

Chapter 5. Unintended Consequences: Tamarisk Control and Increasing Threats to the Southwestern Willow Flycatcher

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Introduction

It is well known that nonnative tamarisk (*Tamarix parviflora*, *T. ramosissima*, *T. chinensis*, and their hybrids; a.k.a. saltcedar) has replaced native riparian woodland vegetation along many streams in the arid Southwest over the last 100 years. Tamarisk can form extensive, dense monocultures and may alter not only the physical structure of the riparian woodland but also soil salinity and fire frequency (Sher 2013). There is significant debate, however, over whether tamarisk is the driver or a passenger of ecological change (Johnson 2013). The decline in the numbers and range of native riparian wildlife has been concurrent with the spread of tamarisk, and numerous studies show that tamarisk-dominated stands may support a lower density and/or diversity of wildlife than do native habitats (Bateman and Ostojka 2012; Sogge et al. 2008; Strudley and Dalin 2013). Consequently, tamarisk is often portrayed as the primary cause for declines in riparian wildlife (e.g., DeLoach et al. 2003a). Although it is now recognized that water use by native vegetation compared to tamarisk depends on site conditions (Zavaleta 2013), tamarisk was also widely blamed for water consumption in excess of native species (Nagler and Glenn 2013). Tamarisk control efforts, many of which were driven by the desire to make more water available for human use, began in the 1940s (Douglass et al. 2013) and continue to the present day, with improvement of wildlife habitat often cited as a goal of tamarisk removal.

Many wildlife species successfully inhabit tamarisk, however, and evidence mounted in the 1980s and 1990s that tamarisk provides important habitat, particularly for birds, in many southwestern riparian systems (see review in Sogge et al. 2008), especially if a small component of native vegetation remains (van Riper et al. 2008). Perhaps the best known, and most controversial, avian occupant of tamarisk habitats is the southwestern willow flycatcher (*Empidonax traillii extimus*; hereafter flycatcher), a riparian obligate songbird that was listed as endangered in 1995 by the U.S. Fish and Wildlife Service. In recent decades, an effective biological control for reducing the vigor and reproductive success of tamarisk was found, and biological control agents were released beginning in 2001. As a result of this biocontrol effort, there have been unintended consequences to the flycatcher and other riparian wildlife. This paper addresses the history of the biocontrol effort and the failure of the scientific community and regulatory agencies to accurately predict the impact of biocontrol releases.

The Search for Biocontrol for Tamarisk

Tamarisk is difficult to control by mechanical means, as it resprouts vigorously following cutting or fire. Heavy equipment can be used to remove entire plants, but this is expensive, causes extensive soil disruption, and is often impractical in riparian areas that are difficult to access. There are several herbicides that are widely used for tamarisk control; however, aerial applications are non-selective, and cut stump treatments, while very effective, are labor intensive (DiTomaso et al. 2013). Given the difficulty and expense of mechanical and chemical control methods, biological control, which would involve using a natural predator, parasite, or pathogen to suppress the tamarisk population, seemed like an attractive alternative. Tamarisk was an ideal candidate for biocontrol; the Tamaricaceae family has no species that are native to North America, and the prospects were therefore good of finding a biocontrol agent that would act selectively on tamarisk and leave other species untouched. Successful biocontrol was expected to reduce the use of conventional pesticides and provide cost effective, self-sustaining, target-specific suppression for tamarisk (USDA Animal and Plant Health Inspection Service 2015a).

The search for biological control for tamarisk began in the late 1960s, led by personnel at the U.S. Department of Agriculture's Agricultural Research Service (USDA ARS). Researchers gathered information on tamarisk and the insects that feed on it throughout its native range to identify potential biocontrol agents—insects that feed selectively on tamarisk and are capable of reducing the population of the host plant (DeLoach et al. 2003a). In 1989, Jack DeLoach of the USDA ARS and colleagues submitted a petition to the Technical Advisory Group for Introduction of Biological Control Agents of Weeds (TAG), a committee of the USDA Animal and Plant Health Inspection Service (APHIS) that is tasked with “providing guidance to researchers and recommendations to regulating agencies for or against the release of nonindigenous biological control agents” (USDA Animal and Plant Health Inspection Service 2015b), asking the TAG's advice on whether proceeding with a biological control program on tamarisk was in the best national interest (DeLoach et al. 2003b). The TAG recommended that the program could proceed, and the search for suitable biocontrol agents continued, with the assistance of several overseas cooperators.

The tamarisk leaf beetle (*Diorhabda* spp.) was identified as one of the promising candidates for biocontrol. It was known to occur in high densities and completely defoliate large areas of tamarisk, and beetles were considered a pest in China in areas where tamarisk was planted for sand dune control (DeLoach 1994). The beetle was brought back to the United States where it underwent extensive host-specificity testing starting in 1992. Tests conducted in 1992 and 1993 showed that beetle larvae developed readily on *Tamarix* hosts and would feed but rarely developed into adults on shrubs in the *Frankenia* (seaheath) genus, the only plants native to the Western Hemisphere that are in the same order as *Tamarix* (Lewis et al. 2003a). Larvae failed to develop on all other host species that were tested (DeLoach 1994).

ARS submitted a petition to the TAG requesting approval for the field release of beetles in Texas and Wyoming in May 1994 (DeLoach 1994). Of the 16 TAG members who responded, nine recommended release with no reservations, six recommended release but had reservations, and one did not recommend release. The most common

concern was the possibility that beetles could feed on *Frankenia*, some species of which were rare. Other concerns were the impact beetles could have on athel (*T. aphylla*, a tree form of tamarisk that is far less invasive than the other *Tamarix* species), which was used as a shade tree in the southwestern United States and Mexico; whether native vegetation would replace tamarisk following biocontrol; and whether there was a means to control *Diorhabda*, if needed. A letter from Jack DeLoach to APHIS on December 22, 1994, clarified that larvae that developed into adults on *Frankenia* were unable to reproduce; this was later confirmed by further host testing (Lewis et al. 2003a). The letter cited the relative rarity of athel among ornamental shade trees as evidence of the limited potential effects to athel.¹ DeLoach conceded in his letter that “Replacement by native vegetation after control ... is circumstantial and not well supported. It is based mostly on biocontrol of other weed species, where native vegetation, desirable range plants, etc., came back strongly after the weed was controlled.” As far as beetle control was concerned, DeLoach cited information from China that local beetle populations could be controlled with insecticides. The letter was sufficient to relieve the concerns of the TAG members, and the TAG chairman recommended to APHIS on June 1, 1995, that *Diorhabda* be approved for release into North America.

Tamarisk leaf beetles feed on the foliage of tamarisk as adults and in each of three larval stages. Beetles overwinter in the leaf litter as adults and emerge in the spring in response to warming temperatures. They aggregate on tamarisk plants to feed, mate, and lay eggs. After progressing through the larval stages, beetles descend to the leaf litter to pupate. The entire life cycle takes 30 to 40 days (Lewis et al. 2003b), and beetles typically go through multiple generations during a growing season. When adult beetles emerge from the leaf litter, they either become reproductively active or are triggered to go into diapause, an overwintering state of suppressed development, by shortening of the photoperiod in late summer (Bean et al. 2007a; Lewis et al. 2003b). If local food resources have been depleted by the previous generation of beetles, adults will disperse, sometimes in large flights, in search of green foliage. Adults that are destined for diapause feed and then descend into the leaf litter instead of becoming reproductively active (Bean et al. 2013).

