, as we contemplate an answer to the question, "What have we lost and what have we gained as a result of the biocontrol?" – or, simply put – "Is *Diorhabda*-induced biocontrol an ecological disaster, or will it eventually lead to a more robust native riparian community?" – at this time we do not find a clear answer.

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