SESSION 12

Negative Economic and Ecological Impacts of Invasive Weeds

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Ecological Interactions in the Biological Control of Saltcedar (*Tamarix* spp.) in the United States: Toward a New Understanding

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Abstract

Saltcedars (*Tamarix* spp. Tamaricaceae) (SC) are exotic, invasive shrubs to medium-sized trees native to the Old World. In riparian ecosystems of the western United States, SC replaces native plant communities, degrades wildlife habitat, reduces biodiversity, alters stream channel morphology, uses large quantities of groundwater, increases wildfire frequency, reduces recreational and agricultural usage, and has contributed to the decline of many wildlife and fish species. In recent years, the southwestern willow flycatcher (*Empidonax trailii extimus*) (sw WIFL) has begun nesting extensively in SC in some of its major breeding areas in Arizona, but not in other areas, since SC has replaced its native willow nest trees. This has caused great concern among flycatcher biologists that the proposed biological control of SC will further reduce sw WIFL populations.

Current understanding of the causes of the SC invasion and of its effects on wildlife appear to be guided mostly by two paradigms. First, that only abiotic (mostly anthropogenic) changes such as altered hydrologic regimes, lowered water tables, high soil salinity, wildfires, and livestock grazing are determinants of SC abundance. These factors make SC appear "better adapted" and "more aggressive" than the native vegetation. SC is said to be only a passive invader, after the ecosystem already had been damaged by human disturbances. Second, that in areas now too dry or too saline, SC communities can act as functional analogs of native plant communities. This concept has been extended recently, but without supporting evidence, to include equivalency in providing habitat for wildlife, including the sw WIFL. Neither concept explains the dramatic invasion and dominance by SC along unregulated streams, often far from human disturbances. The extended equivalency concept is counter to consistent field observations of lower bird species diversity and density in SC, lower sw WIFL reproductive success, lack of fruits, seeds, suitable insects and nesting cavities for birds and other wildlife, and higher frequency of wildfires that destroy active sw WIFL nests in SC. Circumstantial evidence also indicates that SC may provide less protection from nest parasitism and predation and from climatic extremes.

Nevertheless, the sw WIFL nests extensively in SC in some major nesting areas, even though suitable willows grow adjacently. The birds appear to be attracted to the site by dense foliage in moderate to broad floodplains, near or over free water, and with adequate populations of flower-feeding, flying insects. We propose that they nest in SC instead of willow trees because of the superior branching structure of SC for nest placement, even though other traits of SC are inferior and lead to lowered reproductive success - a case of a "super stimulus". We project that biological control, by the introduction of host specific insects of SC from Eurasia, would provide the missing insect herbivory needed to negate the appearance that SC is "more aggressive" and "better adapted" than the native plants, and to reduce it to a non-damaging member of western riparian plant communities. This reduction in competition is expected to allow the native vegetation to recover in areas where soil salinity and depth to water table are suitable, which includes nearly all of the major sw WIFL breeding areas. Also, because of the present synergetic interaction with SC, some degree of improvement in these abiotic factors and wildfire frequency will result from biological control. Biological control is expected to gradually reduce SC density, with a concurrent increase in cottonwood/willow and other native habitat. The sw WIFL will continue to nest in the remaining SC trees and will begin again to nest in native vegetation.

Keywords: *Tamarix*, tamarisk, saltcedar, salt cedar, biological control, *Tamarix* ecology, willow flycatcher, *Empidonax trailii*, WIFL, functional equivalency, super stimulus

Introduction

The invasion by saltcedars (*Tamarix* spp., family Tamaricaceae), exotic shrubs to medium-sized trees from the Old World, is arguably one of the worst ecological disasters ever to befall western riparian ecosystems of the United States. Deciduous saltcedar (SC) has displaced or replaced native plant communities, degraded wildlife habitat, and is probably a major cause in the decline of many native species, including several now threatened or endangered (T&E) species (reviewed by DeLoach 1991, DeLoach and Tracy 1997, Lovich and DeGouvenain 1998). SC was documented as a major cause of decline of the southwestern subspecies of the willow flycatcher (*Empidonux trailii extimus* Phillips) (sw WIFL) when it was listed as endangered (U.S. Fish and Wildlife Service 1995). To date, herbicidal and mechanical controls and manual removal have been the primary tools available for SC control. Although effective in limited areas, these methods are expensive, labor intensive, require frequent retreatments, and (except for manual removal) often harm many nontarget species, resulting in damage to native plant communities whose protection and recovery is typically the reason for control in natural areas.

A program to develop biological controls for SC, by the introduction of host-specific insects from its native range in Eurasia, was begun by one of us (DeLoach) of the U.S. Department of Agriculture (USDA), Agricultural Research Service (ARS), at Temple, Texas in 1986. Concurrence on a petition that the program should proceed was obtained from the Technical Advisory Group for Biological Control Agents of Weeds (TAG) of the USDA's Animal and Plant Health Inspection Service (APHIS) in December 1991. Research then began on overseas exploration and testing and on testing in the ARS

Arthropod Containment Facility (quarantine) at Temple, TX. This research was supported in part by the U.S. Department of the Interior (USDI) Bureau of Reclamation (BOR), and later also by the USDI Bureau of Land Management and by USDA-APHIS.

The first insects were recommended for field release by the TAG in October 1994 and releases were planned for June 1995. However, in March 1995, the sw WIFL was placed on the federal endangered species list (U.S. Fish and Wildlife Service 1995). This bird had begun nesting extensively in SC in central Arizona since SC displaced its native cottonwood/willow (C/W) nesting habitat. This is perhaps the first case in which an invasive plant, scheduled for biological control, has begun to be utilized to an important degree by an endangered species. This situation raises concerns that biological control may harm the endangered species and concerns that not using biological control will perpetuate the harm being done to riparian ecosystems and to many other T&E species by SC (DeLoach 1988, DeLoach *et al.* 1996).

Substantial use by a T&E species triggers the requirement for consultation with the USDI Fish and Wildlife Service (FWS) under the Federal Endangered Species Act of 1973. Therefore, a draft Biological Assessment was prepared by one of us (DeLoach) and submitted to FWS in October 1997 (DeLoach and Tracy 1997). Presently, a 3-year Research Proposal (DeLoach and Gould 1998) is being implemented to release a leaf beetle, *Diorhabda elongata* Brullé, from central Asia and China. FWS signed a Letter of Concurrence on 28 December 1998 (revised 3 June 1999) agreeing with the actions described in the Research Proposal (see S. Stenquist, this symposium). A notice of availability of a draft Environmental Assessment was published on 18 March 1999 (USDA-APHIS 1999). A Finding Of No Significant Impact (FONSI) was completed by APHIS-Plant Protection and Quarantine (the permitting agency) on 7 July 1999, that formalizes this procedure under the National Environmental Policy Act. Permits to release into secure field cages at 10 sites in 6 states (TX, CO, WY, UT, NV, CA) were issued during late July and early August 1999. Concerns still linger, however, regarding the ecological consequences of biological control on the sw WIFL, on other T&E species, and within the riparian ecosystems that continue to be damaged by SC.

In recent years, two concepts have developed that seem to guide understanding of the SC invasion and of its effects on wildlife, and that influence policy to manage these areas for ecosystem recovery and for protection of the sw WIFL. The first concept, that we designate the “anthropogenetic-abiotic paradigm”, explains the SC invasion as caused only by human produced, mostly abiotic changes, which favor SC and harm the native vegetation, especially of cottonwoods and willows (C/W). This leads to the superficial perception that SC is inherently “better adapted” to the changed abiotic environment and is “more aggressive” than the native riparian species (Anderson 1995), that SC was only a passive invader after riparian plant communities already had been damaged by the anthropogenic abuse (Everitt 1998), and that SC cannot be reduced in abundance and be replaced by C/W unless the anthropogenic - abiotic changes are reversed.

The second concept, is that of “functional equivalency” between SC and C/W and as extended to include equivalency in providing ecological goods and services to animal communities, especially to the sw WIFL. This leads to the superficial perception that SC provides satisfactory, and sometimes even superior, habitat for wildlife and the sw WIFL. We argue that the first paradigm is incomplete in failing to acknowledge that biotic factors, such as direct competition, the synergistic interaction between SC and the anthropogenic-abiotic factors, and the lack of insect herbivory, also are major determinants of

SC abundance and dominance. We argue that the second concept omits functional traits that would demonstrate the harmful effects of SC on native plant communities and that its extension to providing satisfactory habitat for wildlife is unsupported and incorrect. Both concepts fail to explain the reality of present conditions in the field - the invasion by SC of both regulated and unregulated streams, the near total displacement of native vegetation following invasion, and the serious decline in many species of animals, including many T&E species and the sw WIFL, since the SC invasion. However, the sw WIFL, in fact, has begun nesting extensively in SC in major breeding areas of central Arizona, but not in other areas or in neighboring states, since the SC invasion. This has caused great concern among flycatcher biologists that SC should be preserved as nesting habitat (Marshall 1996, Sferra *et al.* 1997).

The objectives of this paper are to analyze the ecological relations in western riparian ecosystems at two levels, first the interactions between SC and the physical environment and the plant community, and second, between SC and the animal community, especially of the endangered sw WIFL. We first review the damage caused by SC and how SC has interacted with anthropogenic changes of the past 65 years, and the ecological effects produced by these changes. We then review how animal populations, especially of the sw WIFL, have declined in relation to the SC invasion and how SC exacerbates the negative effects of nearly all known or suspected mortality factors of the sw WIFL.

We present modifications of the above paradigms and hypotheses that better explain the observable field situations - that the biotic factors (lack of insect herbivores, direct competition, and synergistic interactions) are important causes of the SC invasion. We discuss how SC may exacerbate nearly all of the known or suspected mortality factors of the sw WIFL. We argue that the strong attraction of the sw WIFL to nest in SC trees is caused by a single “super stimulus” (the superior branching structure of SC for nest placement), but that this results in lower reproductive success in SC than in the native breeding habitat. We also discuss the role that biological control of saltcedar could play in controlling saltcedar and the effects this might have on native plant and animal communities and on several T&E species, especially on the sw WIFL.

The concerns involved in this program for biological control of SC are examples of the problems that may be encountered in the future, and the kinds of insights needed to resolve them, with other programs for biological control of weeds in ecosystems that include endangered species or species of special concern, and especially if those species have begun utilizing the invading exotic weed.

