TAMARISK BIOCONTROL USING TAMARISK BEETLES: POTENTIAL CONSEQUENCES FOR RIPARIAN BIRDS IN THE SOUTHWESTERN UNITED STATES

EBEN H. PAXTON[1,4], TAD C. THEIMER[2], AND MARK K. SOGGE[3]

[1]*U.S. Geological Survey, Pacific Islands Ecological Research Center, Hawaii National Park, HI 96718*
[2]*Department of Biological Sciences, Northern Arizona University, Flagstaff, AZ 86011*
[3]*U.S. Geological Survey, Flagstaff, AZ 86001*

Abstract. The tamarisk beetle (*Diorhabda* spp.), a non-native biocontrol agent, has been introduced to eradicate tamarisk (*Tamarix* spp.), a genus of non-native tree that has become a dominant component of riparian woodlands in the southwestern United States. Tamarisk beetles have the potential to spread widely and defoliate large expanses of tamarisk habitat, but the effects of such a widespread loss of riparian vegetation on birds remains unknown. We reviewed literature on the effects of other defoliating insects on birds to investigate the potential for tamarisk beetles to affect birds positively or negatively by changing food abundance and vegetation structure. We then combined data on the temporal patterns of tamarisk defoliation by beetles with nest productivity of a well-studied riparian obligate, the Southwestern Willow Flycatcher (*Empidonax traillii extimus*), to simulate the potential demographic consequences of beetle defoliation on breeding riparian birds in both the short and long term. Our results highlight that the effects of tamarisk biocontrol on birds will likely vary by species and population, depending upon its sensitivity to seasonal defoliation by beetles and net loss of riparian habitat due to tamarisk mortality. Species with restricted distributions that include areas dominated by tamarisk may be negatively affected both in the short and long term. The rate of regeneration and/or restoration of native cottonwoods (*Populus* spp.) and willows (*Salix* spp.) relative to the rate of tamarisk loss will be critical in determining the long-term effect of this large-scale ecological experiment.

Key words: tamarisk, Tamarix, *saltcedar, invasive plants, riparian habitat, biocontrol, ecological trap,* Diorhabda.

Control Biológico del Tamarisco por el Escarabajo del Tamarisco: Consecuencias Potenciales para las Aves Ribereñas en el Sudoeste de los Estados Unidos

Resumen. El escarabajo del tamarisco (*Diorhabda* spp.), un agente de control biológico no nativo, ha sido introducido para erradicar al tamarisco (*Tamarix* spp.), un género de árbol no nativo que se ha vuelto un componente dominante de los bosques ribereños en el sudoeste de los Estados Unidos. Los escarabajos del tamarisco tienen el potencial de dispersarse ampliamente y defoliar grandes extensiones del hábitat del tamarisco, pero no se conocen los efectos de una pérdida tan extensa de vegetación ribereña sobre las aves. Revisamos la literatura sobre los efectos de otros insectos defoliantes sorbe las aves para investigar el potencial de los escarabajos del tamarisco de afectar positiva o negativamente a las aves mediante el cambio en la abundancia de alimentos y en la estructura de la vegetación. Combinamos luego los datos de los patrones temporales de defoliación del tamarisco producidos por los escarabajos con la productividad de los nidos de una especie ribereña obligada bien estudiada, *Empidonax traillii extimus*. Simulamos las consecuencias demográficas potenciales de la defoliación de los escarabajos sobre las aves ribereñas reproductivas tanto al corto como al largo plazo. Nuestros resultados destacan que los efectos del control biológico del tamarisco sobre las aves probablemente variarán por especie y población, dependiendo de su sensibilidad a la defoliación estacional dada por los escarabajos y a la pérdida neta de hábitat ribereño debida a la mortalidad de los tamariscos. Las especies con distribuciones restringidas que incluyen áreas dominadas por tamariscos pueden verse afectadas negativamente tanto al corto como al largo plazo. La tasa de regeneración y/o restauración de álamos (*Populus* spp.) y sauces (*Salix* spp.) con relación a la tasa de pérdida de tamariscos puede ser crítica para determinar el efecto de largo plazo de este experimento ecológico de gran escala.

INTRODUCTION

Riparian woodlands, dense stands of woody vegetation found along streams, lakes, and other sources of water, are important breeding, wintering, and stopover habitat for a variety of birds (Rich 2002), especially in the arid southwestern United States (Johnson et al. 1985, Knopf et al. 1988). Unfortunately, riparian woodlands have undergone large-scale loss or degradation through conversion to agriculture, urbanization, overgrazing, and disruption of hydrologic processes (Knopf et al.

