

Erratum

Southwestern Avian Community Organization in Exotic Tamarix: Current Patterns and Future Needs

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***Abstract**—Tamarisk (saltcedar: *Tamarix*), an invasive exotic tree native to the Eastern Hemisphere, is currently the dominant plant species in most southwestern riparian ecosystems at elevations below 1500 m. Tamarisk alters abiotic conditions, vegetation structure, and the plant species composition of native southwestern riparian ecosystems, and, in turn, affects native southwestern animal communities. However, information on the overall effects of tamarisk on avifauna is somewhat conflicting and incomplete. This paper attempts to resolve debate regarding the value of exotic tamarisk to avifauna across the Southwest by gleaning information from the published literature on: 1) which groups of birds use tamarisk; 2) avian species richness and abundance patterns in tamarisk; and 3) which attributes intrinsic and extrinsic to tamarisk are useful in predicting avian use. Use of tamarisk across the Southwest by certain groups of birds is consistently associated with the availability of specific food resources or nesting substrates. For example, frugivores, nectivores, platform-nesting raptors, and cavity nesters all tend to avoid tamarisk due to lack of fruit, tubular flowers, large trees, and pliable wood, respectively. However, use of tamarisk by other groups of birds, such as insectivores, cup nesters, and residency groups, is more complex and is strongly related to the tamarisk vegetation and geographic location being investigated. Avian species richness and abundance patterns in tamarisk are also variable, with evidence from the published literature suggesting that tamarisk vegetation along the lower Colorado River supports a depauperate riparian bird community compared to tamarisk vegetation along the Rio Grande and Pecos River. Overall, avian use of tamarisk is best explained by species-specific nesting and foraging requirements, which in turn covary with vegetation structure and floristics, and are mediated by climatic influences.*

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Background

Evidence that humans impact their local environment dates as long ago as 40,000 years before the present (Drake and others 1989). As human populations on the planet grow, expand, and colonize new landscapes, humans are also beginning to impact the global environment by: 1) increasing concentrations of carbon dioxide in the atmosphere and altering global climatic conditions; 2) producing and releasing persistent organic compounds (e.g., chlorofluorocarbons); 3) changing land cover; and 4) encouraging the spread of invasive organisms, so-called 'biological pollutants' (Coblentz 1990; Soulé 1990; Jobin and others 1996; Vitousek and others 1996; Olson and Harris 1997; Higgins and others 1999; Palumbi 2001). Potential impacts of human activities include local and global species extinctions. Areas where "anthropogenic activities reduce natural habitat in centers of endemism" (Dobson and others 1997:550) are considered 'hot spots' of species endangerment. Within the United States, the Southwest is one of several regions designated as such a hot spot (Dobson and others 1997; Flather and others 1998; Abbitt and others 2000). The Southwest includes southeastern California, most of Arizona and New Mexico, southwestern Colorado, southern Utah, and Texas west of the Pecos River (Bogan and others 1998). The region is topographically and climatically diverse, with elevations ranging from sea level to 4,000 m, and temperatures ranging from mild to extreme cold or intense heat. Precipitation and water availability also vary. The diversity of abiotic conditions, combined with elevational and latitudinal gradients, create a multitude of microhabitats, which have contributed to the evolution and maintenance of biological endemism and diversity (Hubbard 1977; Szaro 1980; Bogan and others 1998). Southwestern ecosystems most threatened by human activities are desert shrubland, arid grassland, and, particularly, riparian.

Southwestern riparian ecosystems occur along streams and rivers and are characterized by narrow bands of mesic vegetation embedded in extensive areas of xeric upland vegetation (Szaro and Jakle 1985; Knopf and others 1988). Anthropogenic alteration, degradation, and destruction of native riparian ecosystems have great potential to negatively impact the long-term stability of southwestern wildlife populations. Southwestern riparian areas are one of the few places where plants and wildlife can find surface or near-surface water

and, consequently, support a large number and variety of southwestern wildlife species (Stamp 1978; Szaro 1980; Knopf and others 1988; Brown and Johnson 1989). Specifically, southwestern riparian areas support more breeding birds than surrounding uplands and attract higher numbers of migratory birds (Carothers and others 1974; Stamp 1978; Szaro 1980; Szaro and Jakle 1985; Hunter and others 1988; Knopf and others 1988; Ellis 1995; Yong and Finch 1997; Patten 1998; Skagen and others 1998; Yong and others 1998; DeLay and others 1999; Kelly and Finch 1999; Kelly and others 2000).