The Saltcedar Plant and the Damage It Causes

Origin, Taxonomy, Invasion of SC

The genus *Tamarix*, with 54 species, is native only in the Old World, with one major center of speciation in the Pakistan - Afghanistan - Iran - Turkmenistan - southern Kazakhstan - western China area and another in the eastern Mediterranean area (Baum 1978). *Tamarix,* together with two other small Asian genera, *Myricaria* and *Reaumuria*, constitute the family Tamaricaceae. *Tamarix* is an ancient genus in Asia that is taxonomically isolated from other plant families (Baum 1978). Some 10 species of *Tamarix* were introduced into the U.S. (Baum 1967, Crins 1989) beginning in 1823 and were widely planted as ornamentals, and in the West also for streambank stabilization and as windbreaks (Brotherson and Von Winkel 1986, DiTomasco 1998). Most species are only weakly naturalized, including several in the Southeast. One species, however, *T. ramosissima* from central Asia (eastern Turkey to western China), spread explosively after the late 1920's and by 1970 occupied large areas of prime riverbottoms and lakeshores in the western United States (Robinson 1965, Horton 1977). Ongoing DNA studies indicate that *T. chinensis* and possibly hybrids between it and *T. ramosissima* occur in some western areas (Gaskin, personal commu.). Another species of SC, *T. parviflora*, is now invading coastal and central areas of California. Athel (*T. aphylla*), a very large, non-cold tolerant, evergreen tree, is widely but not abundantly used as an ornamental and for windbreaks in the southwestern United States and northern Mexico (DiTomaso 1998). Athel is not, or is only minimally, invasive in North America but it has become very invasive and damaging in central Australia (Griffin *et al.* 1989). Only *T. ramosissima* and *T. parviflora* are current targets for biological control in the United States.

The Tamaricaceae, together with the only other closely related family, the Frankeniaceae, are sometimes placed in the order Tamaricales (Thorne 1976, Spichiger and Savolainen 1997), or sometimes in the Violales (Cronquist 1981). *Frankenia* is a more widespread genus native in Asia, Australia, and South America, with 6 species native in the southwestern U.S. and Mexico, one of which, *F. johnstonii*, is endangered (Whalen 1987, Jäger 1992). The great taxonomic isolation of SC means that introduced biocontrol insects are very unlikely to attack any non-target native or economically beneficial North American plant species.

Ecology of SC

SCs are facultative phreatophytic and facultative halophytic plants that propagate by windblown or waterborne seed or vegetatively. They are pollinated mainly by insects but probably also by wind (Shmida 1991), fire tolerant, tolerant of drought and inundation, and difficult to control by herbicides or bulldozing (Hefley 1937, Everitt 1980, DeLoach 1991, 1996). SC qualifies under 10 of the 12 criteria of Baker (1974) that define the ideal weed. SC, being a facultative phreatophyte, can survive on soil water alone, whereas willows and cottonwoods are obligate phreatophytes that can lose contact with the water table only temporarily (Smith *et al.* 1998). As SC stands mature, their extremely high water usage tends to lower water tables to levels that are often below the root zone of cottonwoods and willows, especially of young small plants. SC can utilize saline groundwater and excretes the excess salts through leaf glands, that then falls to and accumulates on the soil surface, killing saline intolerant willows and other plants. The fallen SC foliage is highly flammable, causing increased fire frequency; fires kill native cottonwoods and willows but not SC. Native North American insects cause little or no damage to SC. Over time, desertification and salinization of the watershed results in localized extinction of the native trees and eventually to complete dominance of the floodplain by mono-specific SC thickets. Once this dominance is attained, SC appears to control whole ecosystem processes and to effectively preclude the re-establishment of native species through natural processes (Smith and Devitt 1996, Cleverly *et al.* 1997, Smith *et al.* 1998).

Damage Caused by SC

Native plant communities. The "original" flood-plain vegetation along many of the streams in the arid southwestern U.S. was comprised of gallery forests of native cottonwoods (*Populus* spp.) and willows (*Salix* spp.); thickets of screwbean mesquite (*Prosopis pubescens*), seepwillow baccharis (*Baccharis salicifolia*), arrowweed (*Pluchea sericea*), quailbush (*Atriplex lentiformis*), and seepweed (*Suaeda occidentalis*); and low woodlands of mesquite (*Prosopis glandulosa* and *P. velvtina*) (Grinnell 1914; Ohmart *et al.* 1977, 1988; Tracy and DeLoach 1999). These areas were in dynamic equilibrium, in which semi-predictable natural disturbances maintained the vegetation in an early successional state. The native plants and animals are adapted to those conditions and, in fact, depend upon flood disturbance to maintain diverse structure, age classes, and community composition. The pattern of change was termed "perpetual succession" by Campbell and Green (1968) and fell within well-defined limits (Turner 1974).

By the 1950's, SC occupied most western riparian areas along major streams, from the central Great Plains to the Pacific and from northern Mexico to southern Montana. Major infestations have replaced at least 50%, and often approach 100%, of the native vegetation along large areas of nearly all the major streams within its distribution (Horton and Campbell 1974). SC occupied 900,000 acres by the mid 1960's (Robinson 1965). Today, SC probably occupies 1.5 million acres (Brotherson and Field 1987), including 29,000 acres on 33 western national wildlife refuges (Stenquist 1996).

Ohmart *et al.* (1977) and Turner (1974) describe the demise of the cottonwood forests along the lower Colorado River, from wood cutting and later from replacement by SC. From an original estimated 5,000 to 10,000 acres only ca. 500 acres remained in 1972. Ohmart *et al.* (1977) questioned whether the native plants could have withstood the SC invasion even without dams. On the middle Gila River, SC replaced the native species without the effects caused by dams (Turner 1974). The plant is still spreading rapidly into tributaries, smaller streams and around desert springs throughout the West (Deuser 1997, Lovich and DeGouvenain 1998, Barrows 1998, Tracy and DeLoach 1999). Cottonwoods have been nearly eliminated in many of these areas and willows have been greatly reduced. A near complete replacement of the native plant communities by invasive exotics (SC and Russian olive) is predicted unless human intervention controls their spread and enhances recruitment of native species (Howe and Knopf 1991).

Wildlife. Wildlife habitat has been seriously degraded in many SC infested areas. The population of all birds found in SC on the lower Colorado was only 39% of the levels in native vegetation during the winter and 68% the rest of the year; the number of bird species found in SC was less than half that in native vegetation during the winter (Anderson *et al.* 1977). SC was the most important negatively correlated variable identified with bird populations (Anderson and Ohmart 1984). Frugivores, granivores and cavity dwellers (woodpeckers, bluebirds and others) are absent, and insectivores are reduced in SC stands (Cohan *et al.* 1979). Seven bird species, Arizona Bell's vireo (*Vireo bellii*), Gila woodpecker (*Centurus uropygialis*), gilded northern flicker (*Colaptes chysoides*), vermilion flycatcher (*Pyrocephalus rubinus*), summer tanager (*Piranga rubra*), western yellow-billed cuckoo (*Coccyzus americanus*), and elf owl (*Micrathene whitneyi*) are in serious decline along the lower Colorado River and the Sonoran yellow warbler (*Dendroica petechia*) and sw WIFL have been extirpated from the area (Hunter 1984). Only 2% of the yellow-billed cuckoos were found in SC, 0% of Bell's vireos, 2% of summer tanagers, and 8% of the yellow-breasted chats (*Icteria virens*) (Hunter *et al.* 1985). At Camp Cady in southern California, the bird population was only 49% as great in SC as in cottonwood/willow/mesquite (Schroeder 1993). Bird preference for SC was much lower than for native vegetation along the middle Rio Grande, TX (Engle-Wilson and Ohmart 1978) and somewhat lower on the middle Pecos River (Hildebrandt and Ohmart 1982). Few birds were attracted to dense, monocultural stands of SC but the inclusion of some native trees, especially cottonwoods, willows or mesquites, greatly enhanced the attractiveness of the area to birds (Engle-Wilson and Ohmart 1978, Hildebrandt and Ohmart 1982).

Populations of game animals, furbearers and small rodents are lower in SC than in other vegetation types on the Rio Grande of western Texas (Engle-Wilson and Ohmart, 1978) and on the Pecos of New Mexico (Hildebrandt and Ohmart, 1982). On the Rio Grande of western Texas, SC wetlands ranked fourth and SC sixth in numbers of small rodents caught, among seven vegetative types sampled (Engle-Wilson and Ohmart, 1978). In Big Bend National Park, Ord's kangaroo rat and beavers have been nearly eliminated because of the SC invasion (Boeer and Schmidly, 1977). On the middle Rio Grande, SC types ranked 9th, 15th and 16th among 25 community-structural types in numbers of small mammals trapped (Hink and Ohmart, 1984).

Along the Gila River near Florence, AZ Jakle and Gatz (1985) trapped 3 to 5 times as many lizards, snakes and frogs in native vegetation types as in SC. SC dried up springs and small streams, and forced wildlife to flee or die in Death Valley (Rowlands 1989). Many desert fish species are adversely affected by the narrower, deeper, and more homogenous stream habitats and by the reduction in numbers and types of food insects caused by the SC invasion (Graf 1978, 1979; Blackburn *et al.* 1982, Schoenherr 1988, Bestgen and Platainia 1991). At Ash Meadows National Wildlife Refuge, NV, Kennedy (personal commu.) is testing his hypothesis that the low numbers of speckled dace in sections of the stream infested by SC is caused by the litter being unsuitable for producing the aquatic insects the dace needs. We see a great need for additional information in the area of SC influence and interactions that affect fish habitat and numbers.

Some wildlife can use SC for some components of their needs but SC does not provide for all their needs and they must then forage on other native plants. As SC dominance increases, and the native plants decrease, populations of these wildlife species are likely to decrease for lack of resources, including the type and quantities of insects required by insectivores. SC degrades the habitat and further stresses some 40 T&E species in the southwest (Anonymous 1995, DeLoach and Tracy 1997) (see below).

Stream channel modification. Dense thickets of SC along streams cause increased sedimentation, bank aggradation, narrowing and deepening of channels, filling in of backwaters, modifications or elimination of riffle structure, overgrowth of sand and gravel bars, and changes in turbidity and temperature of the water. Channels sometimes are completely blocked with debris and overbank flooding is more severe (Busby and Schuster 1971, Burkham 1972, 1976; Graf 1978).