1988, Busch and Smith 1995). Concomitant with these losses has been a replacement of native riparian trees by introduced species, particularly the tamarisk (*Tamarix* spp., also known as saltcedar). Tamarisk is currently estimated to be the second-most dominant species complex of woody plants in western riparian zones (Friedman et al. 2005), occupying over 500 000–650 000 ha in the western U.S. (Zavaleta 2000). Tamarisk can form large monotypic stands along rivers, around reservoirs, and in other riparian areas, constituting the only riparian woodland in some areas (Shafroth et al. 2005).

The U.S. Department of Agriculture recently led efforts to release tamarisk beetles (*Diorhabda* spp.; Tracy and Robbins 2009) as a biocontrol agent, leading to the potential for rapid, large-scale eradication of tamarisk across the southwestern United States (DeLoach et al. 2000). Native to Eurasia, tamarisk beetles defoliate tamarisk trees during the growing season, with repeated defoliation over multiple years eventually killing the tree as it depletes its carbohydrate reserves (Fig. 1, Dudley et al. 2001). DeLoach et al. (2000) predicted biocontrol of tamarisk to have large net positive benefits and minimal negative effects, but the ecological consequences of introduced biocontrol agents are notoriously difficult to predict (Simberloff and Stiling 1996, Thomas and Willis 1998, Louda and Stiling 2004, Messing and Wright 2006). Although the research on the tamarisk beetle's herbivory, reproductive success, and host preference prior to release was extensive (DeLoach et al. 2000, Dudley et al. 2001, Dudley 2005), tamarisk beetles have dispersed from sites of release in Colorado and Utah faster and farther than predicted (Bean et al. 2007). Once established in a riparian system, tamarisk beetles can have substantial effects on tamarisk; Dennison et al. (2009) documented as much as 50% of riparian woodland affected by defoliation in some drainages.

The effect of this large-scale biocontrol effort on riparian bird communities is currently unknown. Bird use of tamarisk is often greater than generally recognized; across the western United States, 49 species have been documented breeding in tamarisk, and in Arizona and New Mexico 11 bird species of regional or national concern frequently breed in tamarisk (Sogge et al. 2008). However, there is little research on the ecological ramifications of breeding in tamarisk. A notable exception are studies of the productivity, survivorship, physiology, and diet of the Southwestern Willow Flycatcher (*Empidonax traillii extimus*; Owen et al. 2005, Sogge et al. 2006, Paxton et al. 2007, Durst et al. 2008a, b, Ellis et al. 2008), which indicate that tamarisk is ecologically equivalent to native habitat in at least some areas (Sogge et al. 2008). Likewise, tamarisk can provide shelter for wintering birds and migrants (Walker 2008, van Riper et al. 2008). Cerasale and Guglielmo (2010) found that rates of refueling of migrating Wilson's Warblers (*Wilsonia pusilla*) stopping over at a site in Arizona were higher in tamarisk than in native vegetation (Cerasale and Guglielmo 2010).

Studies evaluating avian use of tamarisk typically compare the value of tamarisk to that of native riparian woody vegetation (Hinojosa-Huerta 2006, Sogge et al. 2008, van Riper et al. 2008). More relevant from the perspective of the effects of biocontrol is the importance of tamarisk habitat relative to what will remain after defoliation by tamarisk beetles and the trees' death (Sogge et al. 2008)—conversion of defoliated tamarisk habitat to native riparian woodlands is not assured (Shafroth et al. 2008, Stromberg et al. 2009). In riparian systems with unaltered hydrology, native trees may establish themselves quickly and outcompete tamarisk (Sher et al. 2000, 2002); such areas will likely transition to native riparian woodlands following tamarisk defoliation by beetles. However, in many areas already affected by beetles, or likely to be so in the near future, soil chemistry and hydrology have been altered to the point that native trees can re-establish themselves only under certain conditions (Bay and Sher 2008) or only with carefully planned and extensive efforts at restoration (Shafroth et al. 2008). Without effective restoration, former tamarisk habitat may be replaced with native or exotic forbs and grasses rather than the shrub and trees needed by most riparian birds (Harms and Hiebert 2006).