Although indigenous peoples have inhabited the Southwest for at least 10,000 years (e.g., the Anasazi, Mogollon, and Hohokam peoples), large-scale anthropogenic impacts to southwestern riparian ecosystems intensified in the 1870s when the Southwest began to be settled by Anglo-Americans, accompanied by development of irrigation, agriculture, livestock grazing, and, eventually, urban and suburban areas (Carothers 1977; Bogan and others 1998). Threats to native riparian ecosystems include: 1) removal of native riparian vegetation (e.g., phreatophyte control); 2) urban and suburban development; 3) groundwater pumping; and 4) river damming, diversion, and channelization (Carothers and others 1974; Carothers 1977; Davis 1977; Johnson and others 1977; Ohmart and others 1977; Knopf and others 1988; Johnson 1989; Howe and Knopf 1991; Marshall and Stoleson 2000). In addition, but perhaps not as widely appreciated, native riparian ecosystems are being altered by the spread and establishment of exotic plants, which can affect ecosystem function and distributions and population dynamics of native species (Knopf and others 1988; Howe and Knopf 1991; Vitousek and others 1996; Westbrooks 1998; Higgins and others 1999; Fleishman and others 2003).

An invasive exotic plant of management concern in the Southwest is tamarisk or saltcedar (*Tamarix*), a long-lived (50-100 years) deciduous tree native to arid regions of the Eastern Hemisphere. Plants within the genus *Tamarix* are generally characterized by: 1) deep pink to almost white flowers (fig. 1); 2) capsule fruit, bearing many tiny seeds; 3) small scale-like leaves with salt-secreting glands; and 4) deep, extensive root systems (up to 100 feet) that extend to the water table. Several species of tamarisk were first introduced into the United States in the early 1800s for stabilization of eroding stream banks and for use as both ornamentals and windbreaks (DeLoach 1997; Westbrooks 1998). By the 1930s,



Figure 1. Flowering tamarisk (*Tamarix*). (Photographs by H. A. Walker.)

tamarisk had successfully invaded riparian areas throughout the western United States (Anderson and others 1977a; Ohmart and others 1977; Brown and Johnson 1989; DeLoach 1997). Initial spread of tamarisk along such rivers as the Gila, Salt, Pecos, Colorado, and Rio Grande was encouraged by the construction of dams and flood control structures, which disrupted natural hydrologic cycles and decreased the competitive ability of native plant species that depended on flood-created regeneration sites (Marshall and Stoleson 2000). Subsequently, tamarisk has successfully invaded riparian areas and ephemeral wetlands (e.g., playas, arroyos, and alkali flats) that are relatively undisturbed by human activities. Introduced tamarisk is now the dominant plant species in most southwestern riparian ecosystems at elevations below 1500 m, where it often forms large monotypic stands to the exclusion of native plants.

The success of tamarisk in replacing native riparian plant species in the Southwest is partially due to its ability to alter ecosystem function and create unsuitable growing conditions for other plants. In particular, tamarisk: 1) increases soil salinity above the tolerance level of most native plants by secreting a salty exudate from its foliage; 2) reduces water availability by drawing down ground water with its deep root systems to depths below root systems of native plants; and 3) increases fire frequency by shedding its foliage and creating thick, fire-prone ground cover (Anderson and others 1977a; Cohan and others 1979; Livingston and Schemnitz 1996; DeLoach 1997). Tamarisk is able to further limit growth of native plant species due to the fact that it: 1) has a 5-month fruiting period that allows it to exploit suitable germinating conditions over a longer period than many native plant species (Howe and Knopf 1991); 2) produces a large seed bank that allows it to out-compete many native plant species for germination sites (Cohan and others 1979; Howe and Knopf 1991; Westbrooks 1998); 3) in the absence of scouring flows, forms thick stands

that shade native plant germination sites; and 4) establishes opportunistically (in both saturated and dry surface soils) after flood disturbance (Stromberg 1997).

By altering abiotic and vegetative conditions of native riparian ecosystems, tamarisk also affects native southwestern animal communities (see DeLoach 1997). However, information on the overall use of tamarisk by wildlife is conflicting and somewhat incomplete. Some authors have reported preferential use of tamarisk vegetation by certain animal species, while other authors have reported that, like many exotic plant species, tamarisk establishment alters animal species compositions and reduces biodiversity (see DeLoach 1997; Olson and Harris 1997). Similar debate exists in the literature regarding the value of tamarisk specifically for avifauna. It is generally accepted that initial spread and establishment of tamarisk in native southwestern riparian ecosystems, and corresponding loss of native vegetation, resulted in population reductions in many riparian bird species (Carothers 1977; Ohmart and others 1977; Cohan and others 1979; Hunter and others 1985; Hunter and others 1987; Hunter and others 1988). However, there is evidence that birds are adjusting to the expansion of tamarisk and are utilizing tamarisk-dominated vegetation for both nesting (e.g., Hunter and others 1988; Brown and Trosset 1989; Fleishman and others 2003) and foraging (e.g., Yard and others 2004).

It is estimated that at the current rate of spread exotic plants will dominate all southwestern riparian ecosystems within 50 to 100 years (Howe and Knopf 1991). Therefore, knowledge of the effects of tamarisk on native organisms will become substantially more relevant as tamarisk becomes the predominant vegetation type available and as the need for habitat management increases (Anderson and others 1977a; Ohmart and others 1977). In this paper, I try to resolve debate regarding the value of tamarisk to avifauna across the Southwest by gleaning information from the published literature on: (1) which groups of birds use tamarisk; 2) avian species richness and abundance patterns in tamarisk; and (3) which attributes intrinsic and extrinsic to tamarisk are useful in predicting avian use. Objectives of the research are to 1) identify broad predictive patterns in use of tamarisk by birds across the Southwest, 2) delineate knowledge gaps in order to direct future scientific research, and 3) provide information useful for management practices that

seek to control or eradicate exotic vegetation while protecting southwestern avifauna.