Water. SC uses great amounts of groundwater in these arid regions where availability is critical for natural ecosystems, agriculture, municipalities and industry (reviewed by Horton 1976, DeLoach 1991). The usage of water by SC has been much studied by various inflow-outflow methods along reaches of rivers (Gatewood *et al.* 1950), for plants growing in lysimter tanks (Gatewood *et al.* 1950, USDI-BOR 1973, van Hylckama 1980) by evapotranspiration measurements over stands growing in river bottoms (Gay and Fritschen 1979, Gay 1985), by stem-flow methods (Busch *et al.* 1992, Cleverly *et al.* 1997) and in river bottoms before and after clearing SC on the Gila River (Culler *et al.* 1970) and on the Pecos River (Weeks *et al.* 1987). Best estimates of usage vary from ca. 5.7 acre feet of water lost through evapotranspiration per year in the lowest and hottest areas along the lower Colorado to 3.2 acre ft. at higher elevations along the middle Rio Grande, NM. In one experiment in lysimeter tanks, SC used 51 to 72% more water at 40 to 60 in. depth to water table than did seepwillow baccharis (Gatewood *et al.* 1950). SC, being much deeper rooted and more salinity tolerant, can grow further back from the river, in more saline areas, and can extract water from a deeper level than can C/W and thus can occupy a larger area and use more water across the floodplain than would be possible by the native phreatophytes. Under natural conditions, less dense communities of mesquites, quailbush or other mesic plants, which use less water than SC (Sala *et al.* 1996, Cleverly *et al.* 1997), would occupy these areas further from the river. Smith *et al.* (1998) discussed that the higher leaf area per unit sapwood area and per unit area of soil surface, tighter stomatal control, and quick recovery after drought gave SC a strong advantage over other riparian plants.

Salinity. SC is able to utilize saline groundwater and excrete the excess salts through leaf glands (Hem 1967). The brine then drips to the soil surface, or falls with the leaves in autumn, forming a layer of salt. This prevents other plants from germinating or growing among SC stands (Shafroth *et al.* 1995). Cottonwoods and willows can tolerate salinity levels of only 1500-2000 ppm but SC can grow at 18,000 - 36,000 ppm (Jackson *et al.* 1990). SC does not favor saline conditions, it only tolerates them better than do most other plants.

Fire. Wildfires are rare in native desert riparian plant communities (Agee 1988). SC-infested areas, however, burn more frequently and more destructively than the native vegetation, especially after dry litter has accumulated under the stands. These fires often kill all cottonwoods, damage other native vegetation, destroy wildlife breeding areas, including nests of the sw WIFL (Paxton *et al.* 1996), and destroy campsites, fences, etc. (Akashi 1988, Ohmart *et al.* 1988, Busch and Smith 1992, Belnap 1997). Efficient post-fire resprouting mechanisms are lacking in willows and cottonwoods but are efficient in saltcedar. Indeed, saltcedar may have developed adaptive characteristics that influence the flammability of the communities where they grow, such as the accumulation of leaf litter. Saltcedar thus can alter whole ecosystem properties including fire (Busch and Smith 1993), nutrient dynamics, and alluvial hydrology (Vitousek 1990).

Recreational usage. SC substantially reduces recreational usage of parks, national wildlife refuges and other riparian areas for camping, hunting and fishing, boating, birdwatching and wildlife photography (Kunzmann *et al.*1989, DeLoach 1991). This occurs not only because SC causes declines in many desirable species but also because SC creates nearly inpenetrable stands that block access to other habitats, it drips brine in humid mornings, and it accumulates dust.

Agriculture. SC reduces livestock stocking capacity by displacing forage grasses and reducing drinking water, by using ground water or irrigation water that otherwise could be available to grow forage or crop plants, by increasing soil salinity, and by increasing the incidence of fires. Also, it is of low palatability to livestock and is inferior to native cottonwood/willow for resting or loafing areas during the summer.

Native American Tribal Lands. Many of these lands have been heavily invaded by SC. Tiernan (1978) contacted some 40 Native American agencies and Pueblos asking the extent of SC infestations and their opinions of using biological control. About half had infestations, totaling over 110,000 acres, and the infestations were increasing. All but a few of the respondees with infestations favored using biological control and the remainder only wanted more information before making a decision. Recent correspondence from several tribes mentions the continued spread of SC as one of the most critical economic impacts on agricultural and livestock producers, because of depletion of soil moisture and salinization of the soil. SC also degrades ceremonial areas, and displaces willows and other native vegetation used in crafts and cultural activities (Welch 1998, Addison 1999, Hemstreet 1999, and Wasburne 1999).

SC vs. Native Plant Communities

Interactions with Human Modifications and Natural Conditions that Give SC a Competitive Advantage

The unique combination of ecological and physiological characteristics of SC allow it to interact to an extraordinary degree with natural factors or human modifications of the riparian ecosystems to increase the damage to native plants and to increase its own competitive advantage (Horton and Campbell 1974, Horton 1976, Everitt 1980, Busch and Smith 1995, DeLoach and Tracy 1997, Lovich and DeGouvenain 1998, Lovich and Bainbridge 1999).

Dams and flood cycles. The construction of large dams has changed the natural hydrologic cycle from a pattern of high, brief, spring floods following the annual spring snow melt or heavy rainstorms, to a pattern of a low flood that extends into the summer or fall, or of no floods. Cottonwoods have evolved with this natural cycle and produce seeds which germinate and establish on the exposed mud banks as the natural spring floods recede. By the time the low, anthropogenic summer floods recede, cottonwoods have ceased producing seeds. However, SC produces seeds throughout the summer and into the fall and can establish whenever the floods recede (Tomanek and Ziegler 1962, Warren and Turner 1975, Everitt 1980, Stromberg 1997). Also, SC establishes on the mudbanks, preempting these potential cottonwood nursery sites and preventing cottonwood establishment even if the flood cycle is natural in following years (Hefley 1937, Smith 1989). For example, along the Green and Colorado rivers in southwestern Utah, willows that established early in the season competed effectively against SC. However, the loss of early flood events may inhibit the establishment of willows and other disturbance - dependent germinators, resulting in greater survival of SC (Belnap 1997, personal commu.).

Channelization, diversion and pumping of groundwater. Long reaches of several western rivers have been channelized by various water management agencies during the past 50 years. Generally, the channel is dredged to 10 to 20 ft. deep and straightened. This was done in an attempt to conserve water and to kill the water-hungry phreatophytic plants, both SC and native species (PSIAC 1966, Carothers 1977). Channelization lowered water tables below the level where shallow-rooted, riparian obligate cottonwoods, willows, seepwillow baccharis, and other plants could reach the water, causing significant mortality of these species, whereas SC survived when separated from the water table and with severe depletion of water from the upper soil profile (Devitt *et al.* 1997). Maximum depth to water table that will allow the growth of healthy cottonwoods and willows is ca. 6 ft., with a 2 ft. annual fluctuation (USDI-BOR 1995). SC roots can penetrate as deep as 100 ft. (Baum 1978) and it can adapt to the lowered water tables (USDI-BOR 1973). SC seedlings allocate almost entirely below ground, so that first-year plants only 10 cm high have a root system more than 2 m deep (Smith *et al.* 1998). Diversion of water in streams and pumping of groundwater, for both agricultural and municipal use, has also critically reduced water tables in many western areas. The large usage of water by SC itself accelerates the lowering of watertables and to a deeper level than is normal (Busch *et al.* 1992, Smith and Devitt 1996). This frequently causes desert springs to dry up and permanent streams to become intermittent (Barrows 1998). Large fluctuations in reservoir levels give SC a similar advantage around the shorelines. Stream incision and downcutting also lower water tables and are of widespread occurrence throughout the west, caused by floods and accelerated by livestock overgrazing (Chambers *et al.* 1998).

Flooding and Inundation. Older SC is more tolerant of flooding than is some native vegetation. Along the shoreline of San Carlos reservoir, AZ, all SC trees died when the root crowns were submerged for 98 or 107 days or when the top growth was completely submerged for 43 days or more (Warren and Turner 1975). Several major infestations of SC established after floods or as high waters declined in reservoirs or lakes (Turner 1974). However, native vegetation tolerates natural flood disturbance better than does young SC. Abnormally high (10-year level) floods caused greater mortality to juvenile SC (less than 5-years old) than it did to native seedlings (cottonwood, coyote willow, seepwillow baccharis, arrrowweed, and mesquite) at Anza-Borrego State Park, CA (D'Antonio and Dudley 1997) and at the study stream (Sycamore Creek, AZ) of one of us (Dudley). However, these floods now are too infrequent, allowing SC to establish. Flooding SC seedlings during the first year's growth has been developed as a control method (Gladwin and Roelle 1998).

Phreatophyte control programs. During the 1950's and 1960's, governmental and private agencies mounted massive programs to control phreatophytic vegetation (exotic and native) in Arizona and New Mexico to conserve water and prevent flooding (PSIAC 1966, Carothers 1977). In the early 1970's, according to Fox (1977), every mile of riparian habitat in Arizona was being cleared or was scheduled for clearing; incredibly, even the cottonwoods in the Verde Valley, AZ were cleared for flood control. These programs were halted by a series of court injunctions in 1970 (Gilluly 1971). Unfortunately, the clearing gave SC a further competitive advantage, and it then rapidly regrew and gained dominance in many of these areas. Clearing of SC and mesquite during the water use experiments along the Gila River near Safford, AZ (Culler *et al.* 1982) gave SC a similar advantage.

Soil salinity. Several western rivers and streams flow through areas of naturally saline soils and groundwater. The natural spring floods leach out these salts but with the present pattern of no flooding or of only low floods, the salts continue to accumulate. SC is much more salt tolerant than are cottonwoods, willows, and most other vegetation of value to wildlife (Jackson *et al.* 1990) and thus gains a great competitive advantage over most other plants in saline floodplain environments (Shafroth *et al.* 1995, Smith *et al.* 1998). Information from one of us (Smith) indicates that SC creates a feed-forward process in which it invades, concentrates salt in its foliage which then drips to the soil surface or falls with the foliage, which forms a saline litter layer and surface soil, which favors SC seedlings over native salt intolerant species, thus further accelerating SC dominance, which causes even more surface and soil salinization, etc.

Wildfires. Wildfires interact with altered flood cycles, drought and salinity to the great advantage of SC. SC is highly tolerant of fire but cottonwoods are highly intolerant. Because of the large quantity of dry leaf litter that accumulates under SC trees, SC thickets are highly flammable and burn frequently (Agee 1988, Busch and Smith 1992). The saline soils, low soil moisture, and dense shade prevent other green plants from growing which could help retard fires. Also, the present lack of scouring floods allows the leaf litter to accumulate. Although wildfires frequently kill nearly all cottonwoods, burned SC commonly regrows to heights of 8 or 10 feet the next year, and thus rapidly dominates an area after a fire (Minckley and Brown 1982, Ohmart *et al.* 1988, Smith *et al.* 1998). At Anza-Borrego State Park, CA, a wildfire originating in SC that one of us (Dudley) is aware of killed a large mesquite stand, after which the SC regrew rapidly and abundantly. Also, SC regrew rapidly at the Kern Wildlife Refuge, CA, after a fire was started to control SC. SC established along the Bighorn River of Montana after a series of fires from 1954 to 1960 (Akashi 1988).