The release of tamarisk beetles as a biocontrol agent represents a large-scale ecological experiment with currently unknown but potentially widespread environmental consequences. The rapid spread of the tamarisk beetle and its potential effects on riparian ecosystems has led to growing concern about the program (e.g., Stromberg et al. 2009, Hultine et al. 2010). On 15 June 2010 the U.S. Department of Agriculture issued a moratorium on interstate transportation and release of the tamarisk beetle in response to concerns about its potential effects on habitat critical to the Southwestern Willow Flycatcher; however, the tamarisk beetle is firmly established in multiple watersheds of the southwestern United States and has continued to expand its range. As an initial step toward understanding how tamarisk defoliation may affect riparian birds, we reviewed literature on the effects of other insect defoliaters and modeled potential outcomes to develop predictions about the effects of biocontrol of tamarisk with beetles. We hypothesized that defoliation by beetles should affect birds in three ways (Fig. 2): (1) altering prey availability, either by inducing a short-term increase in tamarisk beetles as prey or by altering the abundance or composition of other insect prey as a result of defoliation; (2) increasing nest abandonment and predation due to loss of foliar cover; and (3) reducing the quantity of riparian habitat available to breeding birds.

EFFECTS OF INSECT IRRUPTION AND DEFOLIATION ON BREEDING BIRD COMMUNITIES

Biocontrol of tamarisk by tamarisk beetles is characterized by rapid increases in beetle populations during the summer; the larvae defoliate the trees completely (Fig. 1). Other irruptive,

FIGURE 1.   (A) Habitat in which the Southwestern Willow Flycatcher breeds at St. George, Utah, prior to tamarisk defoliation. (B) The same habitat during defoliation. (C) Active flycatcher nest (circle) that eventually failed in tamarisk-dominated habitat at St. George, 2008, during defoliation. Photos by P. Wheeler, Utah Division of Wildlife Resources.

defoliating insects follow a similar pattern. As a first step in investigating the potential effects of tamarisk beetle biocontrol on birds, we searched the literature in Science Citation Index Expanded, accessed via the Web of Science (http://thomson reuters.com/products_services/science/science_products/a-z/ web_of_science), using the terms "defoliation," "insect outbreak," and "insect irruption" combined with the terms "bird," "birds," and "avian." This search returned 21 articles published between 1987 and 2010 that were relevant to the questions we pose, and we obtained another nine articles from the literature cited within those papers. We did not include articles focused on woodpecker responses to insect outbreaks as tamarisk lacks the structural characteristics needed to support breeding by this group of birds (Bateman and Paxton 2010). Of the 30 papers we reviewed, nine focused on the gypsy moth (*Lymantria dispar*; DeGraaf 1987, Thurber et al. 1994, Yahner and
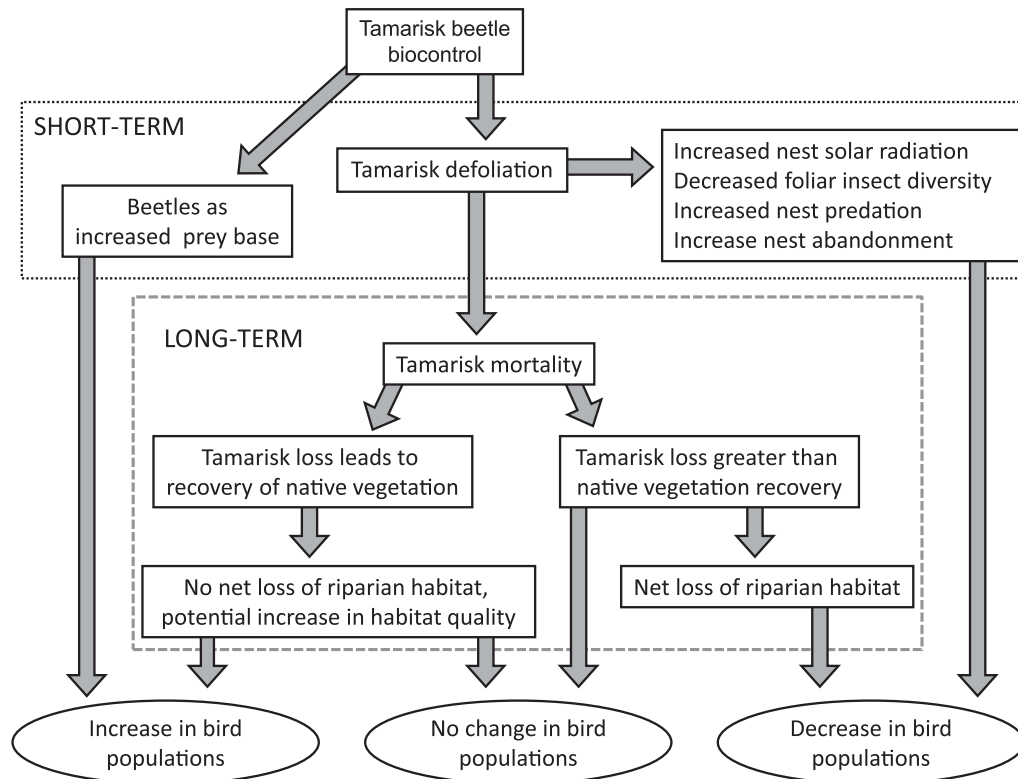
FIGURE 2. Hypothesized model of three primary ways that biocontrol of tamarisk trees by the tamarisk beetle can affect avian populations in riparian systems. In the short term, prior to the trees' death, tamarisk beetles could provide a food source for insectivorous birds as beetle populations expand. Defoliation and mortality of tamarisk, however, will eventually reduce habitat quality by reducing abundance of other insect prey dependent on foliage and by removing canopy cover critical for reducing exposure of nests to predators, brood parasites and the extreme temperatures typical of the southwestern United States. The long-term consequences of tamarisk mortality will depend on the rate of vegetation recovery after the tamarisk dies; these consequences may range from no net loss of habitat if native vegetation recovers at the same rate as tamarisk dies to net loss of habitat when tamarisk mortality is not followed by regrowth of other riparian vegetation.