Which Birds Use Tamarisk?

Presence of a bird species in a particular vegetation type depends on the bird's life history requirements and the availability of physical and biological environmental factors necessary for survival and reproductive success (Szaro 1980; James and others 1984; Cody 1985; Rosenberg and others 1991). Interspecific competition also plays a role in determining species' occurrences, but it is difficult to quantify over broad geographic regions (Carothers and others 1974; James and others 1984). Several predictive patterns of which birds use tamarisk can be gleaned from the literature by grouping birds into guilds according to their shared life histories, specifically their diet, nesting site requirements, and residency status.

Tamarisk Use by Diet Guilds

Food acquisition is important for survival during all phases of a bird's annual cycle and influences seasonal patterns in habitat use. Not all birds use tamarisk to meet food-related requirements and some forage largely or exclusively in adjacent vegetation. Nevertheless, many bird species appear to forage in tamarisk. Few studies investigating the value of food resources in tamarisk to birds used direct measures such as observations of foraging behavior or analyses of stomach and fecal contents. Instead, correspondence between presence of avian diet guilds and abundance of food types is used as a proxy indicator of whether tamarisk vegetation provides necessary food resources.

Five primary diet guilds are discussed in the literature: granivores, frugivores, timber drillers and gleaners (which is often considered to be a foraging, rather than diet, guild, but will be included here), nectivores, and insectivores. As a rule, granivorous bird species prefer or do not avoid tamarisk, while frugivores, timber drillers and gleaners, and nectivores appear to avoid tamarisk (Anderson and others 1977a; Cohan and others 1979; Brush 1983; Anderson and Ohmart 1984b; Rosenberg and others 1991; Ellis 1995). Consistent use of tamarisk by granivores is possibly due to the fact that, though affected by age and water availability, all tamarisk plants produce copious amounts of seeds (up to 100 million seeds per year) from mid-spring to fall.

However, some studies postulate that tamarisk seeds might be too small to provide adequate forage for many granivores. Its lack of fleshy fruits and dense, hard wood result in consistent avoidance of tamarisk by frugivores and timber drillers and gleaners, respectively. Tamarisk floral morphology apparently limits the ability of nectivores to utilize the large numbers of nectar-laden tamarisk flowers available from mid-spring to fall.

Unlike in the above four diet guilds, use of tamarisk by insectivorous birds has been found to vary with location and season; some studies have found that insectivorous birds showed no selection against tamarisk (Anderson and others 1977a; Rosenberg and others 1991; Ellis 1995), while others have found the reverse (Cohan and others 1979; Anderson and Ohmart 1984b). The variability in tamarisk use by insectivores is partially explained by differences in: 1) adjacent vegetation, such as mesquite, which can be good sources for arthropod 'tourist' species that move into tamarisk-dominated vegetation; 2) the composition and diversity of major arthropod taxa between tamarisk and native vegetation and among locations (e.g., Apache cicadas [*Diceroprocta apache*] are less abundant and Orthopterans are more abundant in tamarisk on the middle Pecos River than on the lower Colorado River); and 3) timing of emergence of arthropod prey (e.g., Apache cicadas) (Cohan and others 1979; Hunter and others 1988; Rosenberg and others 1991; Andersen 1994; Mund-Meyerson 1998; DeLay and others 1999; Drost and others 2003). Despite the above, in general, the large number of 1) pollinator species (e.g., *Cotinus* beetles) attracted to flowering tamarisk, 2) the exotic leafhopper (*Opsiastactogalus*) accidentally introduced with tamarisk, and 3) Apache cicadas are all good sources of arthropod prey in tamarisk vegetation for insectivorous birds during spring and summer (Rosenberg and others 1982; Glinski and Ohmart 1983; Glinski and Ohmart 1984; Andersen 1994; Drost and others 2003; Yard and others 2004).

Tamarisk Use by Nesting Guilds

In addition to food resources, the availability of nest sites, which directly affects reproductive success, is an important determinant in habitat selection (Hunter and others 1987). The ability to nest in tamarisk is partly related to nest type (e.g., cavity, cup, platform) and the availability of suitable nesting substrates. Cup nesters (including riparian obligates) are able to use tamarisk vegetation in many areas and sometimes nest predominately in