Transpiration. The physiology of SC, as with several other plant species (including willows), results in partial stomatal closure and transpiration rates considerably below potential during the hottest part of the day. Optimum temperature for photosynthesis of SC is 23° to 28°C, far below the 32° to 45°C typical in the field during the summer (Anderson 1982). During hot periods, transpiration levels off after 10:30 a.m., then gradually decreases throughout the remainder of the day, as air temperature increases and humidity decreases, until late- afternoon (Anderson 1982, Busch and Smith 1995). This enables SC to conserve transpiration losses somewhat, contrary to the notion that it loses unlimited quantities of water. Thus, SC has a higher water-use efficiency (ratio of carbon gain to water loss) than do co-existing phreatophytes, which may be one of the factors in its success along arid-zone floodplains that experience periodic drought conditions (Smith *et al.* 1998).

Livestock browsing. Livestock, native ungulates, and other animals readily browse the foliage or eat the bark of native cottonwoods and willows, frequently killing the young plants and bringing reproduction to a halt (Ames 1977). These animals feed much less on SC, which soon grows taller than the livestock can reach (Stromberg 1997). SC infested areas have been heavily grazed in the past, and continued grazing of riparian areas further increases the dominance of SC.

Conventional controls. Various herbicidal and mechanical controls have been used since the 1940's to control SC. However, these methods often kill the native phreatophytic plants more easily than SC. At present, hand cutting and stump treatment with Garlon® or broadcast treatments with Arsenal® are the most effective (Sisneros 1990). Hand cutting is highly labor intensive and expensive and is feasible only in small areas around springs or small streams, and only if volunteer labor is available. Broadcast aerial applications of Arsenal® provide moderately high control of SC. However, Arsenal® is a broad-spectrum herbicide and so kills much of the native vegetation, whose preservation was the object of control. With all these methods, control is not complete, reinfestation may be rapid, and retreatment every few years is necessary, with continuously increasing damage to the native plants.

Natural enemies. Few native insects feed more than occasionally or sporadically on SC and cause it little damage (Liesner 1971). The one exception is the Apache cicada (*Diceroprocta apache*) whose nymphs feed on the roots of cottonwoods and willows and also of SC (Glinski and Ohmart 1984). The large numbers of insects seen at SC flowers feed on nectar and pollen and cause SC little or no damage. The herbivorous immature stages of these species are produced on nearby native vegetation; SC may provide them an additional advantage in damaging the native plants by providing the adults with an additional food supply.

The high populations of leafhoppers commonly seen on SC in many areas (Liesner 1971, Stevens 1985) are of *Opsius stactogalus* which was introduced from Eurasia by unknown means several years ago; it causes some damage to SC but fails to give control.

Four other Eurasian, SC-specific arthropods also have been introduced by unknown means but cause little or no damage; these are two scale insects (*Chionapsis etrusca* and *C. gilli*) and two mites (*Vasates immigrans* and *Aculops* n. sp.). The lack of insect herbivores that attack SC undoubtedly is a very major factor in the competitive advantage SC has over the native vegetation. Stevens (1985) found that in the Grand Canyon SC had far greater insect numbers and biomass (mostly leafhoppers and Apache cicadas) than did coyote willow but the number of insect species was much greater in the willows.

Active manipulation and direct competition by SC. SC is able to actively manipulate some of the above factors, through habitat modification that favors self-replacement and expansion to increase its own competitive advantage. SC directly increases soil salinity above the normal level, it directly produces highly flammable conditions that promote wildfires, and it directly draws down soil moisture and watertables to a lower level than would occur naturally. It preempts mudbank nursery sites after the abnormal, long-duration, low-level floods now common on regulated rivers so that cottonwoods, willows and other riparian vegetation cannot establish. It creates weedy conditions that encourage herbicidal or mechanical controls that then kill the native vegetation, and it adjusts its physiology to make carbon metabolism more efficient in regions of high temperatures, as discussed previously.

The SC invasion has not been restricted to areas disturbed by past human activities. Examples exist along the Brazos River in Texas (Busby and Schuster 1971), the middle Gila River (Turner 1974), the Colorado River in Canyonlands National Park and the Green River, UT (Thomas *et al.* 1989), the Virgin River, NV (Kasprzyk and Bryant 1989, Smith *et al.* 1998), and the San Miguel River, CO (Richter 1997). It has established at remote mountain springs, streams and washes throughout the west, where no signs of human disturbance are apparent, many miles away from major regulated rivers, and sometimes thousands of feet above grazed or cultivated areas (Deuser 1997, Lovich and DeGouvenain 1998). Along Coyote Creek in Anza-Borrego State Park, CA, SC invaded a watershed in a designated wilderness area; thus, successful invasion occurred without human modifications (D'Antonio and Dudley 1997). In these areas, and also in some areas along regulated rivers, SC "displaces" native vegetation after establishing in any natural openings present. The reduction in density of native riparian plant communities through direct competition from SC has been clearly demonstrated on numerous tributaries and small streams and around desert springs where adverse, changed abiotic conditions were not a factor, or at least not a major factor. In these areas, the native vegetation returned quickly and naturally after SC was controlled (Neill 1985, Inglis *et al.* 1996, Deuser 1997, Egan 1997, Barrows 1998, Lovich and de Gouvenain 1998). SC itself clearly is a direct, major factor in the demise of many western riparian plant communities. The often stated explanation that SC only invades areas already damaged by high soil salinity, low water tables etc. is incomplete.

The lower Colorado is one of the most highly degraded major rivers in the southwest, and SC now dominates large areas along it. In this area, Busch and Smith (1995) experimentally cleared SC thickets from around remnant willow clumps, leaving control clumps uncleared. The following growing season, the willows produced 80% more biomass where SC was removed than at the control plots. This demonstrated the potential for revegetation even here, where recovery is often deemed impossible. This test also demonstrated that direct competition by SC was a significant factor in the suppression of willows here (Smith *et al.* 1998), since depth to water table and soil salinity did not change during the experiment or between control and treatment plots.

Determinants of SC Abundance

Anthropogenic-Abiotic paradigm. The present paradigm for understanding vegetation dynamics in western riparian ecosystems, especially for those on highly regulated streams, seems to be that the major determinants of plant species composition and dominance are *abiotic factors*: primarily water availability and soil type (salinity), but including geomorphic traits, temperature and light intensity. Human-produced changes (discussed above) have modified these factors to produce the present degraded ecosystem. SC invaded and became naturalized, but dominated the native vegetation only after it already had been damaged by high salinity, low water tables, etc. SC was only opportunistic and had no effect on channel narrowing or flood stage; it was only a passive player in the riverine landscape (Harris 1966, Hobbs and Humphries 1995, Anderson 1998, Everitt 1998). Everitt (1998) documented many cases where SC invaded after the construction of dams. SC dominated because it is inherently “more aggressive” and “better adapted” to the new conditions than are the native plants (Anderson 1995). Thus, the argument is made that SC has passively “replaced”, not actively “displaced” the native vegetation. The present SC dominated communities appear to be immutably fixed unless the fundamental abiotic factors change. However, Ohmart *et al.* (1977) questioned whether the native plant community along the lower Colorado River could have withstood the SC invasion even if anthropogenic changes had not occurred.

Soulé (1990) and Hobbs and Humphries (1995) proposed that some exotic invasions represent the exploitation of a new environment by an “aggressive exotic” without anthropogenic ecosystem modifications, but the cause of the aggressiveness is not explained; the effects of this permanent dominance by the exotic would appear to be the same whether or not anthropogenic changes have occurred. Many of these infested areas, when examined carefully, are found to be suitable for vegetation recovery if the SC were removed or thinned; if *any* willows or cottonwoods are present, recovery of the area is probable unless underground structures such as hard clay “lenses” prevent root penetration in localized areas (Fenchel 1998, personal commu.). In many other areas, SC apparently has “displaced” the native vegetation through direct competition even though water tables, soil salinity, etc. remain suitable for the native plants (USDI-BOR 1995, Deuser 1997, Barrows 1998).

The ecosystem changes that cause SC to appear “better adapted” than the native vegetation include altered hydrologic cycles below large dams, lowered water tables, high soil salinity, floods, wildfires, livestock or native wildlife herbivory, or conventional controls. Several inherent, phenotypic and physiological attributes of SC allow it to appear more aggressive and to rapidly dominate the native riparian plant communities. These include high reproduction and dispersal rate, wide geographic and climatic adaptability, deep root system, high water use efficiency, and tolerance of high soil salinity, fire, low watertables, low soil moisture, inundation, resistance to livestock and wildlife browsing, and to mechanical and herbicidal weed controls; the adaptation of its transpiration-carbon metabolism process to high temperature; and, importantly, resistance to attack by native North American insects and plant pathogens.

Biotic paradigm. We believe the “anthropogenetic-abiotic” paradigm to be valid in part but to be inadequate to explain the observed relationships of the SC influence in the ecosystem or to explain the changes expected following an assumed successful biological control program for SC. We propose a new paradigm that includes a major emphasis on *biotic factors* capable of changing not only the species composition but even some of the abiotic factors that affect SC competition. This paradigm considers four important relationships in addition to abiotic factors: 1) that SC competes directly with the native plant community, irrespective of abiotic modifications, 2) that SC itself increases the severity of several of the abiotic factors (such effects then would be reduced after SC control, 3) that SC has invaded many areas where obvious abiotic changes have not occurred, and 4) the effects of natural enemies (especially insects and plant pathogens) on limiting plant abundance, including potential natural enemies that could be introduced to control SC.

Many plant-oriented workers underestimate or ignore the influence that natural enemies (insects, mites, plant pathogens) can have on plant reproduction, growth, mortality, abundance and species composition. Yet, every successful case of biological control of a weed (now at least 10 cases in the continental United States, another 10 in Hawaii, and many others in 50 other countries) clearly demonstrate that only the introduction of one or a few insects or plant pathogens can permanently reduce an aggressive, invading dominant weed to a position of minor importance in the plant community (Huffaker and Kennett 1959, Julien and Griffiths 1999). The apparent "aggressiveness" or being "better adapted to its new environment" is then seen to be only the absence of the natural enemies that normally limit populations of the weed within its native range. The new ecosystem then is seen *not* to be immutably fixed with the exotic plant dominant, but readily changeable, even without difficult, widespread, and expensive changes of the abiotic factors. This lack of natural enemies explains the cases cited by Soulé (1990) and Hobbs and Humphries (1995) of invasions without anthropogenic changes, discussed above.