Mahan 1996, Bell and Whitmore 1997, 2000, Gale et al. 2001, Showalter and Whitmore 2002, Barber et al. 2008, Schill and Yahner 2009), nine on the spruce budworm (*Choristoneura fumerifana*; Kendeigh 1947, Mitchell 1952, Morris et al. 1958, Zach and Falls 1975, Morse 1978, Crawford et al. 1983, Crawford and Jennings 1989, Patten and Burger 1998, Holmes et al. 2009), four on woolly adelges (*Adelges piceae* and *A. tsugae*; Rabenold et al. 1998, Tingley et al. 2002, Becker et al. 2008, Allen et al. 2009), three on the spruce beetle (*Dendroctonus rufipennis*; Matsuoka et al. 2001, Matsuoka and Handel 2007, Werner et al. 2006), two on the processionary moth (*Thaumetopoea pityocampa*; Pimental and Nilsson 2007, 2009), two on the tent caterpillar (*Malacosoma disstria*; Sealy 1979, Pelech and Hannon 1995), and one on the elm spanworm (*Ennomus subsignarius*; Haney 1999). The response of southwestern riparian birds to tamarisk defoliation will undoubtedly vary somewhat from that of birds in defoliated eastern and northern forests, so our discussion emphasizes general patterns and important differences between the tamarisk system and systems studied elsewhere.

Of the 25 papers documenting responses of avian populations to defoliating insects, 10 reported positive responses, 13 reported some species increasing and others decreasing, and two reported overall negative responses. Population increases were attributed to increased abundance of the defoliating insect as prey or to changes in habitat caused by defoliation. Some defoliating insects, like the spruce budworm, are highly palatable and consumed by a wide variety of birds, as well as by a smaller suite of "budworm specialist" warblers, so birds' positive response was likely due to increased abundance of the budworm as prey. Even in areas of outbreaks of this highly palatable insect, however, few birds had guts containing >40% budworm by volume (Mitchell 1952), and a diet of budworms alone would likely be nutritionally deficient (Morse 1978). Other defoliating insects were taken by a smaller suite of birds (e.g., the processionary moth; Pimental and Nilsson 2007, 2009) or were palatable for only a limited period of the life cycle (e.g., the tent caterpillar [Sealy 1979, Pelech and Hannon 1995] and gypsy moth [Bell and Whitmore 1997, Gale et al. 2001]) or apparently did not serve as prey at all (woolly

adelges; Rabenold et al. 1998, Tingley et al. 2002, Becker et al. 2008, Allen et al. 2009). These papers illustrate that a positive numerical response by birds to increased abundances of defoliating insects as prey depends on the palatability of the defoliating insect. Currently, nothing is known about the palatability or nutritional value of tamarisk beetles for riparian birds. Although coleopterans constitute a significant portion of the diet of many southwestern riparian birds (Drost et al. 2003, Yard et al. 2004, Wiesenborn and Heydon 2007, Durst et al. 2008a), the tamarisk beetle is a member of the family Chrysomelidae, which produce secondary chemicals distasteful to some birds (Hilker and Köpf 1994, Rowell-Rahier et al. 1995), so it may be less palatable than other coleopterans.