Tamarisk leaf beetles are sensitive to chemicals released by tamarisk and also to chemicals released by other *Diorhabda* individuals (Bean et al. 2013). This sensitivity allows beetles to occur in large aggregations that can exceed 1,000 beetles per plant (Bean et al. 2013; Jashenko n.d.), resulting in rapid and complete defoliation. The defoliation period can last for several weeks, but the tamarisk then typically puts on new leaves. An individual plant can be defoliated multiple times within a growing season. The response of tamarisk to multiple defoliation events is variable and is likely influenced by numerous factors, including age of the plant, access by the plant to resources such as water, seasonal timing of defoliation, and plant genetics (Bean et al. 2013). A single defoliation event can result in mortality, but more typically several defoliation events are required, if the plant is killed at all. When plants do re-leaf, they often exhibit reduced vigor, with dieback of terminal branches, reduced foliage volume, and

¹ Further research suggested that beetles would not affect athel as strongly as they affected other *Tamarix* species, although the researchers conceded the possibility of “transient but substantial damage” to athel (Moran et al. 2009). Damage to athel in northern Mexico was described as “conspicuous” (Estrada-Muñoz and Sánchez-Peña 2014), and treating individual athel trees with insecticide was recommended for beetle control (Muegge 2010).

reduced flowering. The response of other vegetation to tamarisk dieback and mortality is also variable and is influenced by soil condition, hydrological regime, and local seed sources.

Conflict With the Southwestern Willow Flycatcher

By the time beetles had been recommended for release by the TAG, another concern had surfaced. The southwestern willow flycatcher was listed as endangered on February 27, 1995 (60 FR 10694-10715). The flycatcher breeds in Arizona, New Mexico, southern California, southern Nevada, southern Utah, and western Texas, placing its nests in dense, wet thickets of trees and shrubs approximately 4–7 m or more in height. The southwestern willow flycatcher was historically a common species in riparian areas throughout its range, but flycatcher numbers dwindled as southwestern wetlands and riparian habitats, particularly those vegetated by cottonwood and willow, suffered large-scale losses during the 1900s as the result of dams, diversions, livestock grazing, increase in agriculture, urbanization, and wood cutting. By the time the flycatcher was listed, the range-wide population was estimated at around 500 pairs (60 FR 10694-10715). The decline in flycatcher populations coincided with the spread of tamarisk, which proliferated with the modifications in the natural hydrograph caused by dams and diversions. Tamarisk was regarded by some researchers as providing poor habitat in comparison to native vegetation for various bird species because of reduced structural diversity, changes in the arthropod community (Carothers and Brown 1991), and a hotter microclimate (Hunter et al. 1987). At the time of listing, flycatchers were known to nest in thickets dominated by tamarisk, but it was unclear whether the long-term reproductive success of flycatchers nesting in native vegetation differed from the success of those nesting in tamarisk.

Because of the potential effect of beetle-caused defoliation on flycatchers, consultation with the U.S. Fish and Wildlife Service (USFWS) was required prior to release of the beetles. ARS and APHIS submitted a draft Biological Assessment (BA) to the USFWS in October 1997 (DeLoach and Tracy 1997). The action proposed in the draft BA was to release both the leaf beetle and a mealybug, *Trabutina mannipara*, at sites across seven States. All proposed release sites were at least 100 miles from areas where flycatchers were known to nest in tamarisk. The BA considered direct and indirect effects of biological control agents on flycatchers not only at the release sites themselves but also across the region, after the control agents had resulted in an estimated 75–85 percent reduction in the density and cover of tamarisk.

The analysis of effects in the BA rested on several assumptions: (1) biocontrol agents would not spread more than 2–4 miles each year; (2) the decrease in the density of tamarisk would be gradual and would be accompanied by a “consequent and concurrent increase in the native plant community”; (3) biocontrol agents would provide food for flycatchers; and (4) tamarisk is “only partially suitable as habitat for flycatchers” and was “a major factor in [the flycatcher’s] extirpation from . . . the lower Colorado and the lower Gila rivers.” In particular, the BA proposed that tamarisk provides unsuitable habitat for flycatchers at lower elevations because tamarisk stands are “intrinsically hotter” than cottonwood/willow vegetation, resulting in the exposure of flycatchers to temperatures that are lethal for eggs and nestlings. It then followed that, if biocontrol

resulted in the replacement of tamarisk with native vegetation, the suitability of formerly tamarisk-dominated areas for nesting flycatchers would increase. The BA concluded that biological control of tamarisk “is not likely to adversely affect the southwestern willow flycatcher.”

The authors of the BA overlooked a few key factors about the effects of the beetles on tamarisk. Although mortality of tamarisk might be gradual, defoliation by tamarisk leaf beetles was known to be sudden and complete. If, as the project proponents maintained, exposure of flycatcher nests to lethal temperatures was a cause of extirpation of flycatchers from some areas, surely the removal of shade during the height of flycatcher breeding season should have been a concern.

In addition, there was no evidence, at the time the BA was written, that native vegetation would return to areas where tamarisk had been controlled. The BA did not completely address the role that changes in hydrology (e.g., the construction of Hoover Dam) likely played both in the invasion of tamarisk and in the reduction of habitat suitability for willow flycatchers via stream channelization and the reduction in spring floods that create the dense thickets of young vegetation preferred by flycatchers.

Despite assurances by beetle proponents, some scientists gave unequivocal warnings against beetle releases (see Appendix IV in DeLoach and Tracy 1997). In response to concerns voiced within and outside of the USFWS and APHIS, a meeting was called in June 1998 with the USFWS, ARS, and other Federal agencies to discuss the BA.

As a result of these concerns, ARS and APHIS submitted a revised research proposal to the USFWS in August 1998 (DeLoach and Gould 1998). This proposal requested the release of tamarisk beetles and mealybugs at 13 sites in seven western States, with one of the criteria for site selection being a distance of at least 200 miles from areas where flycatchers nest in tamarisk. The proposal specified two phases—research and implementation—of the biocontrol program. The research phase included both cage and field releases and was intended in part to evaluate whether remedial actions, such as manual revegetation, would be needed prior to the arrival of beetles in areas occupied by flycatchers. The proposal stated that biocontrol agents would be contained within the defined release sites; some of these release sites, however, encompassed over 100 miles of river. The implementation phase would entail release of biocontrol agents at additional sites, with the goal of widespread control of tamarisk, but would still exclude releases in areas where flycatchers nest in tamarisk.