tamarisk even when native vegetation is available (Hunter and others 1988; Brown and Trosset 1989; Rosenberg and others 1991; Brown 1992; Ellis 1995). However, evidence suggests that midsummer breeders with open cup nests are less likely to use tamarisk than are birds with insulated nests (e.g., sphere nests or cup nests with shade structures) on the lower Colorado River (Hunter and others 1988). This pattern cannot be explained by the lack of suitable nesting substrates for open cup nesters on the lower Colorado. A number of other species are also generally unable to meet their nesting requirements in tamarisk vegetation, including ground nesting charadriiformes (e.g., Least Tern [*Sterna antillarum*], Snowy Plover [*Charadrius alexandrinus*]), large raptors, and cavity nesters (e.g., woodpeckers, nuthatches) (Anderson and others 1977a; Cohan and others 1979; Brush 1983; Hunter and others 1987; Rosenberg and others 1991; Ellis 1995; Koenen and others 1996; Taylor 2003). Large raptors might be absent from tamarisk due to the lack of tall, large trees needed for placement of platform nests (Hunter and others 1985). Cavity nesters might be absent from tamarisk because (1) tamarisk wood is too hard to excavate, (2) the body sizes of North American woodpeckers (and required cavity sizes) generally exceed the maximum size of tamarisk trunks and limbs, and (3) the absence of woodpeckers affects secondary cavity nesters that require woodpeckers for cavity excavation (Anderson and others 1977a; Brush 1983). A notable exception is the Ladder-backed Woodpecker (*Picoides scalaris*), which was the first New World woodpecker to be documented breeding in tamarisk, most likely due to the fact that it is the smallest and best excavating woodpecker in the range of introduced tamarisk (fig. 2; Brush 1983).

Tamarisk Use by Residency Guilds

Avifauna of southwestern riparian ecosystems can be categorized into four principal residency groups: 1) residents (also called permanent residents), which tend to be present throughout the year; 2) summer residents (also called summer visitors or summer breeders), which are only present during late spring and summer; 3) winter residents (also called winter visitors), which are only present for varying lengths of time between September and April; and 4) transients (also called *en route* migrants), which are only present for narrow time periods during fall and spring migration (Szaro 1980; Hunter and others 1985; Hunter and others 1987; Hunter and others 1988; Finch and others



Figure 2. Cavity nesting birds generally avoid tamarisk (*Tamarix*) and are restricted to native vegetation. A notable exception is the Ladder-backed Woodpecker (*Picoides scalaris*). The Ladder-backed Woodpecker (left photographs) was the first New World woodpecker to be documented breeding in tamarisk, which is most likely due to the fact that it is the smallest and best excavating woodpecker in the range of tamarisk. Note the stout bill morphology of the Ladder-backed Woodpecker compared to that of the Red-shafted Flicker (right photographs: *Colaptes auratus cafer*). (Photographs by S. Guallar, S. Ogle, and J. Puschock.)

1995). Most research on avian use of tamarisk has focused on residents and summer residents during the summer breeding season. Little research has been completed on winter residents and even less on transients.

Studies on residents and summer residents during the breeding season indicate that peak timing of egg laying is a confounding determinant in breeding bird use of tamarisk (Hunter and others 1985, 1988). Use of tamarisk by early summer breeders generally increases from east to west (Hunter and others 1985, 1988). In contrast, most midsummer breeders are largely restricted to native vegetation on the lower Colorado River, but they occur in greater or equal densities in tamarisk as native vegetation on the middle Pecos River, the Rio Grande, and higher-elevation stretches of the Colorado River (Anderson and others 1977a; Cohan and others 1979; Hunter and others 1985; Hunter and others 1987; Hunter and others 1988). Research during the winter season indicates that avian densities and species richness in tamarisk also follow geographic patterns; densities and species richness of wintering birds are generally lower in tamarisk than in native vegetation types on the lower Colorado River and Rio Grande, while wintering birds use tamarisk heavily on the middle Pecos River (Anderson and others 1977a; Cohan and others 1979; Anderson and Ohmart 1984b; Hunter

and others 1988; Rosenberg and others 1991). There is some evidence to suggest that, as with breeding and wintering birds, use of tamarisk by transients is also related to geographic location. However, the only published studies that specifically addressed use of tamarisk by transients were from the middle Rio Grande. I found no published studies on transient use of tamarisk on the Pecos River and the few studies that measured avian use in tamarisk during the spring and/or fall migratory periods along the lower Colorado River provided little specific information on migrating birds. The lack of work on transient use of tamarisk makes conclusions problematic. Nevertheless, it appears that transients sometimes use tamarisk in equal numbers to the native vegetation along the middle Rio Grande (Leal 1994; Ellis 1995; Yong and others 1998; Kelly and Finch 1999; Kelly and others 2000; Yong and Finch 2002), while both spring and fall birds (of all residency groups, not just transients) avoid tamarisk along the lower Colorado River (Anderson and others 1977a; Cohan and others 1979; Anderson and Ohmart 1984b).