While tamarisk beetles may provide a temporarily abundant food source, cascading effects of defoliation on the broader arthropod community could reduce the diversity of prey available to riparian insectivores. Tamarisk trees flower profusely and attract a variety of native insects (Durst et al. 2008a, Wiesenborn et al. 2008) as well as supporting populations of the introduced tamarisk leafhopper (*Opsius stactogalus*), itself important prey for riparian birds (Yard et al. 2004, Wiesenborn 2005, Durst et al. 2008b). Thus, foliage-feeding insects, important to gleaners, and pollinators, important to aerial foragers, are likely to be reduced by defoliation. Although termites, carpenter ants, and some general wood borers (e.g., Buprestidae, Cerambycidae, Platypodidae, Siricidae) may be attracted to beetle-killed tamarisk, we know of no studies that have quantified their abundance in dead tamarisk. Birds that would exploit an increase in these insects, such as woodpeckers, nuthatches, and chickadees, don't breed in many of the regions likely to be affected, although they could prey on these insects during migration or winter. Overall, there is little evidence to suggest that positive responses by these insects necessarily follow tamarisk mortality or that these insects would have a significant effect on breeding birds. For avian insectivores that specialize on specific taxa, require a diverse prey base, or find chrysomelid beetles unpalatable, the increase in tamarisk beetles may not offset the loss of other important arthropods. Of the 42 species of breeding birds documented to use tamarisk in the southwestern United States, we estimate that at least 26 are likely to be affected by changes in arthropod abundance because of their dependence on insects as prey during the breeding season (Table 1).

Even if tamarisk beetles are palatable to birds, landscape-level characteristics of southwestern riparian woodlands may reduce the net positive effect of the increased abundance of prey that has been documented in other communities. In at least three cases, numerical responses to defoliating insects were due to recruitment of birds from neighboring nondefoliated habitat (Morris et al. 1958, Gale et al. 2001, Barber et al. 2008). Whereas these birds were colonizing defoliated patches from surrounding unaffected forest, the highly fragmented riparian patches in the southwestern United States typically are surrounded by human-modified agricultural and urban lands or upland desert or shrub-steppe that are unsuitable for riparian-breeding birds. In many drainages tamarisk is the dominant tree, and defoliation by the beetles can be extensive and widespread (Dennison et al. 2009), leaving little unaffected habitat to support bird populations that could invade and take advantage of areas of insect outbreak. Therefore, although birds from adjacent nonriparian areas may benefit from dense tamarisk beetle populations during the breeding season, benefits are less certain for birds that are restricted to riparian woodland habitat.

Changes in woodland structure and composition after defoliation, which drove avian population responses to insect defoliation in many of the studies we reviewed, may not affect southwestern tamarisk habitats in the same way either. In eastern and northern forests, mortality of defoliated canopy trees typically results in more standing snags and stimulated growth of the shrub layer, thereby benefiting cavity nesters (Showalter and Whitmore 2002) and shrub- and ground-nesting birds (e.g., Bell and Whitmore 1997, 2000) while negatively affecting canopy feeders and tree nesters (DeGraaf 1987, Rabenold et al. 1998, Gale et al. 2001, Tingley et al. 2002, Werner et al. 2006). In areas with both native willows and cottonwoods and non-native tamarisk, defoliation may stimulate growth of native components that could offset any negative consequences of tamarisk defoliation. However, monotypic stands of tamarisk typically lack a shrub layer that could respond positively to defoliation, and primary cavity nesters are lacking in tamarisk habitats. As a result, shrub and cavity nesters are unlikely to benefit in these tamarisk habitats, while the negative effect on birds dependent on the canopy would remain. Alternatively, in some areas where tamarisk grows with large native willows and cottonwoods, tamarisk acts as the shrub layer, and the loss of tamarisk could have negative consequences for shrub nesters.

Last, vegetation density and canopy cover may be more important to avian communities in southwestern riparian forests than in other forest types. First, in the low-elevation deserts where tamarisk now dominates, foliar cover likely plays a more important role in ameliorating the microclimate at the nest (e.g., Tieleman et al. 2008). Many areas reach or exceed ambient air temperatures lethal to eggs (43–44 °C; Webb 1987), and high summer daytime temperatures and aridity can quickly stress birds' ability to dissipate heat and balance their water demands (Wolf and Walsberg 1996). We estimate that at least 19 of the bird species recorded breeding in tamarisk habitat could experience higher nest temperatures because of defoliation (Table 1) while some, like herons and egrets that use tamarisk primarily as a structural component to support nests, may be less affected. Second, several lines of evidence indirectly link vegetative cover and density with occurrence or productivity of southwestern riparian breeders. Many riparian birds breed in those areas of riparian habitat where vegetation is densest (Fleishman et al. 2003, Sogge et al. 2005,

TABLE 1. Birds documented to breed in tamarisk habitat in the southwestern U.S. (from Sogge et al. 2008) and likely to be affected by tamarisk beetle biocontrol because of (a) alteration in insect prey abundance due to dependence on insects as prey during the breeding season, either positively if beetles serve as prey or negatively if defoliation leads to a decrease of insect abundance and diversity or (b) seasonal defoliation that increases nest failure due to increased predation or abandonment.