The proposal acknowledged, however, that the control insects would eventually disperse to areas occupied by flycatchers, though this was projected to take 10 to 20 years. This estimate of dispersal speed (200 miles in as little as 10 years, or an average of 20 miles in a year) was quite different from the 2–4 miles per year stated in the 1997 BA, but there was no direct acknowledgment in the proposal that the dispersal estimate had changed, and subsequent analysis by the USFWS did not consider this faster dispersal rate. The proposal expressly stated, “Unprecedented safeguards and precautions are herein proposed to insure that biological control does not adversely affect the [flycatcher], especially through the process of reducing its potential breeding habitat (which presently includes saltcedar) before the recovery of its native habitat (willows, cottonwoods and other native trees and shrubs) can occur.”

The proposal refers to the BA for these safeguards and precautions, and the BA contains only the very general statement that in the “very improbable” event that beetles

needed to be controlled, "...the areas of the most dense and most damaging control agents populations will be treated by ground or aerial applications of appropriate insecticides at sub-lethal or borderline lethal rates in order to slow the reproduction and spread, but without exterminating all control agents at the release site." There was no consideration of the possibility that by the time it would become obvious that control was progressing too rapidly, the beetles would occupy too large an area for insecticide to be a reasonable solution.

The Flycatcher Recovery Team reviewed the revised research proposal and submitted a letter to the Southwest Regional Director of the USFWS, expressing its concerns that tamarisk might not be replaced by native vegetation with equal function with respect to the needs of the flycatcher, particularly in areas with site conditions such as altered flooding regimes, high salinity, and grazing. There was also concern that the biocontrol agents might escape the proposed release areas, either by natural dispersal or by transport by humans (USFWS 2014).

Despite the concerns of the Flycatcher Recovery Team and the presence of flycatchers nesting in tamarisk along the Rio Grande (USFWS 2002), the USFWS issued concurrence on December 28, 1998, that the proposed releases at all 13 sites would not adversely affect the flycatcher. It cited safeguards such as the 200-mile distance from areas where flycatchers nested in tamarisk. The concurrence was rescinded the following April, based on "new information" regarding flycatchers nesting in tamarisk along the Rio Grande. An amended concurrence was issued on June 3, 1999, following a meeting between USFWS and USDA personnel and agreement from the project proponents that all sites along the Rio Grande would be removed from consideration.

The concurrence required a separate consultation before the implementation phase of the project could be started, and it also required separate consultation for the addition of any new sites. Despite the prediction in the project proposal that beetles could spread as much as 20 miles per year, the concurrence cited "convincing argument[s]" presented by USDA personnel at the meeting that the geographic isolation of the remaining release sites would prevent the control agents from reaching areas where flycatchers nested in tamarisk, given that "research ... indicates [the control agents] should move on the order of tens of feet per year."

A final draft Environmental Assessment (EA) on the biological control of tamarisk was released by APHIS in July 1999. The EA addressed the release only of the tamarisk leaf beetle, *Diorhabda elongata* Brulle, and did not include the mealybug. The proposed action included the release of beetles at 10 sites, all of which were at least 185 miles from flycatcher nesting areas, and stated that the spread of beetles would be slowed through chemical or mechanical means if the beetles appeared to "consume saltcedar too rapidly." The EA did not predict a rate of spread for these particular beetles but implied that the rate would be slow, given that other chrysomelid beetles "appeared to spread relatively slowly at a maximum of several tens of meters per year," and stated that invasion of flycatcher nesting areas by beetles and the death of tamarisk faster than native plants could regenerate was "highly improbable." A Finding of No Significant Impact (FONSI) was signed on July 7, 1999, and APHIS immediately began issuing permits for the establishment of field cages.

Beetle Releases

Northern Beetles

Field cages were established as soon as permits were obtained, but because permits were not issued until mid-July, research at the field cages during 1999 was largely limited to one generation of beetles. Despite having data only from a single generation of beetles in a single year, a report issued later that year (Gould 1999) concluded that “the data ... indicate that *D. elongata* will require at least several years to reduce even local saltcedar stands to a significant degree.” A second summer of cage studies was completed in 2000, and beetle populations at several of the sites increased to very high numbers, resulting in the consumption of all foliage in the cages and causing complete mortality of some large plants (DeLoach et al. 2003b).

In the spring of 2001, APHIS issued permits for the open release of beetles, and beetles were released in May at sites in Texas, Colorado, Wyoming, Utah, Nevada, and California. Little defoliation was seen during the summer of 2001, but the summer of 2002 produced “spectacular defoliation” at some sites (DeLoach et al. 2003b). By September of 2002, beetles had dispersed no farther than approximately 100 m from the release points.

The beetles that were released into cages in 1999 and then into the field in 2001 all originated either from Fukang, China, or Chilik, Kazakhstan (classified at the time as *Diorhabda elongata deserticola* and later reclassified as *D. carinulata*, the northern tamarisk beetle; Tracy and Robbins 2009). The cage and field tests revealed that beetles originating from these northerly latitudes did not overwinter successfully at southerly latitudes (DeLoach et al. 2003b). Laboratory experiments and field observations on the northern tamarisk beetle showed that this ecotype entered diapause at a day length of ≈ 14 h 39 minutes; south of $36^{\circ} 20'$ N (approximately 50 miles south of the northern borders of Arizona and New Mexico), the longest day is shorter than this critical day length. Researchers therefore concluded that this northern ecotype was unlikely to succeed as a biocontrol agent south of 38° N (approximately 70 miles north of the northern borders of Arizona and New Mexico) because premature diapause would increase mortality (Bean et al. 2007b).

Other Beetle Species

Beetle proponents began testing other ecotypes, which were also later reclassified as separate species, originating from Uzbekistan (*D. carinata*, the larger tamarisk beetle), Crete (*D. elongata*, the Mediterranean tamarisk beetle), and Tunisia (*D. sublineata*, the subtropical tamarisk beetle) (Tracy and Robbins 2009) for control of tamarisk at latitudes below 38° N. By the end of the summer of 2002, all four beetle species had been tested in cages, and a request was submitted on February 14, 2003, to the USFWS for the release of beetles of all four subspecies at the 10 existing sites as well as 20 new sites, many of which were in Texas and New Mexico and included sites on the Rio Grande where flycatchers were known to breed (DeLoach et al. 2003b). Beetle releases at these flycatcher sites were requested as a demonstration that beetles would have no adverse effects on flycatchers that nested in areas with abundant willows.

Subsequent discussion between ARS and the USFWS resulted in all sites along the Rio Grande that were within 200 miles of occupied flycatcher habitat being removed from consideration, and the USFWS issued a letter on June 13, 2003, concurring that release of beetles at the additional sites “may affect, but is not likely to affect” the flycatcher. This determination relied on distance and geographic barriers (i.e., expanses without tamarisk) to be “effective as a means of keeping the control agents from sites on the Lower Colorado River in Arizona and the Rio Grande in New Mexico where flycatchers are nesting in saltcedar.” Concurrence was also given by the USFWS on July 23, 2003, for the release of multiple species of beetle near Kingsville, Texas, and at several sites along the Pecos River. Concurrence for release at sites in western Texas followed on September 1, 2004. Between 2003 and 2009, beetles of all four species were released at about 70 sites in Texas, and the larger, subtropical, and Mediterranean species became established at various sites (DeLoach et al. 2011). Beetles were first released on the Rio Grande in Texas in 2007, and subtropical beetles became established at multiple sites along the Rio Grande in 2009.