The Biological Control Program

The lack of effective natural enemies of SC in invaded ecosystems of North America, caused by its introduction from Eurasia without the insects and plant pathogens that attack it there, is a major cause of its domination of our riparian plant communities. The biological control program we are undertaking seeks to introduce those highly host specific and most effective natural enemy species into the United States. SC sometimes dominates areas in its native range in the Old World, but seldom to the extent seen in the western U.S. In the Old World, its populations are considerably suppressed by herbivory from many host specific insect species (Mityaev 1958, Zocchi 1971, Gerling and Kugler 1973, Habib and Hasan 1982, Kovalev 1995), even though these herbivores are often heavily attacked by their own parasitoids and predators. We may expect better control in the U.S. than in the Old World because these parasitoids and predators will not be introduced.

Testing has begun on some 20 species of insects by cooperating scientists in France, Israel, Turkmenistan, Kazakhstan and China. Seven of these have been received into quarantine at Temple, TX for further testing, and testing has been completed on 3 species: a leafbeetle, *Diorhabda elongata,* from central Asia and China; a mealybug, *Trabutina mannipara* Hemprich and Ehrenberg, from Israel; and a foliage-feeding weevil, *Coniatus tamarisci* F., from France (DeLoach *et al.* 1996). *Diorhabda elongata* has now received APHIS and FWS approval for experimental release.

Extensive host-range testing at Temple, TX of adult feeding and survival, ovipositional host-plant selection, and larval feeding, survival and development of *D. elongata* and *C. tamarisci*, and similar no-choice testing of nymphs and adults of *T. mannipara*, have demonstrated that these 3 candidate control insects are completely restricted in host range to species of *Tamarix*. Museum records and field surveys in Europe and Asia confirm this. The test results for *D. elongata* and *T. mannipara* were critically reviewed by the USDA-APHIS multi-agency Technical Advisory Group for Biological Control Agents of Weeds (TAG), and by FWS (test results for *C. tamarisci* have not yet been submitted). These agencies have approved the experimental release of *D. elongata*. The release of *T. mannipara* is pending for demonstration that it can be confined in field cages during the first of year of the research phase.

A 3-year program began during the summer of 1999 to make research releases of *D. elongata* at 10 sites in Texas, Colorado, Wyoming, Utah, Nevada and California. These sites are all from 200 to 800 miles from the nearest areas where the sw WIFL is nesting in SC, all are isolated by ecological barriers and without connecting SC stands, and none are in watersheds that drain into sw WIFL nesting areas. Releases will be made into secure field cages during the first year. After overwintering, the cages may be removed during the second and third years. Intensive monitoring will be done during this period, and for some years thereafter, of 1) the effects of the control insects on SC and of any possible attack on non-target plants, 2) vegetation recovery following SC control, and 3) wildlife recovery after vegetation recovery (DeLoach and Gould 1998). Any other introduced biological control insect species that might be introduced in the future probably will be released and monitored in a similar manner.

The major objectives are to determine the rate of dispersion of the control insects and the rapidity with which they control SC. This is to provide guidance on whether the control insects are likely to rapidly invade SC in sw WIFL nesting areas that possibly would leave this bird with a shortage of nest trees until the willows have time to recover sufficiently to provide nesting habitat. Our expectation is that dispersal will be slow and that SC control will be gradual over several years at a given site, allowing time for the concurrent recovery of willows and other native plants without loss of habitat for the sw WIFL. We predict an ultimate 75 to 85% level of control, after several years and with the release of several insect control agents.

If, after appropriate review, the research releases demonstrate the safety of biological control for the sw WIFL, then authorization may be granted to begin the implementation phase in which wider distribution may be made. We project that a 75 to 85% level of control will allow for a substantial recovery of both the native riparian plant community and of the several declining and T&E species of birds and other animals and plants, including the sw WIFL, that have been negatively impacted by the SC invasion.

Vegetation Recovery After SC Control

The presumption that SC infested areas can no longer support native vegetation needs further examination. The assumption of the unsuitability of the present riparian areas appears to be based on the fact that SC has indeed invaded and that the native vegetation has not been able to displace it. This attitude is further influenced by human-produced changes in flood cycles, soil salinity, depth to water table, increased wildfires frequency, and overgrazing in some areas, and that early attempts at manual revegetation mostly failed. Many areas can recover, but some probably cannot, without reversing the human changes.

Manual revegetation. Several large-scale, expensive revegetation projects along the lower Colorado during the late 1970's and early 1980's were carried out, mostly using cottonwood poles but also using willows, mesquites and other plants (Pinkney 1992). Little experimentation was conducted to develop the techniques that were implemented. Mortality was high throughout and eventually most of the trees died. However, some plantings of mesquite survived and grew well. Causes for the failure include poor site selection (water table depth, soil salinity), improper planting methods and irrigation, and failure to protect against livestock and wildlife browsing, weeds and insect damage. Later, Briggs (1992) surveyed 27 different revegetated sites in Arizona (apparently not planted with a view to success potential), and found that 13 of the revegetation attempts were successful and that at 10 sites natural revegetation was good. Recently, the USDA-NRCS Plant Materials Center at Los Lunas, NM has developed manual revegetation methods that produce 95% survival and continued growth of cottonwoods, willows and other native plants in riparian areas (Swenson and Mullins 1985, Dreesen *et al.* 1999).

Site suitability. Surveys conducted recently along the lower Colorado River recorded substantial areas where conditions for revegetation are suitable. Anderson (1995) reported that, in 28% of his 3,465 samples along streams in California, Arizona, New Mexico and Texas, depth to water table and salinity were suitable for cottonwoods and willows. USDI-BOR (1995) surveyed 18,762 acres of monotypic SC stands, also along the Lower Colorado; 10% was suitable for cottonwoods, 45% for mesquites, and 45% for quailbush, all valuable wildlife plants. The suitable area for C/W included nearly all of the major sw WIFL breeding area at Topock Marsh. Ten percent of the present total 44,460 acres of monotypic SC stands present along the lower Colorado (4,446 acres) equals approximately the amount of cottonwood/willow originally present. Some areas now may be too saline, or the water tables too low, for re-establishment and growth of cottonwoods and willows (but probably not for mesquite or quailbush) but these areas are smaller than often implied. The assertion that extensive areas, including much actual or potential sw WIFL habitat, are unsuitable for revegetation has not been adequately documented. Controlled flooding, which prepares substrates, distributes seeds, and dilutes salts, should be a component of promoting site suitability where possible, especially in areas of high soil salinity.

Clearing along small streams. Numerous projects have been conducted in recent years to clear SC from small streams and from around desert springs. These areas are along unregulated or minimally regulated streams where soil salinity has not increased and where channelization or groundwater pumping has not occurred. Such areas represent a large proportion of western riparian areas and they are being rapidly invaded by SC. In many cases, the native plant communities recovered quickly and naturally after SC control, and without manual revegetation; desert springs flowed again, intermittent streams became permanent and extended for a longer distance and wildlife species, including fish, returned (Neill 1985, Inglis *et al.* 1996, Egan 1997, Deuser 1997, Barrows 1998, Kennedy 1999, personal commu.).

Natural revegetation following floods. During the large floods of the mid-1980's, large areas of SC were washed out along the lower Colorado. The floods also probably leached out the accumulated salts from the soils. Willows rapidly and naturally revegetated in these areas and soon grew to a size suitable for wildlife habitat and remain so today (Solomon 1997, personal commu.). The experimental flooding of the Grand Canyon in 1996 also leached out accumulated salts but did not scour out much SC. The water table and salinity conditions there should now be near ideal for willows and cottonwoods except for the remaining direct competition from SC. During the large floods along the middle Rio Grande in the mid 1980's, SC was washed out near the river, areas further back were flooded for long periods drowning the SC, and extensive sedimentation occurred. When the waters receded, willows regrew rapidly in those areas and now provide good wildlife habitat; SC persists further back from the river in drier areas (Ahlers 1999).

At the Bosque del Apache National Wildlife Refuge on the Rio Grande of central New Mexico, successful natural revegetation has been routinely obtained by flooding areas cleared by mechanical control, and allowing the waters to recede just as cottonwoods are producing seeds; this produces almost a monoculture of cottonwoods. Coyote willows also revegetated naturally around pond margins, and now form dense stands. The sw WIFL now nests in the willows and remaining SC, whereas it did not nest here before the SC was removed and the willows regrew (Taylor, personal commu. 1998). Farley *et al.* (1994) found, on the middle Rio Grande, NM, that revegetated sites provided good bird habitat after only 3 years and that 5-year old sites were used by as many bird species as the 30-year old sites; also, cottonwoods, and especially willows, reached suitable height classes of 3 to 6 m earlier (within 2 to 5 years) than did SC. In Colorado, beavers moved into SC areas, cut down the SC to build their dams and lodges but fed little on it; when the pools flooded, willows returned abundantly but SC did not because of the high water table, and the beavers then fed on the willows. This resulted in a form of biological control of SC and natural revegetation by willows (Baker 1995).

A large experiment currently is in progress along streams in western Colorado to mimic the effects of the proposed biological control program through herbicidal applications and careful monitoring of vegetation recovery (Gladwin 1998, personal commu.). Both native vegetation and bird usage has recovered well along the Mojave River, CA after SC removal followed by both active or passive vegetation restoration (West 1999, personal commu.).

SC vs. Animal Communities

Effects of SC on Declining and Endangered Species

Populations of many animal and plant species have declined drastically during at least the past 50 years. During this time the ecosystem also has changed drastically. The most obvious ecosystem changes have been the construction of dams along all major rivers, channelization and phreatophyte control programs along many rivers and smaller streams, the enormous invasion of SC and the decline of native vegetation in nearly all riparian areas, and the invasion of nest parasitizing cowbirds into the southwest from the Central Great Plains of the U.S. These changes appear to have caused or contributed to the decline of many species of native animals, including several endangered species.

DeLoach and Tracy (1997) reviewed 51 T&E species, or proposed T&E species, that occupy western riparian areas infested by SC, from a list provided by the U.S. Fish and Wildlife Service's Region 2 (Albuquerque) in August, 1995. These included 2 mammals, 6 birds, 2 reptiles, 2 amphibians, 34 fish, 1 arthropod, and 4 plants. Several of these T&E species may utilize SC to some extent, but not to a degree that would make it appear important to them or as valuable as the native vegetation it has replaced (Anonymous 1995). The evidence (mostly from the review by DeLoach and Tracy 1997) suggests that biological control would have a beneficial effect on 39 species, insignificant or beneficial effect on 8 species, and no effect on 4 species.