Species	Sensitivity to alteration of insect prey	Sensitivity to seasonal defoliation
Gambel's Quail *Callipepla gambelii*		
Cattle Egret *Bubulcus ibis*		
Black-crowned Night Heron *Nycticorax nycticorax*		
White-faced Ibis *Plegadis chihi*		
Roseate Spoonbill *Platalea ajaja*		
Common Moorhen *Gallinula chloropus*		
Mourning Dove *Zenaida macroura*		•
White-winged Dove *Zenaida asiatica*[a]		•
Yellow-billed Cuckoo *Coccyzus americanus*[a]		•
Greater Roadrunner *Geococcyx californianus*		
Elf Owl *Micrathene whitneyi*		
Black-chinned Hummingbird *Archilochus alexandri*[a]		•
Belted Kingfisher *Megaceryle alcyon*		
Willow Flycatcher *Empidonax traillii*[a]	•	•
Black Phoebe *Sayornis nigricans*	•	
Bell's Vireo *Vireo bellii*[a]	•	•
Chihuahuan Raven *Corvus cryptoleucus*		•
Northern Rough-winged Swallow *Stelgidopteryx serripennis*	•	
Cliff Swallow *Petrochelidon pyrrhonota*		
Verdin *Auriparus flaviceps*	•	
Bewick's Wren *Thryomanes bewickii*[a]	•	
Cactus Wren *Campylorhynchus brunneicapillus*	•	
American Dipper *Cinclus mexicanus*	•	
Black-tailed Gnatcatcher *Polioptila melanura*	•	•
Brown Thrasher *Toxostoma rufum*	•	•
Crissal Thrasher *Toxostoma crissale*	•	•
Lucy's Warbler *Oreothlypis luciae*[a]	•	
Yellow Warbler *Dendroica petechia*[a]	•	•
Common Yellowthroat *Geothlypis trichas*	•	
Yellow-breasted Chat *Icteria virens*[a]	•	•
Summer Tanager *Piranga rubra*[a]	•	•
Abert's Towhee *Melozone aberti*	•	•
Song Sparrow *Melospiza melodia*	•	•
Pyrrhuloxia *Cardinalis sinuatus*	•	•
Blue Grosbeak *Passerina caerulea*[a]	•	•
Lazuli Bunting *Passerina amoena*	•	
Indigo Bunting *Passerina cyanea*	•	•
Red-winged Blackbird *Agelaius phoeniceus*	•	
Tricolored Blackbird *Agelaius tricolor*	•	
Yellow-headed Blackbird *Xanthocephalus xanthocephalus*	•	
Brown-headed Cowbird *Molothrus ater*	•	•

[a]Species of regional or national conservation concern that breeds in tamarisk-dominated habitats and may experience local declines following tamarisk defoliation (see Sogge et al. 2008).

Hinojosa-Huerta 2006). The normalized difference vegetation index (NDVI), a measure of foliage density and vigor (Avery and Berlin 1992), is highly informative in predicting the breeding habitat of the Southwestern Willow Flycatcher (Hatten and Paradzick 2003, Hatten et al. 2010). Annual variation in the NDVI of breeding sites is strongly correlated with variation in the flycatcher's annual productivity (Paxton et al. 2007). Even relatively small decreases in foliar cover may render a site unsuitable for the Southwestern Willow Flycatcher (Allison et al. 2003). Dennison et al. (2009) have documented decreases in the NDVI of extensive stretches of riparian woodland occupied by beetles in Colorado, indicating decreases in vegetation

density and vigor due to tamarisk beetle defoliation. If other riparian birds are affected by loss of foliar cover in the same way as the flycatcher, tamarisk defoliation will likely have widespread effects on local and regional bird communities.

Of the studies we reviewed that examined nesting success during or after defoliation, most found no increase in nest predation, parasitism, or abandonment (DeGraaf 1987, Bell and Whitmore 2000, Matsuoka and Handel 2007, Allen et al. 2009, Schill and Yahner 2009). In contrast, Thurber et al. (1994) and Yahner and Mahan (1996) reported that artificial nests placed in defoliated areas were depredated at rates higher than nests placed in nondefoliated areas, although Thurber et al. (1994) found no association between canopy cover and nest success, suggesting that defoliation influenced predation indirectly, perhaps by altering predator abundance. Holmes et al. (2009), following the trajectory of defoliation over 33 years, found an increase in bird numbers during initial phases of an outbreak was followed by a decline even before insect populations reached their peak, suggesting that negative effects on habitat were offsetting the initial benefit of increased prey availability.

SEASONAL DEFOLIATION: AN ECOLOGICAL TRAP FOR RIPARIAN BREEDERS?