Implementation Phase of Biocontrol Program

While additional release sites were being approved by the USFWS, USDA personnel were also working toward the implementation phase of the biocontrol program. The implementation phase considered only the northern tamarisk beetle, *D. carinulata*. Under the implementation phase, beetles would be established at “nursery” sites in up to 13 western and midwestern States, north of 38° N latitude. Beetles would then be available for distribution anywhere in those States. Utah was excluded from the plan since beetles had already been distributed there.

A BA for the implementation phase was released in March 2005 and an EA followed in June. The effects analysis in both documents determined that there would be no effect to flycatchers, and this determination relied on critical day length for *D. carinulata* precluding beetles from establishing populations in areas south of 38° N. The EA did concede that beetles from the northern ecotype could eventually adapt to conditions below 38° but stated that this adaptation would not be rapid because beetles were documented to disperse only 1.5 miles in 3 years. Later in the same document, however, dispersal was noted as being over an order or magnitude larger than this, 50 miles in 4 years.

In the concurrence letter, the USFWS indicated that APHIS provided additional information and clarification to the USFWS before the concurrence was issued. The USFWS concluded that *D. carinulata* is “capable of occurring between 36 and 38 degrees north latitude in substantial numbers at some locations” and also acknowledged that the beetles “are expected to eventually adapt to diapause at lower latitudes” but still maintained that beetles were expected to have “little success in reducing saltcedar stands in areas at or south of 38° north latitude.” The concurrence letter also recognized that suppression of tamarisk without active management to restore native vegetation might result in riparian habitat of degraded quality, thereby reducing habitat quality for flycatchers. Despite these apparent misgivings, the USFWS concurred on July 11, 2005, that the proposed action was not likely to adversely affect the flycatcher, and the FONSI, which predated the concurrence, was issued for the EA in June 2005.

Beetles Spread Into Flycatcher Habitat

Virgin, Muddy, and Lower Colorado Rivers

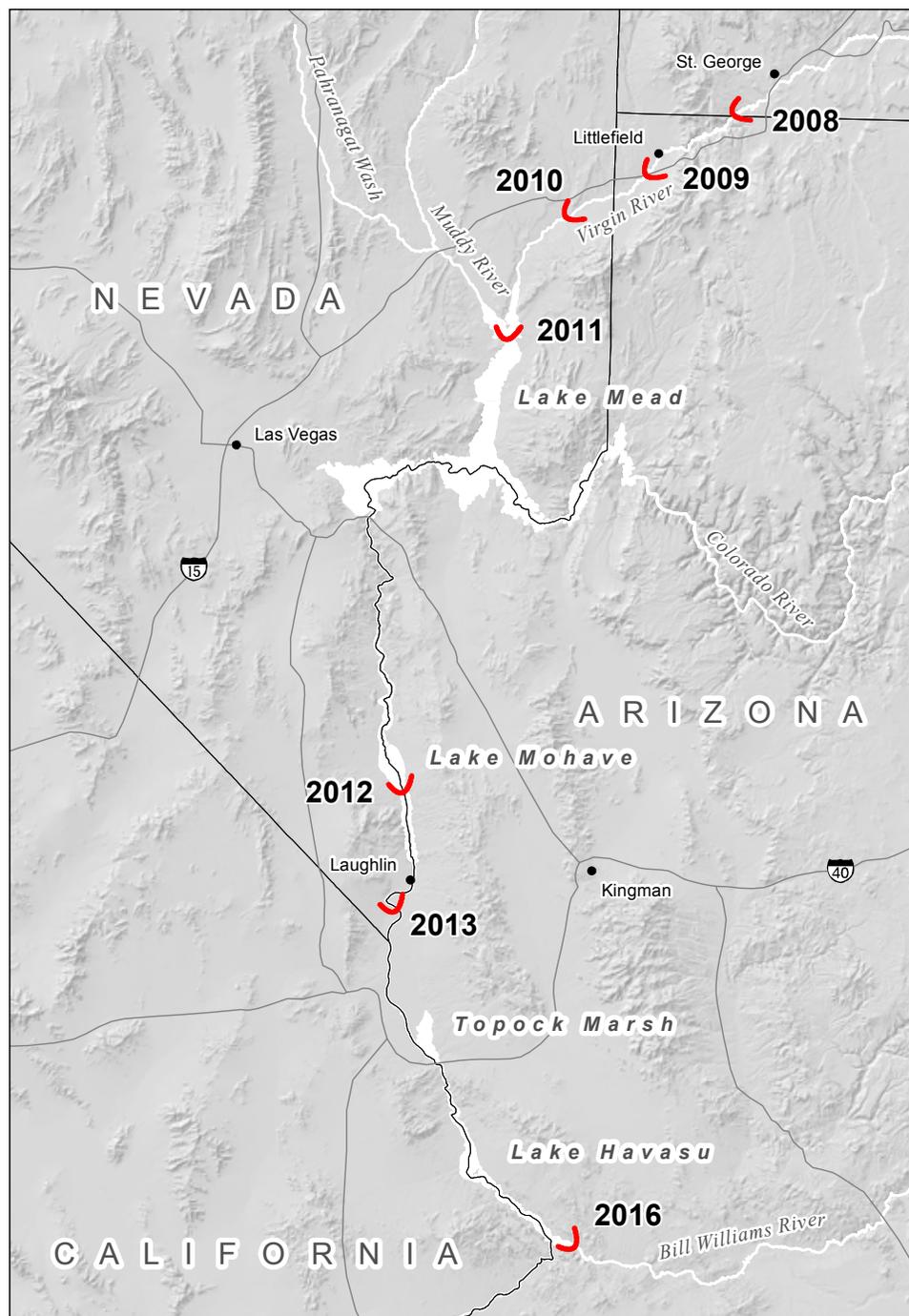
The 2005 EA for the implementation phase of the beetle program acknowledged that the eventual outcome of the no action alternative and the proposed action alternative were the same; the only difference was the rapidity with which beetles would spread. As was soon to be demonstrated, however, beetles are capable of rapid spread even without human assistance. In 2004, beetles were released along the Colorado River near Moab, Utah. This release was not done under the USDA program but rather by the Grand County weed management department, which had collected beetles (*D. carinulata*, from the Chilik, Kazakhstan strain) from Delta, Utah, one of the original 10 test sites, and re-distributed them near Moab. The first major defoliation along the Colorado River was recorded in 2006 and encompassed around 990 acres over approximately 20 miles of river. By the end of the following year, around 10,000 acres were defoliated over approximately 70 miles of the Colorado River, and beetles had spread into the Green and Dolores Rivers (Tamarisk Coalition, n.d.). In subsequent years, these beetles continued to spread in the upper Colorado River Basin.