In the central Great Plains, SC has overgrown the gravel bars along streams, preempting this essential nesting habitat of the interior populations of the least tern (*Sterna antillarum*) (Koenen *et al.* 1996). The Yuma clapper rail (*Rallus longirostris yumanensis*) along the lower Colorado River Valley is harmed because SC has replaced its necessary cattail/bullrush habitat and reduced its crayfish food supply. Least Bell's vireo (*Vireo bellii pusillus*) in southern California has been harmed by the replacement of its native cottonwood/willow/sycamore habitat by SC; its population has shown some recovery where cowbirds have been trapped. The bald eagle (*Haliaeetus leucocephalus*) (proposed for delisting in July 1999) has been harmed by the great reduction in the large cottonwoods that are one of its preferred nest trees (Anonymous 1995, DeLoach and Tracy 1997).

The peninsular bighorn sheep (*Ovis canadensis cremnobates*) has been forced from some of its critical areas in southern California because its watering sources were dried up by SC. Also, SC provides cover for mountain lions that prey on it. Clearing SC at Anza Borrgo State Park increased the flow from Cimmarron Spring (Wright 1997). The Concho water snake (*Nerodia paucimaculata*) is found only in the Concho and Colorado rivers of western Texas; SC has reduced its critical habitat of rocky banks, riffle areas and hibernation sites and the recovery plan calls for SC removal (Anonymous 1995). SC dries up water remaining in southern California streams and modifies the channel geomorphology, diminishing the habitat value and further threatening the protected western pond turtle (*Clemmys marmorata*) in the Mojave River, and potentially, the endangered desert slender salamander (*Batrachoseps aridus*) in isolated canyons near Palm Springs (Lovich and DeGouvenain 1998, Lovich *et al.* 1994). The arroyo southwestern toad (*Bufo microscaphus californicus*) and the California red-legged frog (*Rana aurora draytonii*) are potentially threatened by SC sedimentation of critical marsh habitat, overgrowth of exposed weeds, and reduction of the insects on which they feed.

Some 34 species of T&E fish are found in SC infested areas. Their habitat is seriously degraded by reduced water levels, modified channel morphology, silted backwaters, altered water temperature, and probably by reduced and modified food resources. Examples of SC degradation of endangered fish habitats include the loss of shallow sandbar habitat for the Rio Grande silvery minnow (*Hybognathus amarus*), loss of critical low velocity nursery habitat for the Colorado squawfish (*Pytocheilus lucius*), and reduction in water levels in springs for the desert pupfish (*Cyprinodon macularis*). The threatened Pecos sunflower (*Helianthus paradoxus*) is harmed by SC encroachment into its habitat; in some areas it was found for the first time after SC was removed (U.S. Fish and Wildlife Service 1999; Radke 1998, personal commu.; Tracy and DeLoach 1999).

The Southwestern Willow Flycatcher

Five subspecies of the willow flycatcher, *E. trailii*, have been designated that breed over most of the U.S. except the southeast, and also breed into southern Canada, but identification is uncertain. They probably overwinter in Central America and northern South America. Only the southwestern subspecies, *E.t. extimus* (sw WIFL), is endangered. In mid-elevational areas of Arizona, it now nests significantly in SC since SC has replaced its native nest trees; sometimes it even appears to prefer SC to the native willows for nesting (Sferra *et al.* 1997, McKernan and Braden 1999). This, together with the critically endangered status of the bird, causes great concern about its welfare if SC is controlled. We present arguments here that these concerns are largely unfounded and that biological control of SC more likely will have a positive effect on sw WIFL populations.

Ecology. The sw WIFL has been labeled a cottonwood/willow obligate species

(Rosenberg *et al.* 1991). It is a neo-tropical migrant, riparian obligate, mid-summer breeding bird. It breeds in areas of dense shrubs or small trees with a dense (90-95%) canopy cover and often with a high upper canopy of cottonwoods, in moderate to broad floodplains, and near or over water. At middle elevations in Arizona, males arrive on territories in late April or early May, and the birds may be present until early or mid-August (Hunter *et al.* 1987). First and last egg laying was 29 May to 27 July, egg hatching from 9 June to 6 August, and fledging from 22 June to 12 August (Sferra *et al.* 1997). Pair fidelity appears to be low and mate swapping occurs between broods (Netter *et al.* 1998). The sw WIFL usually nests within 100 m of water in temporarily flooded areas, in branches overhanging water or near water or over wet ground, and if the soil dries out it may not nest or may abandon the nest. Narrow strips of trees only a few meters wide are not suitable nesting habitat (Tibbitts *et al.* 1994, Sferra *et al.* 1997). It nests in willow in several areas but at several major sites it nests in coastal live oak, boxelder maple, or button bush, with a few nests in seepwillow baccharis or other native shrubs. Since the invasion of SC, the sw WIFL nests significantly in it in mid-elevational areas of Arizona but not in other areas. However, it is generally absent where monotypic SC stands have replaced the native riparian vegetation (Tibbitts *et al.* 1994). Site fidelity in the sw WIFL appears to be rather high, but not absolute. Within a site, most adults settled within 50 m of the previous year's territories but banded birds have been recorded moving 94 km (1 male) and 190 km (1 female) the next year (Paxton *et al.* 1997).

Distribution and population. Historically, the sw WIFL bred from southern California (as far north as the Santa Inez River), along the Lower Colorado from the Mexican border to the southern tip of Nevada, maybe into southernmost Utah and Colorado, throughout Arizona, in western New Mexico to and including the Rio Grande valley, and occasionally in Trans-Pecos Texas (Browning 1993). The 34 nests collected near Yuma, AZ in 1902 by Herbert Brown (Unitt 1987) indicate that it was a common breeder along the lower Colorado River.

By 1996, the total known population of the sw WIFL range-wide had been reduced to ca. 550 territories at 62 sites. Only 7 populations of more than 20 territories were known, with 78% of the sites comprised of 5 or fewer territories and 20% occupied by a single unmated male (Marshall 1996). Recently, an additional ca. 45 breeding adults have been found in the southeastern half of Utah (Peterson *et al.* 1998) and 45 in the southwestern fourth of Colorado (Sogge 1997, personal commu.). The sw WIFL still nests throughout most of its historical range. At the mid-elevational sites in Arizona, 72% of the nests found during 4 years (1993-1996) occurred in SC and those in the east-central mountains nest entirely in willows; statewide, 60% nested in SC (Muiznieks *et al.* 1994, Sferra *et al.* 1997). In 1998, 77.6% of the nests in all sites in Arizona were in SC (Paradzick *et al.* 1999).

The largest population, with ca. 135 territorial pairs, breeds along the upper Gila River near Cliff, NM, entirely in native trees, mainly boxelder maple (*Acer negundo*) (Hull and Parker 1995, Skaggs 1996). The second largest, with ca. 84 pairs in several sites occurs near the San Pedro/Gila River confluence in southwestern Arizona, nesting mainly in SC but also in native willows and native buttonbush (*Cephalanthus occidentalis*) at some sites. The third largest population is at Roosevelt Lake in south-central Arizona. Here, ca. 23 pairs breed in mixed SC/willow stands at the Tonto Creek inlet and another ca. 20 pairs in monotypic SC stands at the Salt River inlet - all nests were in SC trees at both areas (Paradzick *et al.* 1999). Another population of at least 20 pairs breeds in SC at Topock

Marsh (in the Havasu National Wildlife Refuge) on the lower Colorado River near Needles, CA (McKernan and Braden 1999). Populations of ca. 20 pairs breed at each of 4 locations along California coastal rivers: the San Luis Rey (Hass, personal commu., 1997), at Camp Pendleton (along 3 streams) (Griffiths, personal commu., 1997), and along the Santa Ynez, and inland along the Kern River (Whitfield, 1996, Greenwald 1998); these nest mostly in coastal live oak (*Quercus* sp.) but also in willows and a few other native plants. In Colorado, ca. 45 adults breed in willows at 10 sites in the southwestern fourth of the state (Sogge, personal commu. 1997). In New Mexico, ca. 23-28 pairs breed along the middle Rio Grande, mostly in willows (Cooper 1997, Maynard 1994, Ahlers and White 1995, 1996, 1998).

Breeding populations of the sw WIFL appear to have been extirpated in low elevational areas along the lower Colorado north to Topock Marsh, along the lower Gila to Roosevelt Lake (Sferra *et al.* 1997, Greenwald 1998, McKernan and Braden 1999) and in western Texas. Populations along the upper Verde River that were small but healthy only 3-4 years ago now seem to be declining. A 20-pair population nesting only in willows at the Virgin River delta has been lost because of the rising water level in Lake Mead. The sw WIFL has extended its range into the Grand Canyon where it nests in SC (but with a negative reproductive rate) (Sogge *et al.* 1995) but has not expanded into the Pecos River Valley that has been massively invaded by SC. Populations at Cliff, NM and Roosevelt Lake and possibly the San Pedro/Gila, NM sites, Topock Marsh and the Virgin River area seem to be increasing but populations at the 3 upper elevation sites at Greer/Alpine, AZ have declined by half since 1993, although others may nest in unsurveyed areas. Critical habitat for the sw WIFL has been established in the coastal rivers and the Kern River, CA, 5 areas of Arizona, and southwestern New Mexico (Fish and Wildlife Service 1997).

Sw WIFL Mortality Factors and Detrimental Interactions with SC

Although the sw WIFL apparently is attracted to nest in SC, several of its needs may not be provided by this exotic plant and its very limited associated flora and fauna. Several major mortality factors have been identified but the degree of importance of each is not very clear and varies from site to site. We here propose some additional factors and discuss how most of these factors could be exacerbated by SC, a possibility that heretofore has been little discussed.

The reasons for the sw WIFL's precipitous decline toward extinction are poorly known. Since 1993, a major effort has gone into surveying populations and in documenting nesting success and causes of mortality. This is extremely difficult and time consuming work and in spite of dedicated efforts the picture remains incomplete. However, enough information has been gained to better understand some aspects. We here propose hypotheses that may explain the ecological relationships involved, or at least that may suggest further investigations. The relatively well understood facts are these:

1) The sw WIFL probably was never abundant but now is critically endangered. Its populations were first noticed to be declining in 1948 and apparently are still declining.
2) The population decline is strongly correlated with the increase in SC and decrease in native habitat but a cause and effect relationship has not been proven.
3) The sw WIFL appears to be strongly attracted to nest in SC trees. In Arizona, ca. 60% of the 255 nests found annually during the 4 years from 1993 to 1996,

and 78% of those found in 1998, were in SC, even though apparently suitable willows are present at several of the SC sites. In several areas, all nests were in SC.