Tamarisk beetles typically defoliate a tamarisk over several annual cycles before the tree dies (Dudley 2005). Given that defoliation typically occurs in early summer, after many riparian birds have begun but not yet finished nesting, the multi-year cycles of defoliation and refoliation have the potential to create an "equal preference" ecological trap (Robertson and Hutto 2006). Such traps arise when an animal attempts to breed in a site that it perceives as suitable but in which reproductive success is poor. Under such a scenario, breeding birds could be caught in a negative feedback loop by repeatedly returning in spring to breed in tamarisk-dominated areas, finding trees refoliated and habitat apparently suitable, only to experience defoliation later in the summer. This trap is especially likely for species whose year-to-year fidelity to a breeding site is high.

The timing of defoliation relative to the timing of breeding will largely determine how the reproductive success of each bird species will be affected by seasonal tamarisk defoliation. To better understand this dynamic for a well-studied riparian nester, we combined data on tamarisk defoliation near Dolores, Colorado (Bureau of Reclamation, unpubl. data), with nest-productivity data (average number of young fledged per day of year) from a long-term study of the Southwestern Willow Flycatcher in central Arizona (Ellis et al. 2008; Fig. 3). Because information on nesting success and timing of tamarisk defoliation does not exist for any one site, we combined information from two sites for the sake of illustration. At Dolores, defoliation by beetles spans the period responsible for 80% of the Southwestern Willow Flycatcher's annual productivity. If we assume that the flycatcher's nest success is at its typical level prior to full defoliation but that no nests are successful after full defoliation, beetle herbivory would reduce its annual population productivity by at least 40% (Fig. 3). If nest success declines during the period of defoliation, not simply after its peak, productivity could be reduced as much as 80%. Although timing of defoliation and nesting will vary by site and species, and so the degree to which defoliation affects a species' reproductive success will vary, this simulation
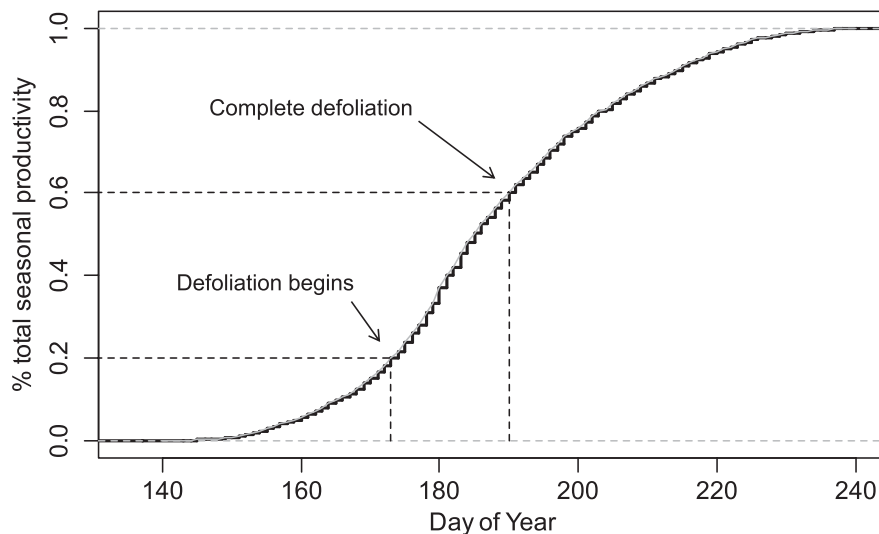

FIGURE 3.   Percentage of cumulative nest productivity (average number of young fledged per day; *y* axis) by day of year (*x* axis) of Southwestern Willow Flycatchers nesting at Roosevelt Lake, Arizona, 1996–2004. Near Dolores, Colorado, defoliation by tamarisk beetles begins on day 173 (~22 June) and is complete by day 190 (~8 July). If the flycatcher were to nest near Dolores on the same schedule as at Roosevelt Lake, over 80% of its nest productivity would occur after defoliation begins.

underscores the potential for defoliation to significantly reduce productivity of birds nesting in tamarisk stands being defoliated by beetles. Reduction in reproductive success is likely greatest for birds, such as many migratory species, that initiate nests later in the season, before defoliation. Open-cup nesters are also vulnerable because defoliated tamarisks offer less protection from higher temperatures. For riparian bird species with small populations, repeated cycles of defoliation after nest initiation followed by regrowth the next spring could lead to local extirpation. Any negative effects of an ecological trap would end when death of tamarisks makes the site no longer attractive to breeding birds; subsequent long-term consequences of the introduction of tamarisk beetles would depend on the rate of the habitat's recovery after the tamarisks are dead.