In 2006, another *D. carinulata* release occurred, this time by the city of St. George, Utah. St. George lies along the Virgin River just above 37° N latitude and has a small population of nesting flycatchers. Although beetle researchers had claimed that *D. carinulata* was unlikely to do well below 38° N, widespread defoliation around St. George occurred beginning in August 2008 (Dobbs et al. 2012). As the beetles progressed southward, it became abundantly clear that the assumption that northern beetles would not succeed as a biocontrol agent below 38° N was wrong. Further experiments in 2007 and 2008 on *D. carinulata* showed that critical day length had decreased over the previous 5 years, with the magnitude of the decrease being inversely proportional to latitude (Bean et al. 2012).

The area around St. George was again defoliated in 2009, this time beginning in June, and by the end of that summer, complete defoliation had spread over 25 miles downstream of St. George, to a point between Littlefield, Arizona, and Mesquite, Nevada. Beetles continued to spread downstream on the Virgin River, traveling another 20 miles and encompassing another flycatcher breeding site in 2010, reaching the Gold Butte area by the end of the summer, and extending another 20 miles to reach a third flycatcher breeding site and encompass the entire lower Virgin River to the Overton Arm of Lake Mead (approximately 36.4° N) by the end of 2011. By the end of 2012, beetles occurred all along the Muddy River, including at another flycatcher site, and had reached the lower end of Lake Mohave. By the end of 2013 they were at Big Bend State Park, south of Laughlin, Nevada, at 35.1° N, having dispersed a straight-line distance of 150 miles in the 7 years since their release in St. George (fig. 15). This was an average dispersal distance of slightly over 20 miles per year, exactly what had been stated in the 1998 project proposal as the maximum likely dispersal rate.

Over the next 2 years, beetles spread very little south of Big Bend State Park. In July 2015, extensive defoliation was apparent at Big Bend State Park (M.A. McLeod, Biologist, SWCA Environmental Consultants, personal observation, Big Bend State Park, July 23, 2015), and a few individual beetles but no defoliation were observed

Figure 15—Spread of tamarisk beetles along the Virgin and Lower Colorado Rivers in 2008 to 2016 (map by Glenn Dunno, SWCA Environmental Consultants).



approximately 5 miles south of Big Bend (Tom Dudley, University of California Santa Barbara, personal communication, August 7, 2015). Some people speculated that the northern beetles had finally reached the latitude where southerly dispersal would be limited by critical day length. However, by July 2016, beetles and defoliation were apparent at Topock Marsh, on both sides of Lake Havasu, and at the mouth of the Bill Williams River, over 60 miles from Big Bend and within a quarter mile of nesting fly-catchers along the Bill Williams River (M.A. McLeod, Biologist, SWCA Environmental Consultants, personal observation, Lower Colorado River, July 21 and 22, 2016).

Rio Grande

While *D. carinulata* were spreading along the Virgin River and downstream along the Lower Colorado River, they were also spreading elsewhere. By the end of 2014, *D. carinulata* were found throughout much of the upper Colorado River Basin, including the San Juan River, as well as through Grand Canyon and the Little Colorado River as far east as Holbrook, Arizona. *D. carinulata* were also defoliating tamarisk along the Rio Grande around Albuquerque and as far south as Socorro, New Mexico, near 34° N (Tamarisk Coalition 2014). By the end of 2015, northern beetles had moved southward on the Rio Grande almost to Elephant Butte Reservoir. Subtropical beetles expanded northward along the Rio Grande from Texas at the same time as the northern beetles advanced southward. Subtropical beetles were found north of Las Cruces at Rincon, New Mexico, by fall of 2014; in August of 2015 beetles and defoliation were noted at Caballo Reservoir, about 30 miles south of Elephant Butte (James Tracy, Texas A&M University, College Station, Texas, personal communication, August 6, 2015).

Beetles, presumed to be of the subtropical species but awaiting species verification at the time of this writing, arrived at Elephant Butte during the summer of 2016 and began defoliating tamarisk close to areas with large numbers of flycatchers nesting in tamarisk (Dave Moore, U.S. Department of the Interior, Bureau of Reclamation, Denver, Colorado, personal communication, July 2, 2016). Nesting flycatchers are found along the Rio Grande from north of Albuquerque south to Radium Springs near Las Cruces. The Elephant Butte area hosts one of the largest populations of nesting flycatchers, with over 300 territories documented in 2014 (Moore 2015). Nesting habitat along the Middle Rio Grande was dominated by native vegetation in 2002, but native habitat declined in subsequent years, partly as the result of drought, and by 2014 less than 40 percent of flycatcher nest sites were dominated by native vegetation (Moore 2015).

The subtropical beetle had been projected to reach Elephant Butte Reservoir by fall of 2014 and the middle Gila River in Arizona by the spring of 2017 (Tracy 2014). Given that the arrival of beetles at Elephant Butte was later than initially thought, beetles will likely not arrive on the Gila River as soon as was anticipated. The middle Gila River also hosts a large flycatcher population, and almost all flycatcher breeding sites are dominated by tamarisk (Graber et al. 2012; Heather English, Salt River Project, Phoenix, Arizona, personal communication, April 30, 2013).

Cessation of Biocontrol Releases

The Center for Biological Diversity (CBD) and Maricopa Audubon Society filed suit against the USFWS and APHIS on March 27, 2009, seeking reinitiation of consultation between APHIS and the USFWS, after beetles defoliated flycatcher habitat around St. George and research showed that northern beetles were adapting to more southerly latitudes. Consultation was reinitiated later that year. In May 2010, APHIS submitted a new BA to the USFWS, asking for concurrence that cessation of the beetle release program would have no adverse impacts to the flycatcher. An official moratorium on the beetle program, cancelling all existing permits for release and interstate transport of all *Diorhabda* species and discontinuing issuance of new permits, was announced by APHIS on June 15, 2010. However, beetles were already widely established by then, and shutting down the release program had no effect on preventing the spread of the

beetle. CBD and Maricopa Audubon Society filed a second suit in 2013, seeking, in part, a “mitigation plan to address impacts of the beetle populations on flycatchers and their critical habitat.”

Response by Flycatchers to Tamarisk Defoliation

St. George, Utah

Breeding flycatchers and beetle defoliation first overlapped in St. George, Utah, in late July of 2008. This was, coincidentally, also the year that the Utah Division of Wildlife Resources began intensive monitoring of nesting flycatchers in St. George after doing general presence/absence surveys since 2001. Flycatchers along the Virgin River typically arrive on their territories beginning in early May, with late arrivals coming in the middle of June. The average start of incubation is in the middle of June, and the latest nests fledged by the middle of August (Bureau of Reclamation, n.d.; Sogge et al. 2010). Therefore, defoliation that begins in late July has little effect on flycatchers. Eight breeding pairs and 10 nesting attempts were documented in St. George in 2008; seven of the 10 nests were built in areas dominated by tamarisk (Edwards and Woodhouse 2015). The eight pairs produced 17 young (fecundity, or young produced per female, was 2.1; fig. 16) (Fridell et al. 2009).