Species Richness and Abundance Patterns in Tamarisk

When attempting to derive broad patterns in avian species richness and abundance in tamarisk from the published literature, it became immediately apparent that most research investigating avian use of tamarisk is biased towards riparian ecosystems that were historically dominated by native cottonwood (*Populus*), willow (*Salix*), and/or mesquite (*Prosopis*) along the Rio Grande and Pecos and Colorado Rivers in New Mexico, Texas, and Arizona. Furthermore, it also became apparent that geographic location is a strong determinant of avian community structure and that avian species richness and abundance differ consistently among the three southwestern river valleys. A predominant geographic pattern is that tamarisk-dominated vegetation along the lower Colorado River supports a depauperate riparian bird community compared to similar tamarisk vegetation along the Rio Grande and Pecos River (Hunter and others 1985; Hunter and others 1987; Hunter and others 1988) (fig. 3). Furthermore, tamarisk vegetation along the lower Colorado River supports lower avian densities and species richness than the native vegetation types. In

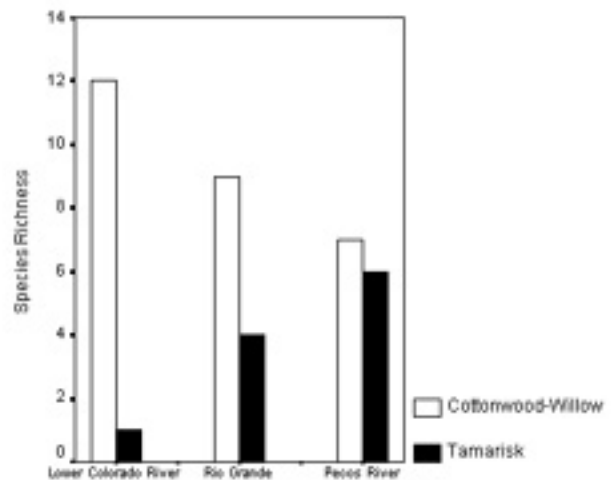


Figure 3. Number of bird species (N = 13), common to the Rio Grande and the Pecos and lower Colorado Rivers, with more than fifty percent of their detections in either cottonwood-willow (*Populus-Salix*) or tamarisk (*Tamarix*) vegetation, when evaluating presence only in those two vegetation types. Adapted from data published in Hunter and others (1985, 1988).

contrast, along the middle Pecos River, where a substantial riparian woodland was absent prior to establishment of tamarisk, total densities and species richness in tamarisk surpasses that of the native Chihuahuan grassland and shrub communities (Anderson and others 1977a and 1977b; Cohan and others 1979; Anderson and Ohmart 1984b; Hunter and others 1985; Hunter and others 1988; Rosenberg and others 1991; Livingston and Schemnitz 1996). Tamarisk invasion has even promoted expansions of several bird species within the Pecos Valley (Hunter and others 1988; Livingston and Schemnitz 1996). On the Rio Grande, several published studies report that avian densities and species richness are lower in tamarisk relative to native vegetation (Anderson and Ohmart 1984b; Hunter and others 1988; Kelly and Finch 1999), while other studies report that avian densities and species richness are either similar or higher in tamarisk (Hunter and others 1985; Ellis 1995; Livingston and Schemnitz 1996; Kelly and Finch 1999).

Which Attributes of Tamarisk Predict Avian Use?

Variation in both physical and biological environmental factors is apparent in tamarisk-

dominated sites. Due to its ability to tolerate a wide range of environmental conditions, tamarisk can flourish along both permanent and ephemeral water sources and in a wide variety of soil types (saturated and dry), elevations, and climates. In addition, both the structure of tamarisk vegetation and the floristics of adjacent and associated vegetation are variable (Brotherson and others 1984). As a result of differences in environmental features among tamarisk vegetation types across local and broad geographic scales, tamarisk provides a variety of abiotic microclimates, food resources, and foraging and nesting substrates. Thus, variation in environmental features must be examined in relation to avian life history requirements in order to tease apart the factors that confound region-wide patterns in avian use of tamarisk (James and others 1984; Sogge and Marshall 2000).

As discussed in the previous section, availability of food resources and nesting substrates are two predictors of avian presence in tamarisk, specifically of various diet and nesting guilds. However, these attributes cannot explain the geographic variation in use of tamarisk by residency groups nor can they explain the geographic patterns in species richness and abundance in tamarisk. Geographic variation in use of tamarisk appears to pose an obstacle to drawing sweeping region-wide conclusions about the value of tamarisk to avifauna: few region-wide generalizations regarding avian community structure in tamarisk can be derived from information based on any one river valley. However, several underlying factors are confounding patterns seen at the geographic scale. In the following paragraphs, I will evaluate the extent to which vegetation structure, plant species composition, and climate underlie two somewhat consistent patterns in avian use of tamarisk: 1) Tamarisk vegetation along the lower Colorado River supports fewer total species and individuals of midsummer breeding and wintering birds than tamarisk vegetation along the Rio Grande and middle Pecos River; and 2) early summer breeders are more abundant in tamarisk along the lower Colorado River than in tamarisk along the Rio Grande and the middle Pecos River.