LONG-TERM CONSEQUENCES OF WIDESPREAD TAMARISK LOSS DUE TO BIOCONTROL BY BEETLES

Under favorable ecological conditions, restoration of native cottonwoods and willows to the size and structure required by riparian woodland birds can proceed relatively quickly (3–6 years; e.g., Kus 1998, Taylor and McDaniel 1998, Rood et al. 2003). However, abiotic and biotic conditions in many areas now occupied by tamarisk have been so altered anthropogenically that recolonization by native willows and cottonwoods is unlikely without intensive restoration efforts (Harms and Hiebert 2006, Shafroth et al. 2008). Given the cost and effort required for active restoration over the large areas likely to be affected by the tamarisk beetle, widespread tamarisk mortality will likely result in a net loss in riparian habitat for at least a decade or more. In some areas, such as the Colorado River in the Grand Canyon (Holmes et al. 2005, Sogge et al. 2005) and the Pecos River in New Mexico (Hunter et al. 1988), where riparian birds' abundance and distribution expanded when tamarisk created new riparian woodlands where none existed in recent times, loss of tamarisk will likely result in the loss of at least some species from the riparian breeding bird community (e.g., Brown 1992). Large-scale aerial spraying of tamarisk along the Pecos River in New Mexico resulted in the loss of tens of kilometers of riparian forest and the subsequent extirpation of breeding Yellow-billed Cuckoos (*Coccyzus americanus*) from the treated areas (Livingston and Schemnitz 1996, Travis 2005), a possible analog of the effects of biocontrol. Critical habitat for the endangered Southwestern Willow Flycatcher includes stretches of tamarisk-dominated riparian woodland (USFWS 2005), with approximately 28% of known territories rangewide found in such habitat (Durst et al. 2007), so a rapid loss of tamarisk across the Southwestern Willow Flycatcher's range could slow or jeopardize its recovery. Another consideration is the ability of locally or regionally rare species to recolonize habitat regenerated at a treated site. An important factor in the Southwestern Willow Flycatcher's colonization of new sites is distance from source populations (Winkler et al. 2004).

Colonization of new sites is high up to 30 km from a source population then decreases with distance (Paxton et al. 2007). Thus, predicting how biocontrol with beetles will affect populations of riparian birds over the long term will require knowledge of the spatial extent of affected areas, the probability and length of habitat recovery, and the rate at which avian populations will recolonize recovered habitat.

MANAGEMENT IMPLICATIONS AND SUGGESTIONS FOR FUTURE RESEARCH

Tamarisk has been viewed almost exclusively as a management problem and has been the subject of extensive efforts at control and eradication. Perceptions of its ecological role, however, are changing, and the challenges of control and restoration of native riparian habitat are now better understood (Shafroth et al. 2008, Stromberg et al. 2009, Hultine et al. 2010). Our review highlights that birds' response to biocontrol of tamarisk is likely to be complex, with different species responding differently according to (1) their ability to exploit tamarisk beetles as prey, (2) their sensitivity to the seasonality of defoliation, and (3) their dependence on current tamarisk stands as productive habitat (Table 1). Although the majority of species documented to use tamarisk likely have populations large enough or are widespread enough in other habitats to withstand large-scale loss of tamarisk, species that use tamarisk extensively and with distributions confined to areas dominated by tamarisk may experience significant population declines, locally or regionally.

Given the potentially rapid and widespread loss of tamarisk due to biocontrol by the beetle, and the uncertainty of how such loss may affect riparian bird populations, proactive actions to minimize negative consequences are prudent. Those actions could include (1) giving priority to sustaining and protecting existing stands of native-dominated riparian vegetation that may act as important refugia in areas currently or likely to be affected by the beetle, including ensuring supplies of water adequate to maintain these woodlands as well as protection from any further loss or degradation, (2) actively restoring native willows, cottonwoods, and other native riparian vegetation in areas now dominated by tamarisk and known to harbor breeding populations of sensitive riparian birds, and (3) long-term planning with the goal of balancing the spatial and temporal loss of tamarisk habitat with restoration, particularly with restored sites near enough (e.g., within 30 km) to allow successful colonization through dispersal as tamarisk succumbs to defoliation.

We suggest several aspects of the tamarisk beetle–bird interaction that warrant future research: (1) the potential for tamarisk beetles to act as food for riparian birds, (2) the effects of loss of foliar cover on other native and non-native insect prey, (3) the effect of loss of foliar cover on nest success and annual productivity, and (4) the rate at which native vegetation recovers after tamarisk beetle attack in areas of mixed vegetation versus that in monotypic stands of tamarisk.

ACKNOWLEDGMENTS

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