The following year, defoliation was noted beginning in early June, after territories had been established and when nesting was already underway, and a second defoliation event occurred in late July to August. The Utah Division of Wildlife Resources documented 10 breeding pairs and 18 nests, three of which were abandoned before eggs were laid. As was the case in 2008, the majority of nests (11 of 15 nests with flycatcher eggs) were placed in areas dominated by tamarisk (Edwards and Woodhouse 2015). Defoliation of the tamarisk was complete, leaving nests without shade or concealment (fig. 17). Productivity was markedly lower than in 2008, with a total of two young produced (fecundity = 0.2) (Fridell et al. 2009; fig. 16). Primary causes of nest failure were depredation and failure of the eggs to hatch after at least 18 days of incubation. Six nests (46 percent of nests that failed after eggs were laid) failed to hatch, indicating that embryos died in the egg (Dobbs et al. 2012). Failure to hatch is not typically a common reason for a nest to fail, accounting for less than 9 percent of failures on the lower Virgin River in 2003 to 2010 (McLeod and Pellegrini 2013). The high rate of added nests in 2009 could have been the result of eggs at unshaded nests being exposed to lethal temperatures.

In 2010, defoliation was again noted in St. George beginning in early June, with a second defoliation in late July to August (Dobbs et al. 2012). Nine breeding pairs of flycatchers were detected in 2010. The marked difference between 2010 and prior years was where the flycatchers established territories. In previous years, flycatchers had nested primarily in tamarisk-dominated sites; in 2010, 16 of 20 nests were built in willow-dominated areas that had been previously either unoccupied or sparsely occupied by flycatchers, including one site where willow planting had occurred following a large flood in 2005. Fecundity in 2010 rose to 1.3 young per female (Dobbs et al. 2012). Tamarisk around St. George has been defoliated each year since 2008, although the timing and number of defoliation events has varied among years. Despite annual defoliation, the tamarisk shows little sign of mortality or reduced vigor (Hultine et al. 2015;

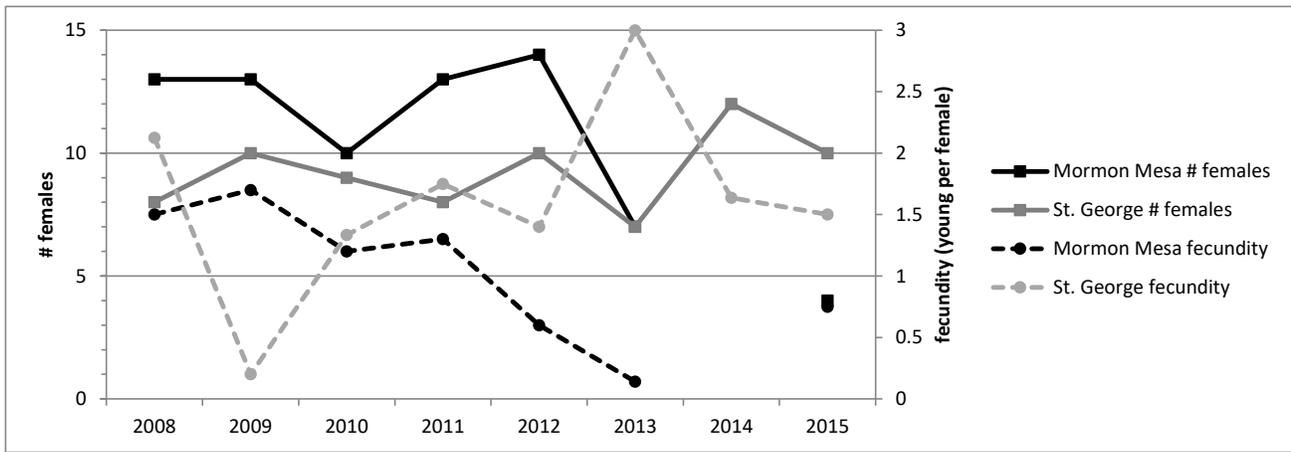


Figure 16—Number of female southwestern willow flycatchers and annual fecundity (young produced per female) documented at St. George, Utah, and Mormon Mesa, Nevada, 2008 to 2015.

Figure 17—Female southwestern willow flycatcher panting as she shades her nest in a defoliated tamarisk stand, St. George, Utah (photo by Pam Wheeler, Utah Division of Wildlife Resources).



M.A. McLeod, Biologist, SWCA Environmental Consultants, personal observation, St. George, Utah). Flycatchers around St. George continued occupying native-dominated areas in 2011 to 2015, though flycatchers again occupied tamarisk-dominated areas in 2014 and 2015 (Edwards and Woodhouse 2015). The total number of flycatcher pairs fluctuated between 7 and 12, and fecundity varied between 1.4 and 3.0 young per female (fig. 16; Dobbs and Edwards 2012; Dobbs et al. 2012; Edwards and Dobbs 2013; Edwards and Woodhouse 2014, 2015).

Flycatchers typically demonstrate a high degree of site fidelity, with half of all adults that are detected in multiple years returning to nest within 40 m of the place where they nested the previous year (McLeod and Pellegrini 2013). However, site fidelity is strongly influenced by reproductive success, with flycatchers that fail to produce offspring being far more likely to attempt breeding at a different site in the following year (McLeod and Pellegrini 2013; Paxton et al. 2007). This local plasticity in site selection, as demonstrated by the flycatchers in St. George, is what should be expected from a species that was adapted to the southwestern riparian system, which was characterized by scouring floods and a constantly shifting mosaic of vegetation.

Mormon Mesa, Nevada

When beetles progressed downstream on the Virgin River in 2009 to 2011, they affected the two flycatcher breeding sites on the lower Virgin River. Flycatchers along the Virgin River in Arizona and Nevada have been monitored annually since 1997 under a contract funded by the Bureau of Reclamation. Two areas, one in the vicinity of the town of Mesquite, Nevada, and the other approximately 19 miles downstream, across Mormon Mesa from Overton, Nevada, have been consistently occupied by breeding flycatchers since monitoring began (McLeod and Pellegrini 2015). Although flycatcher occupancy and nest success at Mesquite declined markedly from 2010 to 2013 (McLeod and Pellegrini 2014), this was likely a response to the site being dry for extended periods in 2011–2013 and the resulting decline in vegetation health.

The flycatcher breeding site at Mormon Mesa contained patches of coyote willow and a few emergent Goodding's willows (*Salix gooddingii*) surrounded by a sea of tamarisk. Defoliation was first observed at Mormon Mesa in mid-July 2011, and the breeding area was fully defoliated by early August. In 2012, widespread defoliation was observed in late May, and a second defoliation event occurred at the beginning of August. No defoliation events occurred during the flycatcher breeding season in 2013, but defoliation from the previous 2 years had resulted in 84 percent dieback at Mormon Mesa by 2013 (Hultine et al. 2015). This dramatic change in the vegetation is readily apparent on satellite imagery (fig. 18).

As was the case in St. George, the first defoliation event at Mormon Mesa occurred late in the breeding season, after most flycatcher nesting activity was over. The number of female flycatchers (13) and fecundity (1.3 young per female) documented in 2011 were typical of previous years (fig. 16; McLeod and Pellegrini 2013). In the following year, defoliation occurred as flycatchers were establishing territories and choosing nest sites. Fourteen female flycatchers nested at Mormon Mesa in 2012, and every nest found was placed in or on the edge of a willow patch.