Confounding Variables: Vegetation Structure and Plant Species Composition

The vegetation structure (physiognomy) and plant species composition (floristics) of tamarisk-dominated vegetation are variable across the Southwest (fig. 4). Structure of individual tamarisk



Figure 4. The vegetation structure (physiognomy) of tamarisk is variable. Individual tamarisk plants can vary from thin-stemmed shrubs to multi-trunked trees and from ground cover seedlings to trees of 10 meters or more in height. (Photographs by K. Lair and H. A. Walker.)

plants can vary from thin-stemmed shrubs to multi-trunked trees and from ground cover seedlings to trees of 10 meters or more in height (Brotherson and others 1984). In addition, tamarisk-dominated vegetation can vary from mixtures of native and exotic plant species to stands comprised solely of tamarisk. Furthermore, vegetation adjacent to tamarisk stands can vary from native woodland to grassland or agricultural fields. Variation in both physiognomy and floristics of tamarisk-dominated vegetation is perhaps more useful in explaining geographic variation in avian use of tamarisk than variation in food resources or nest site availability alone. Physiognomy and floristics influence the types and availability of food resources and of foraging and nesting substrates (Szaro 1980; Fleishman and others 2003), and, therefore, are proxies for a large number of environmental factors necessary for birds to fulfill their life history (MacArthur and MacArthur 1961; Robinson and Holmes 1984; Szaro and Jakle 1985; Allison and others 2003; Fleishman and others 2003).

Though there are few consistent structural and floristic differences among tamarisk vegetation of the Rio Grande and the Pecos and Colorado Rivers, two primary differences exist among tamarisk vegetation examined in the published literature: 1) tamarisk stands on the lower Colorado River tend to be lower-statured and sparser than stands along the Pecos River, the Rio Grande, and upper elevations of the Colorado River; and 2) a larger number of

adjacent shrubs and annual plant species are present along the middle Pecos River. These geographic differences in physiognomy and floristics alone are probably insufficient to explain geographic patterns in avian community structure in tamarisk. Nevertheless, variation in physiognomy and floristics is correlated with local patterns in avian community composition and structure in tamarisk. Tamarisk vegetation with similar physiognomy as native vegetation generally supports similar avian densities and species richness (Brown and Trosset 1989; Livingston and Schemnitz 1996; Fleishman and others 2003), and tall, dense tamarisk stands that are structurally diverse are generally most often used by birds (Carothers and others 1974; Anderson and others 1977a; Stamp 1978; Szaro and Jakle 1985; Rosenberg and others 1991; Farley and others 1994; Livingston and Schemnitz 1996). Thus, in some situations, riparian communities dominated by tamarisk can be the structural or ecological analogs of native communities that are the required habitat of native riparian birds. Compared to physiognomy, avian species composition is generally more similar when floristics is more similar (Anderson and others 1977a; Fleishman and others 2003). Therefore, tamarisk stands that contain some attendant native plant species are more likely to support unique avian species that are usually closely associated with the native vegetation (Ellis 1995). In addition, floristics of adjacent plant species influences avian species composition and abundance in tamarisk vegetation by increasing availability of food and nesting substrates (Carothers and others 1974; Szaro and Jakle 1985). Due to the effect of floristics on avian communities, many studies suggest that addition of native trees and shrubs that provide high quality nesting and/or foraging substrates enhances the value of tamarisk vegetation to birds (Beidleman 1971; Anderson and others 1977a; Cohan and others 1979; Glinski and Ohmart 1983; Hunter and others 1987; Hunter and others 1988; Brown 1992; Livingston and Schemnitz 1996; Kelly and Finch 1999).

Confounding Variables: Climate

Birds select among available habitats using information on both physical and biological environmental attributes to meet energetic and reproductive needs and to maximize fitness: the vegetative component alone does not determine whether a bird will be present in a particular area. Thus, although availability of food resources and nesting substrates, which covary with physiognomy

and floristics, help to explain patterns in avian use of tamarisk, the physical environment is also an important causal factor. In the Southwest, elevation decreases and temperatures increases from east to west (e.g., from the Pecos River to the Colorado River) and from north to south (e.g., from the upper Colorado River to the lower Colorado River). These gradients influence abiotic environmental features extrinsic to tamarisk-dominated sites and help to explain the conflicting patterns seen in breeding birds (i.e., why midsummer breeders are absent in tamarisk on the lower Colorado River while early summer breeders rarely use tamarisk on the middle Pecos River).

Along the lower Colorado River, June and July temperatures frequently exceed 42 °C. Such high temperatures are detrimental to developing eggs and young. As tamarisk stands along the lower Colorado River tend to be lower-statured and sparse, it has been hypothesized that they might not provide adequate foliage cover for eggs and young during midsummer months (Anderson and others 1977a; Hunter and others 1985; Hunter and others 1987; Hunter and others 1988; Rosenberg and others 1991; Marshall and Stoleson 2000; United States Fish and Wildlife Service 2001). This hypothesis is supported by the fact that midsummer breeders with insulated nests are more likely to use tamarisk on the lower Colorado River than are open cup nesters (Hunter and others 1988). Opposite to summer temperatures, winter severity decreases from east to west. Hunter and others (1985, 1988) hypothesized that the low numbers of early breeding residents in tamarisk along the middle Pecos River and Rio Grande are due to the fact that tamarisk might provide suboptimal habitat for wintering early breeding Sonoran or Chihuahuan bird species in western Texas and eastern New Mexico. Physiological stress and associated mortality might prevent resident species from spreading into tamarisk and surviving to breed the next year.