4) In the lowest, hottest areas along the lower Colorado and lower Gila rivers, where the sw WIFL was once common, only a few territorial males (or pairs), no more than 2 or 3 nests, and no reproduction have been found for at least the last 20 years.
5) Outside of Arizona, the sw WIFL nests almost entirely in native trees, except for 6 nests found in SC and 1 in Russian olive at various sites on the Rio Grande, NM in 1995 and 1996. In southern California it nests mostly in coastal live oaks and willows, in New Mexico mostly in boxelder maples or willows, and in southwestern Colorado in willows; at the higher elevations of Arizona it nests only in willows.
6) Although it nests extensively in SC in mid-elevational areas of Arizona, large areas of nearly monotypic SC and other areas of mixed SC/native vegetation remain uninhabited, such as along the lower Colorado, lower Gila, Pecos and Virgin rivers, and along many smaller streams in CA, AZ, NV, and NM, unless native vegetation grows nearby.

Loss of native breeding habitat. Loss and fragmentation of native breeding habitat is given as the primary cause for the decline in sw WIFL populations in nearly every discussion of the topic by flycatcher biologists (U.S. Fish and Wildlife Service 1995). The most widespread and obvious change in habitat is the replacement of the native willow/cottonwood western riparian forests by invading, exotic SC. During the past 60 to 70 years, SC has increased to occupy half or more of the total vegetation on most southwestern streams and now exceeds 90% replacement on many. The sw WIFL population decline over time, first noted by Phillips (1948), clearly is correlated with the decline in native plant communities and the increase in SC over the same time period (Hunter *et al.* 1987, 1988; Rosenberg *et al.* 1991; U.S. Fish and Wildlife Service 1997), though a causal relationship has not been proven. Anthropogenic changes undoubtedly have detrimentally altered the environment of the native plants, but direct competition from SC and interactions between SC and the anthropogenic changes also have been major causes, especially along small streams but also along major regulated rivers (Lovich and Bainbridge 1999).

The sw WIFL continues to breed well in several areas of native vegetation outside of Arizona. Conversely, several large areas dominated by SC are not occupied, including the lower Colorado and lower Gila where the bird formerly was a common breeder. For the most part, large monotypic stands of SC seem to be unsuitable habitat (Tibbitts *et al.* 1994), perhaps in part due to the sw WIFL's lack of preference for the extensive drier riparian areas that SC now occupies and helped to create, or to the lack of certain species of critical food insects. The Pecos River floodplain of Texas and New Mexico from the Rio Grande to Santa Rosa has contained very large, almost monotypic SC stands since the 1930's. This apparently was never part of the sw WIFL breeding range; however, willow flycatchers migrate through here, and this could be an expansion area for the species, but no nesting has been reported here (Cooper 1997, Williams 1997). One exception to this scenario is at the Salt River inlet of Roosevelt Lake. Here, the sw WIFL nests substantially in monotypic stands of very large SC trees; however, areas of mesquite and other plants grow nearby which could supply resources.

Cowbird nest parasitism. Nest parasitism by the brown-headed cowbird (*Molothrus ater*) is one of the most important direct mortality factors for the sw WIFL, and surpasses predation in importance in some areas (Tibbitts *et al.* 1994). Average percent parasitism for all sites in Arizona increased from 6.3% in 1995 to 12% in 1996. In 1996, parasitism of sw WIFL nests at high elevations in Arizona was 38% (Sferra *et al.* 1997) and reached 80% in the Grand Canyon (Sogge and Tibbitts 1994). By 1998, cowbird trapping programs had reduced parasitism at several sw WIFL nesting sites to less than 1% while it remains at 25 to 38% at several sites without trapping (Griffith and Griffith 1995, Paradzick *et al.* 1999). The cowbird trapping program at Camp Pendleton, CA is attributed to greatly increasing the populations of least Bell's vireo. However, cowbird trapping there (Griffith and Griffith 1996), on the Kern River, CA (Whitfield and Strong 1995) and on the lower San Pedro, AZ (Paradzick *et al.* 1999) has reduced parasitism but still has produced no, or only slight, increase in sw WIFL populations.

Some evidence indicates a synergistic interaction between cowbirds and SC abundance that could increase the rate of parasitism. On the Pecos River, the ratio of cowbirds to other birds was three times higher in SC than in native vegetation types, suggesting that rates of parasitism also might be higher in SC there (Livingston and Schemnitz 1996), and confirming similar findings there by Hildebrandt and Ohmart (1982). McKernan and Braden (1999) reported greater levels of cowbird parasitism in near monotypic SC at Topock Marsh (6 of 21 nests) than in near monotypic willows at Pahranagat NWR (0 of 21 nests). Surveyors have noted that sw WIFL nests could be more easily spotted in SC because of less foliage in the area of the plant where the nests were located (Sogge and Tibbitts 1992, 1994; McDonald *et al.* 1995). Perhaps nests in SC also are more easily found by cowbirds (Tibbitts *et al.* 1994). Although the sw WIFL selects SC thickets with a dense canopy cover, it places its nests in the area of little cover just underneath the canopy. The dense foliage in willow thickets extends further below the canopy, hiding the nests more completely. Cowbird parasitism also delayed successful nesting by 13 days at the Kern River, which substantially reduced survival of the fledged young (Whitfield and Strong 1995).

Sw WIFL adults sometimes build an additional bottom in the nest that covers the cowbird eggs, preventing them from hatching (Sogge *et al.* 1995, Sferra *et al.* 1997). Rarely, they may eject the cowbird eggs from the nest (Hull and Parker 1995). They sometimes are able to chase away nest-searching female cowbirds (Whitfield 1990), but she cautioned that aggressive behavior toward cowbirds does not necessarily deter parasitization.

Predation. Nest predation was documented as the greatest cause of nest failure of the sw WIFL at sites in Arizona (Sferra *et al.* 1997, McCarthey *et al.* 1998). Of a total 203 nests found during 1998, 64 (31.5%) were depredated (Paradzick *et al.* 1999). At 19 nests of sw WIFL and other similar bird species monitored continuously (day and night) by video cameras, 5 were depredated by common kingsnakes (*Lampropeltis getulus*) and one by a spotted skunk (*Spilogale gracilis*) at night. Two of those depredated by kingsnakes were the sw WIFL (Paradzick *et al.* 1999). Other animals, such as rodents and birds are also suspected of preying on eggs or the young. Flooded conditions and standing water under nest trees (that the birds favor for nesting) may give some protection from predators such as rodents and snakes (Greenwald 1998). Willows may provide more protection from predators than does SC, since nests there are less visible than in SC. On the other hand, McKernan and Braden (1999) reported higher levels of nest predation in near monotypic willows at Pahranagat NWR (12 of 21 nests) than from almost monotypic SC at Topock Marsh (7 of 21 nests), perhaps because predator populations may have been higher in the native vegetation. Jakel and Gatz (1985) reported higher populations of reptiles in native vegetation than in SC.

Fires and floods. Sw WIFL populations are susceptible to elimination by stochastic events especially since most populations are small and tend to occur in small areas. The increased likelihood of fire is one of the most serious threats to the sw WIFL caused by SC (DeLoach and Tracy 1997, Greenwald 1998). Fires are rare in native riparian plant communities, but SC stands burn relatively frequently (Agee 1988). Also, the driest part of the year often is during the breeding season for these birds. A large fire in SC stands at the PZ Ranch on the lower San Pedro River in 1996 burned 75% of the habitat and several active nests (Paxton *et al.* 1996). A fire in SC at Topock Marsh on the lower Colorado in 1998 burned much habitat and may have burned some active nests and fires at Mittry Lake and Martinez Lake burned habitat with territories but without nests. The birds thus increase their risk of breeding failure by choosing to nest in SC.

Recent flooding on Lake Mead has nearly eliminated a 20-pair, and apparently increasing, sw WIFL population breeding only in willows because the flooding eventually killed the willows (Sferra *et al.* 1997). Authorization to raise the level of Roosevelt Lake threatens that large 43-territory population, and release of water from Alamo Lake on the lower Bill Williams River in 1983 eliminated much good potential, although maybe unoccupied, habitat (Hunter 1987, Hunter *et al.* 1987). Overfilling of Lake Isabella on the Kern River, CA threatens a 25-pair population on the Kern River Preserve and the South Park Wildlife Area (Greenwald 1998).

Lethal high temperatures. The interaction of the sw WIFL with extremely high temperature and vegetational type could explain the extirpation of the sw WIFL along the lower Colorado and lower Gila rivers according to a theory advanced by Hunter (1987; Hunter *et al.* 1987, 1988; Rosenberg *et al.* 1991). Webb (1987), after reviewing the research on various bird species (not including the sw WIFL), reported that for most species optimal development occurred between ca. 35-38°C, 80% mortality occurred above 41°C, and most embryos died above 43°C for exposure periods of less than 10 hrs. In these lowest and hottest areas of the Southwest (the Lower Colorado River Subdivision of the Sonoran Desert Scrub Formation) (Brown and Lowe 1980), maximum temperatures during the breeding season frequently exceed 43°C (109°F) (USDC-NOAA 1993). The area delineated, from the Salton Sea and the lower Colorado River to Lake Mojave, to just east of Phoenix, to Hayden and just east of the Santa Cruz River, closely corresponds to the area where the sw WIFL has been extirpated, or nearly so. The relatively large populations at Roosevelt Lake, on the lower San Pedro, at Topock Marsh on the lower Colorado River, and on the upper Bill Williams River all lie just outside this area, at higher and cooler elevations. The successful nesting areas of the sw WIFL at Topock Marsh are all within the vast mesic area of seasonally standing water immediately adjacent to the large marsh (McKernan and Braden 1999). Although at a low (140 m) elevation, this area probably is cooled below the critical 43°C by evaporation from the water. All the populations in California, New Mexico, Colorado, and other areas of Arizona occur in cooler and/or higher areas.