Figure 18—The Mormon Mesa area of the Virgin River in August 2010 before tamarisk beetles arrived (left) and in May 2013, after 2 years of defoliation (right). The 2013 image was not taken during a defoliation event and depicts the mortality and dieback of tamarisk caused by the prior 2 years of defoliation. The areas in the 2013 image that appear grayish-green are vegetated by arrowweed (*Pluchea sericea*), and the bright green areas are coyote willow (*Salix exigua*) or Goodding’s willow (*S. gooddingii*). Yellow outline shows the area surveyed for flycatchers (base photo by Google Maps, outlines by SWCA Environmental Consultants).

Despite nests being placed in willow patches, fecundity in 2012 was 0.6, just half that recorded in the prior year (McLeod and Pellegrini 2013). Nest desertion during the laying phase, without any sign of cowbird parasitism or partial depredation of the clutch, accounted for half (4 of 8) of the nest failures; in 1997 to 2010, only two other instances of this were observed on the lower Virgin River, accounting for 1 percent of nest failures (Bureau of Reclamation, n.d.). Nest desertion may be indicative of poor habitat quality; flycatchers in Arizona were observed to forego nesting altogether under severe drought conditions (Ellis et al. 2008). In 2013, only seven females nested at Mormon Mesa, producing one fledgling among them (fecundity = 0.14 young per female; fig. 16; McLeod and Pellegrini 2014). Four nests were abandoned before eggs were laid, and two of the four nests (50 percent) that failed after eggs were laid had added clutches.

Flycatchers at Mormon Mesa were not monitored in 2014 because all Federal agency personnel and their contractors were barred from visiting the lower Virgin River

because of safety concerns following the Bureau of Land Management's attempt to remove Cliven Bundy's trespass cattle. The Nevada Department of Wildlife (NDOW) completed surveys and intermittent monitoring for flycatchers at Mormon Mesa in 2015. Only two breeding male flycatchers were detected, each of which was confirmed to have one mate and suspected to have two (NDOW, n.d.). Two of the females were confirmed to have produced three fledglings between them, for a minimum fecundity of 0.8 young per female (fig. 16).

It is unlikely that a substantial number of the flycatchers at Mormon Mesa moved to other locations, where they went undetected, in the years following 2012. Estimated annual survival of adult flycatchers along the Virgin River in 1997–2012 was 61 percent (McLeod and Pellegrini 2013). In 2012, 20 adult flycatchers were individually identified, via unique color-bands, at Mormon Mesa. Thirteen (65 percent, essentially what would be expected given annual mortality) of those flycatchers were detected again in 2013, and all 13 were detected at Mormon Mesa; none were detected at other flycatcher sites despite all known flycatcher breeding areas in southern Nevada and western Arizona being monitored as part of various projects. In addition, all of the adult flycatchers detected at Mormon Mesa in 2013 had been there the year before; i.e., for the first time in 17 years of monitoring, no new adults entered the population at Mormon Mesa (McLeod and Pellegrini 2014; Bureau of Reclamation, n.d.).

St. George vs. Mormon Mesa

Flycatchers at both St. George and Mormon Mesa had a sharp decline in productivity in the first year when defoliation significantly overlapped the flycatcher breeding season. The response after that first year differed dramatically between the two areas, however, and the two populations took very different trajectories. Flycatchers in St. George moved into native-dominated stands in subsequent years, the total number of breeding flycatchers remained the same, and productivity recovered from the low observed in the first year of defoliation; flycatchers at Mormon Mesa continued attempting to breed in the same stands but the number of breeding flycatchers dropped sharply and productivity remained very low through the second year, despite no defoliation events occurring during that breeding season.

There are two key differences between St. George and Mormon Mesa that likely contributed to the differing trajectories of the flycatcher population. One is the response of tamarisk to beetle defoliation. Tamarisk around St. George has experienced little mortality or dieback as a result of repeated defoliation; unless a defoliation event is occurring, the tamarisk still provides shade and concealment. In the Mormon Mesa area, in contrast, two seasons of defoliation resulted in widespread mortality and dieback.

The other striking difference is the overall species composition of the vegetation in the riparian zone. St. George is on the upper Virgin River, where native trees are common. Prior to 2009, St. George had stands of native trees that looked like suitable flycatcher habitat and had been surveyed, but where few or no resident flycatchers were found (Rob Dobbs, Utah Division of Wildlife Resources, Hurricane, Utah, personal communication). Flycatchers moved into these existing native sites in 2010, following defoliation and widespread nest failure at tamarisk-dominated sites in 2009. The lower Virgin River, in contrast, has relatively little native vegetation; there were

no sites, consisting of either native vegetation or tamarisk, that looked like they could be suitable flycatcher habitat but were unoccupied (M.A. McLeod, Biologist, SWCA Environmental Consultants, personal observation, lower Virgin River). When tamarisk was defoliated, flycatchers at Mormon Mesa had nowhere nearby to go. The closest flycatcher sites to Mormon Mesa were at Mesquite (~19 miles away) and at Overton on the Muddy River (~7 miles away). Both were in poor condition; Mesquite had been dry, and Overton was suffering both from changes in streamflow that left a portion of the breeding site dry and from tamarisk defoliation (McLeod and Pellegrini 2015).

Short-Term Consequences

The proponents of the tamarisk biocontrol program claimed that decline in tamarisk would be gradual and would be accompanied by a concurrent increase in the native plant community. They also cited examples of how quickly native vegetation could become suitable habitat for nesting flycatchers as evidence that no gap in habitat availability would occur. However, beetles can cause complete defoliation that results in greater solar insolation, lower humidity, and higher temperatures (Bateman et al. 2013), which have been associated with low reproductive output in flycatchers (Dobbs et al. 2012; McLeod and Pellegrini 2013). While it is true that riparian vegetation can grow into suitable flycatcher nesting habitat in as little as 2 or 3 years (Paxton et al. 2007; M.A. McLeod, Biologist, SWCA Environmental Consultants, personal observation, Virgin and lower Colorado rivers), this typically occurs in areas that have been scoured by a flood or on sediments that are newly exposed when water levels in a reservoir decline.

A resurgence of willows on the stream margins of areas that have been defoliated by tamarisk beetles has been observed in some areas, such as along the upper Colorado River (S. Carothers, SWCA Environmental Consultants, personal observation, upper Colorado River; Graham et al. 2016), but in other areas, the reduction in canopy cover of tamarisk has allowed weed species to proliferate. At Mormon Mesa, beetles caused rapid dieback and mortality of tamarisk, without concurrent recovery of native vegetation. No expansion of the willows was apparent as of the summer of 2016, 5 years after beetles became established in the area, but whitetop (*Lepidium* sp.), an invasive weed, had become much more widespread than it was prior to the arrival of beetles (M.A. McLeod, Biologist, SWCA Environmental Consultants, personal observation, Mormon Mesa, June 16, 2016). In short, it is now clear that beetles can cause a gap in habitat availability that lasts for several years, and possibly much longer.