Synthesis of Current Patterns

Southwestern riparian bird populations are affected by a complex set of interacting factors, including competition, diet preference, nesting requirements, psychological preferences for habitat attributes (e.g., vegetation structure, plant species composition, patch size), and physiological tolerance to microclimatic factors of the physical environment

(Szaró 1980; James and others 1984; Sogge and Marshall 2000). As factors necessary for the survival and reproductive success of birds fluctuate spatially and temporally, discussion of avian community composition and structure in tamarisk must involve biogeographic considerations. An evaluation of the variation in avian use of tamarisk across the Southwest generated several broad predictive patterns regarding which birds use tamarisk, species richness and abundance patterns in tamarisk, and which attributes intrinsic and extrinsic to tamarisk are useful in predicting avian use.

Use of tamarisk across the Southwest by certain groups of birds is consistently associated with the availability of specific food resources or nesting substrates. For example, frugivores, nectivores, ground nesting charadriiformes, platform-nesting raptors, and timber drillers, timber gleaners, and cavity nesters all tend to avoid tamarisk due to lack of fruit, tubular flowers, bare ground, large trees, and pliable wood, respectively, while granivores tend to prefer or at least do not avoid tamarisk regardless of locality possibly due to high seed abundances. In contrast, use of tamarisk by other groups of birds, such as insectivores, cup nesters, and residency groups, is more complex and is strongly related to the tamarisk vegetation and geographic location being investigated. Nonetheless, two predictive geographic patterns are evident for residency groups: 1) Tamarisk vegetation along the lower Colorado River supports fewer total species and individuals of both midsummer breeding and wintering birds than similar tamarisk vegetation along the Rio Grande and middle Pecos River; and 2) early summer breeders are more abundant in tamarisk along the lower Colorado River than in tamarisk along the Rio Grande and the middle Pecos River.

Evidence from literature published on avian species richness and abundance patterns in tamarisk suggests that tamarisk vegetation along the lower Colorado River supports a depauperate riparian bird community compared to tamarisk vegetation along the Rio Grande and Pecos River. However, as breeding birds (especially midsummer-breeding summer residents) are the most abundant group in riparian areas (Szaró and Jakle 1985) and are the most well documented, patterns in breeding bird use of tamarisk drive the patterns that have been described for avian species richness and abundance.

Overall, documented patterns in avian use of tamarisk are best explained by species-specific nesting and foraging requirements, which in turn covary with physiognomy and floristics, and are

mediated by climatic influences. Tamarisk vegetation most used by birds generally occurs as tall, dense, structurally and floristically heterogeneous stands. Such stands tend to have more nesting and foraging substrates, provide cover from thermal stress and predation, and support more food resources.

Future Needs

Despite the numerous studies that have been published on avian use of tamarisk, large gaps exist in our knowledge base:

1. Most research has focused on the lower Colorado River, which is vegetatively and climatically distinct from tamarisk-dominated sites elsewhere. As a result, broad conclusions made on the value of tamarisk to avifauna would be erroneous if based solely on data from the lower Colorado River (Brown and Johnson 1989). More studies are needed not only from the Rio Grande and the Pecos River, but from associated tributaries and other major southwestern river systems (Hunter and others 1985).
2. The majority of research has been completed during the breeding season. Although some information exists for wintering birds, there is much left to discover regarding tamarisk use by migrating birds.
3. Use of tamarisk by insectivorous birds has been found to vary with location and season, but little information is available to explain the observed variability. Studies are needed comparing insect biomass and availability of foraging substrates to foraging behavior and diet requirements.
4. Published literature on avian use of tamarisk has been largely limited to inventory – that is, simply recording the presence or absence of bird species in tamarisk vegetation. However, occupancy of a habitat alone does not imply optimality, only that the habitat meets the selection criteria for those species present (Sogge and Marshall 2000). Ultimately, the suitability of a habitat must be measured by reproductive success and survivorship (Sogge and Marshall 2000). The suitability (in terms of productivity and survivorship) of tamarisk-dominated vegetation to avian species in the Southwest is not well studied and has been mostly limited to work on one species, the Federally Endangered Southwestern Willow Flycatcher (*Empidonax traillii extimus*) (see Sogge and Marshall 2000). Notable exceptions are studies by Yong and others (1998) and Kelly and Finch (1999)

that looked at energetic condition (e.g., fat scores and mass) of transients on the middle Rio Grande, New Mexico. Additional studies quantifying survivorship and reproductive success should better determine the value of tamarisk habitats and should resolve whether tamarisk habitats are sinks for southwestern bird populations.

5. More studies (particularly experimental studies) are needed to tease out which factors delimit avian use of tamarisk at different scales. Hunter and others (1985, 1987, 1988) and others have put forth several hypotheses to explain observed patterns in avian use of tamarisk, but no studies have attempted to determine their validity. More data are needed to determine whether, for example, the relative insulation properties of tamarisk, availability of food resources, and/or vegetation structure limit bird use of tamarisk along east-west gradients.