Flycatchers, like most small passerines, are relatively short-lived birds. Estimated juvenile mortality along the Virgin River in 1997–2012 was 68 percent (i.e., only 32 percent of fledglings survive to their second summer; McLeod and Pellegrini 2013), and estimated annual adult mortality over that same period was 39 percent. If flycatchers are unable to reproduce, the flycatcher population experiences a precipitous decline. In the complete absence of reproduction, the adult flycatcher population would decline by 77 percent in just 3 years and 91 percent in 5 years, given the estimated annual mortality rate. Even if each adult female produces, on average, one fledgling per year, the population would decline 73 percent after 5 years. Flycatchers do not have the longevity to be able to wait out several years of poor reproduction if tamarisk defoliation renders entire river reaches unsuitable as breeding habitat.

In areas where flycatchers nest primarily in tamarisk-dominated habitats, alternative breeding sites are needed so that local populations can persist during the period when tamarisk no longer provides nesting habitat but native vegetation has not recovered. These alternative sites should be close to existing breeding sites; in multiple drainages where flycatchers have been studied, the vast majority of between-year movements by adult flycatchers resulted in distances moved of less than 25 miles (McLeod and Pellegrini 2013; Paxton et al. 2007).

In addition, when a large area of formerly suitable habitat became unsuitable, no large-scale dispersal to other breeding locations was observed (Paxton et al. 2007), illustrating the need for local refugia. Following biocontrol, any areas that recover native vegetation in sufficient density to become flycatcher breeding habitat should be readily colonized by flycatchers if a local population is present. Colonization of new habitats that are adjacent to occupied areas has been observed in multiple flycatcher studies (McLeod and Pellegrini 2014; Moore and Ahlers 2008; Paxton et al. 2007), and flycatcher populations can increase rapidly in response to an increase in suitable habitat (Graber et al. 2012; Moore and Ahlers 2008; Paxton et al. 2007).

Long-Term Prospects

Beetles are expected to be eventually found in all areas of North America that have tamarisk (Bean et al. 2013), and these areas completely overlap the breeding range of the southwestern willow flycatcher. In the long term, tamarisk biocontrol may have exactly the effect on tamarisk that its proponents advertised: reducing the density of tamarisk by up to 85 percent. The authors of the 1998 biocontrol proposal suggested this would “reduce the abundance of saltcedar to below the level where it causes important damage to western riparian ecosystems.” At this level of suppression, however, tamarisk would also no longer provide much ecological value. Recovery of native vegetation is unlikely to occur in many areas that will be affected by the tamarisk beetle, and in these places, biocontrol will result in a long-term reduction in habitat quality.

Tamarisk is a symptom as well as a cause of the degradation of riparian ecosystems, and removing the tamarisk does not address the underlying changes that limit native riparian species and allow tamarisk to proliferate. The Flycatcher Recovery Team identified this concern early on and reiterated it in the letter sent to the Regional Director of the USFWS in 1998 expressing their concerns about the proposed beetle releases, pointing out that without extensive regional changes in the management of water and land, existing conditions would continue to preclude the establishment of native riparian vegetation.

The long-term effects of tamarisk beetles on vegetation conditions are likely to vary widely between river systems and between reaches, depending on the prevalence of tamarisk and on the many factors, such as flood regimes, groundwater levels, and soil and water salinity, that influence whether native riparian vegetation can become established and persist. The fact that some of the largest flycatcher populations occur in sites dominated by tamarisk makes the flycatcher, among riparian obligate wildlife, particularly susceptible to the detrimental effects of tamarisk beetles. Based on the observed responses of flycatchers to tamarisk defoliation, flycatcher productivity will almost certainly decrease immediately following the arrival of beetles in any area

where flycatchers nest in vegetation with a significant tamarisk component, including at Elephant Butte Reservoir and on the Gila River.

Whether beetles cause a long-term reduction in, or even extirpation of, the flycatcher population in these areas remains to be seen. The health, and possibly persistence, of flycatcher populations in reaches that can still support native vegetation may depend on active restoration of native vegetation prior to and immediately following the arrival of beetles. Even beetle researchers have recently acknowledged that defoliation and subsequent dieback of tamarisk can have adverse effects on flycatchers, including in stands that are not dominated by tamarisk (Tracy et al. 2014). Researchers have advocated restoration efforts in advance of the arrival of beetles (Tracy 2014).

Beetle proponents and opponents differ, often passionately, on whether tamarisk bio-control was a good idea, but both sides ostensibly have the same goal: the preservation and improvement of riparian health. Now that the beetle has been set loose and is spreading rapidly, the common focus should be on mitigating the detrimental effects and maximizing the beneficial results of the inevitable arrival of beetles. The lawsuit that was filed in 2013 against APHIS and the USFWS by CBD and Maricopa Audubon Society sought, in part, a declaration that the defendants had violated the Endangered Species Act and the development of “an appropriate mitigation plan to address the impacts of the beetle populations on flycatchers and their critical habitat.” The District Court found that APHIS was in violation of section 7(a)(1) of the Endangered Species Act, which requires Federal agencies to take actions to preserve endangered species (Center for Biological Diversity et al. v Vilsack et al., Dkt. 87), and issued a remedial order instructing the defendants to take several measures, including considering funding intensive third-party restoration efforts (Center for Biological Diversity et al. v Vilsack et al., Dkt. 104).

Flycatchers have received much attention because of their status as a Federally endangered species, but they are, of course, not the only species affected by tamarisk defoliation. A study of riparian-nesting birds on the Virgin River showed that species richness and abundance were higher in 2009 and 2010, prior to the arrival of beetles, than they were in 2013, after 2 or 3 years of defoliation, with yellow warblers (*Setophaga petechia*) being particularly affected (Johnson 2015). Similarly, herpetofauna were less abundant after defoliation in both monotypic tamarisk and stands of mixed vegetation (Bateman et al. 2014). No study of riparian-nesting birds has been undertaken to compare the pre- and post-beetle nest success of species other than the flycatcher.

For the sake of all riparian obligate wildlife, restoration of native vegetation is urgently needed wherever tamarisk constitutes a significant portion of the woody riparian vegetation and the arrival of beetles is imminent or has already occurred. Restoration is often costly and labor intensive, and it will likely be prohibitively so in places where soil treatments are needed or depth to groundwater is such that irrigation would be required in perpetuity. Restoring habitat where flycatchers can nest successfully is even more difficult, given their propensity to select dense vegetation close to surface water.

One strategy in places where beetles are already present is to target monotypic or mixed tamarisk stands that supported breeding flycatchers prior to the arrival of beetles. These stands likely still have the same surface water conditions that attracted breeding flycatchers but no longer have suitably dense vegetation. This strategy has been employed around St. George, and two successful flycatcher nests were located in one of the restored areas in 2017 (Christian Edwards, Utah Division of Wildlife Resources,

personal communication, September 11, 2017). Prior to the arrival of beetles, restoration efforts should target sites that can support dense vegetation in proximity to breeding flycatchers, as nearby sites are the most likely to be colonized. This approach is being used on the Gila River in the Safford Valley. Either approach requires careful planning and close coordination with the USFWS. These strategies represent a change from more traditional flycatcher management, which required avoiding nesting sites and their surroundings, but this kind of proactive management may be critical to the long-term success of the southwestern willow flycatcher.

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