6. Tamarisk vegetation is variable in structure and floristics. Hunter and others (1985) suggest that, in order to better quantify avian value of tamarisk, bird communities should be surveyed in a large range of tamarisk vegetation types. However, the diversity of tamarisk vegetation types hampers discussion of the types of tamarisk most preferred or avoided by birds. I propose that a classification system be developed for tamarisk vegetation based on such attributes as plant species composition, structure, and hydrology. Similar classification systems have been developed for streams (see Rosgen 1985), riparian forests (see Brown and others 1979; Szaro 1980), and tamarisk structural types (see Anderson and others 1977a). Only by formulating standardized terminology can the complexity of tamarisk vegetation types be addressed by both managers and researchers.

Discussion

Riparian ecosystems in the Southwest provide mesic sanctuaries from surrounding arid and semi-arid landscapes for a host of wildlife species (Patten 1998). Although riparian ecosystems represent only 1 percent of the total area in the southwestern United States, they support 75-80 percent of southwestern wildlife species (Knopf and others 1988). Specifically, riparian ecosystems support more breeding bird species than surrounding uplands (Johnson and others 1977; Hunter and others 1988; Knopf and others 1988; Ellis 1995; DeLay and others 1999; Kelly and Finch 1999) and, according to Hunter and others (1988), over 40 percent of all the bird species found in southwestern river valleys

depend, either partially or entirely, on riparian vegetation. In addition, southwestern riparian areas attract high concentrations of migratory passerines en route to their wintering or breeding grounds (Yong and Finch 1997; Skagen and others 1998; Yong and others 1998; Kelly and others 2000).

Over the last century, an estimated 90 percent of native riparian ecosystems in Arizona and New Mexico has been lost or degraded due to anthropogenic land clearing, fragmentation, river damming and impoundment, overgrazing, and addition of fertilizers and agricultural chemicals (Howe and Knopf 1991). Native cottonwood/willow (*Populus/Salix*) riparian forest is now considered one of North America's rarest forest types (Johnson 1989). Resulting from and compounding these anthropogenic changes is the widespread establishment of exotic plant species (Westbrooks 1998). It has been estimated that at the current rate of spread exotic plants will dominate all southwestern riparian ecosystems within 50 to 100 years (Howe and Knopf 1991).

A particularly successful exotic in the Southwest is tamarisk or saltcedar (*Tamarix*), an exotic tree from the Eastern Hemisphere that was introduced to the United States in the early 1800s for stabilization of eroding stream banks and use in wind breaks (DeLoach 1997). Tamarisk is quickly becoming the dominant vegetation type in southwestern riparian ecosystems (Hunter and others 1985; Brown and Johnson 1989) and it is thought that potential increases in average global temperatures and aridity will only further the spread of tamarisk and the decline of native plant species (see Marshall and Stoleson 2000). Introduced tamarisk alters the abiotic environment of southwestern riparian ecosystems by changing soil salinity, ground water availability, and fire frequency (Cohan and others 1979; Brotherson and others 1984; DeLoach 1997; Lovich and DeGouvenain 1998). In addition, tamarisk introduction, and associated loss of native riparian vegetation, is affecting faunal communities and could potentially result in the loss of approximately half of the avian species that breed in the Southwest (Knopf and others 1988).

In order to curtail future negative impacts of tamarisk on native ecosystems, many federal, state, and tribal agencies are undertaking aggressive campaigns to reduce or eradicate tamarisk in the Southwest through mechanical, chemical, and biological control (Fleishman and others 2003). However, many such efforts are being undertaken on a site-specific basis without sufficient quantitative

data on the value of tamarisk to wildlife, specifically avifauna. Although development of broad management guidelines is difficult due to the variability of tamarisk vegetation and the scale of infestation (Szaro 1980; Knopf and others 1988), site-specific data and management policies can lead to erroneous conclusions regarding the desirability and efficacy of tamarisk removal programs across the Southwest (Knopf and others 1988). In this paper, I recommend that more research be completed on the local and regional use of tamarisk by avifauna and that a classification system of tamarisk vegetation types be developed to aid in defining which types of tamarisk are most useful and detrimental to wildlife. However, tamarisk control actions already underway or planned for the near future cannot wait for the results of future scientific projects. For those control programs, results from this paper suggest that monotypic stands of tamarisk that are sparse and lower-statured should be a priority for removal, while stands that are structurally and floristically diverse can function as temporary replacements for native vegetation for a number of riparian bird species. Regardless of which types of tamarisk are removed, intensive tamarisk removal projects that eradicate tamarisk and leave areas bare of woody overstories and/or understories, without restoring native vegetation in the near term, might threaten the local persistence of many native birds. At the very least, tamarisk removal projects should be accompanied by studies of birds and other organisms. Such studies are essential to determine whether tamarisk control projects achieve their targeted goals.

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