The extensive willow stands (often with denser shade than SC thickets) that were present along the lower Colorado River in the early 1900's, together with a tall overstory of cottonwoods that provided shade and additional cooling, probably kept temperatures below the lethal level for bird eggs. Maximum summer temperatures probably have changed but little since the early 1900's, but vegetation has changed drastically. The SC thickets of today, coupled with the complete lack of a cottonwood overstory, allow temperatures to frequently exceed the lethal level for bird eggs during the summer. The combination of lack of upper canopy shade from cottonwoods and lack of air mixing in the SC thickets results in dramatically increased temperatures and humidities within SC canopies during the summer months. Observations by one of us (Smith) indicate that the probable mechanism is first, that the SC thickets may have an open canopy with small, fairly reflective leaves that poorly shade the ground, especially compared to the tall, broadleafed cottonwoods and willows. Second, the architecture of the SC upper canopy forms a boundary layer below which air mixing is poor. The result is a layer of still air overlying a poorly shaded surface that maintains higher temperature and humidities than in the well-mixed air above the canopy, especially compared to a cottonwood/willow stand that has a "rougher" surface with better air mixing and that provides denser shade. The general lack of seasonal flooding, with its cooling evaporative effect, may also contribute to higher temperatures here. The sw WIFL and 6 other mid-summer breeding, riparian obligate bird species have been extirpated or are in serious decline in the lower Colorado River valley below Topock Marsh (Hunter 1987). Spring breeding birds are able to complete their nesting before temperatures become excessive and their populations are not in decline. The status of the summer-breeding birds in this area, including the sw WIFL, probably will not improve until SC is controlled and willow thickets and tall cottonwoods return.

Anderson (1994) found that, in SC/mesquite vegetation along the lower Colorado River, mean daily soil temperatures at the 10-cm depth were 2-5°C higher, and maximum daily temperatures were up to 10°C higher, than in a cottonwood/willow grove, presumably because of the greater amount of shade in the C/W grove. On the other hand, willows, but few cottonwoods, have regrown since the 1983 floods at some sites along the lower Colorado south of Yuma (Solomon 1997) but the sw WIFL has not begun nesting there (Sferra 1999, personal commu.).

McKernan and Braden (1999) reported temperature and humidity at the nest, in the territory, and in similar unoccupied habitat at Topock Marsh (monotypic SC), the Virgin River area (mixed SC/willows), and the Pahranagat NWR (monotypic willow), all areas where the sw WIFL breeds successfully. However, their measurements could not clarify the hypothesis of Hunter (1987) because they did not report temperatures in the hottest areas south of Topock Marsh where the birds do not reproduce and because they reported average daily and not maximum daily temperatures.

Food. The feeding behavior of the sw WIFL, like most birds, probably is restricted to catching certain kinds of insects to which it is attracted, which are nutritionally adequate, and which are sufficiently abundant to provide for energy, body maintenance and development of the young. Early studies indicate that the willow flycatcher (*E. trailii*) fed mostly on wasps and bees, beetles, flies and sometimes moths (including caterpillars) and bugs but not on any homopteran species, which includes leafhoppers and cicadas (Beal 1912). However, the food preferences and needs of the southwestern subspecies (*E.t. extimus*) have been little studied. As a food resource, SC provides the exotic *Opsius* leafhoppers and also insects that feed on pollen and nectar (Liesner 1971, Stevens 1985), all of which are abundant throughout most of the growing season, and the native Apache cicada, which is abundant only briefly in mid-summer and only in more southern areas (Glinski and Ohmart 1984). Other types of phytophagous insects (and immature insects including caterpillars) are almost entirely lacking in SC. The flower-feeding insects all develop on nearby native vegetation and the adults fly to the SC flowers, so their larvae are absent in SC trees. The diversity of insect species in the native plant communities thus is far greater than in SC, and these are the insect species and stages with which the sw WIFL evolved. If sw WIFL (or other bird species) nestlings require particular types of insects, for example caterpillars (Beal 1912) at some time during their development, they cannot be obtained from SC. Caterpillars may be especially important for the nestlings, not only for nutrition but as a critical source of water during the hot, dry summers of the sw WIFL breeding range.

Recent observations indicate that the sw WIFL feeds to a limited extent on *Opsius* leafhoppers (Drost *et al.* 1998) but not on Apache cicadas. At Roosevelt Lake and several other sites in Arizona and Colorado, Drost *et. al.* (1998) found that for adult sw WIFL, in both willow and mixed habitat, caterpillars constituted 8% and leafhoppers 4% of the number of prey insects in the diet but in SC habitat caterpillars only 3% and leafhoppers 14% of the diet. For nestlings and fledglings, in willows and mixed habitat combined, caterpillars constituted 17% (tied with Diptera for first place) but leafhoppers only 5% of the diet (SC habitat not sampled). Caterpillars are much larger than leafhoppers, so on a volume or biomass basis, caterpillars would constitute perhaps half of diet of nestlings in willow habitat, though this comparison was not made by Drost *et al.* (1998). The biological control insects themselves may also become a food resource for the various insectivorous birds and other animals.

The sw WIFL does not usually occupy the interior of large monotypic SC stands but nests nearer the edges, where a greater variety of insects would be available in adjacent native vegetation. Paradzick *et al.* (1999) speculated that the higher rainfall created by El Niño in 1998 may have produced an increase in the abundance and diversity of food insects compared with previous years, which led to the increased nesting success and productivity seen from 1997 to 1998. Along the lower Colorado River, increased soil temperature in SC/mesquite groves causes the Apache cicada to emerge a month earlier than in C/W groves, causing the cicada emergence to peak and decline in the SC/mesquite before the peak food needs of birds that feed on them (Anderson 1994). They speculated that this lack of synchronization between cicada emergence and bird food needs in the SC/mesquite could be an explanation for the population decline of some summer-breeding bird species in this area. Similar SC induced asynchrony between other insects and birds has not been reported but could be a factor in the decline of other bird species. An abnormally extended development period is a common characteristic for insects feeding on less than optimal host plants. SC might not only harbor reduced populations of sw WIFL food insects but also might either accelerate or delay their development outside of the period of the peak of food needs.

Shortage of females. A very noticeable condition in sw WIFL ecology is the large number of singing but apparently unmated males, reported at many of the survey sites. This indicates the possibility of a substantial shortage of females in the breeding population, not just that the sexes are unable to find each other. The magnitude of this apparent shortage of females could make this one of the greatest, and possibly the greatest, causes of the overall low reproductive rate of the sw WIFL. For example, at Roosevelt Lake, survival of banded females was only 34% but was 56% for males from 1996 to 1997, although survival of females and males was about equal at 56 to 57% from 1997 to 1998 (Netter *et al.* 1998). Possible sources of the problem may lie in 1) a difference in basic sex ratio (a lower proportion of female eggs when laid), 2) lower survival of female nestlings or fledglings (male nestlings more aggressive?), or 3) lower survival of female adults during migration, overwintering or during the breeding season. Sampling bias (females more difficult to find) could account for part of the differences observed, but we also should look for factors that have changed during the past 50 years.

One clue we found was the observation by Sedgwick and Knopf (1989) that the males in north-central Colorado (probably *E.t. trailii*) assist but little in feeding the young. They did not note differences in participation in nest building. They hypothesized that biparental care of nestlings for the WIFL may not be mandatory. Male strategy of survival may dictate that protecting the territory from other intruding males is more productive in passing along his genes than is helping to feed the young, especially in view of the observation of promiscuity by the females and polygyny by the males. Differential sex ratio or survival in the nest may be impractical to measure in the field because the required sampling might cause nest abandonment or mortality of the young. However, nestlings and fledglings now are being banded and blood samples taken for DNA analysis. Chromosome studies or a measure of hormone levels from these same blood samples could determine sex ratios. Perhaps females on nests are more frequently killed by wildfires in SC than are males. Differential mortality of male and female adults during the breeding season has not been reported. However, differential mortality of overwintering adults could be possible, for example, if females, already stressed from the breeding season and migration, were further weakened by feeding on insects that originated in insecticide-treated agricultural fields in Central America.

Increased metabolic stress on the female could explain the observations. The major energy requirements of the sw WIFL would appear to be for migration, defending the territory, nest building, egg production, and feeding the young. The latter two of these appear to be borne entirely or mostly by the female, placing more metabolic stress on her than on the male. The reproductive stresses are compounded by the common practice of a female producing 2 or even sometimes 3 broods during the breeding season, or of nesting again if the first or second nest, eggs or young are lost. Also, Sogge (1999, personal commu.) observed that the males sometimes leave the territories during the second brood, leaving *all* care to the female. If females are so reduced in vigor that they die during the migration from the southwestern United States to southern Central America and back just 1 year sooner than normal, the overall female population would be reduced by from 25 to 33%, given the average life span of 3 to 4 years. If searching for food is more metabolically demanding for females in SC this could be another way in which SC might adversely affect the sw WIFL. We could not find information to resolve these questions; more research obviously is needed.

Overwintering habitat. Loss of overwintering habitat in Central and/or South America possibly is of critical importance in the sw WIFL population decline. In January and February 1998, 20 willow flycatchers (subspecies not identified) were found in Costa Rica (Koronkiewicz *et al.* 1998). There, more than half of the forests have been cleared, mostly for beef cattle pastures, since 1940. The wetland areas where the flycatchers were found are mostly surrounded by agricultural fields and pastures, often with substantial usage of pesticides. The effects on overwintering flycatchers and other birds is not known, but further encroachment of agriculture into the wetlands could threaten these birds. The banding program that began in 1997 may soon reveal the overwintering locations of the sw WIFL. The first banded sw WIFL (from Ash Meadows NWR, NV) was recovered in

Costa Rica during the 1998-99 winter and was seen again at Ash Meadows in late June 1999 (Sogge, personal commu.). The limited information available to date does not indicate overwintering mortality as a major cause of the sw WIFL decline.

Other factors. Livestock sometimes may push on the trees causing the eggs or young to fall from the nest and disturbance by humans can cause nest, abandonment (Sferra *et al.* 1997). Knowledge of sw WIFL ecology is not very complete and other factors, or interactions, may yet be discovered that influence the observed population decline.

Attractiveness of SC to the sw WIFL vs. Lack of Adequate Resources

The sw WIFL obviously evolved with its summer breeding grounds in native riparian vegetation, and we must assume that these areas provided for all its needs. Now that SC has invaded and replaced most of the willows, creating an artificial, exotic habitat in many areas, the sw WIFL is nesting in SC, and often seems to prefer SC even if suitable willows are present. Obviously, something about SC attracts the bird. Nevertheless, sw WIFL populations continue to decline. Based on these conditions, we must assume that SC does not provide for all its needs. We here review these conditions and propose hypotheses to explain this phenomenon.

The major behavioral patterns that influence population levels of the sw WIFL would appear to include site selection and nest tree selection. The birds appear to be influenced by both site fidelity and opportunism. Several of the requirements of the sw WIFL are supplied by both its native habitat vegetation and by SC. The birds are influenced in selection by certain site attributes that served them well within the native plant communities in which they evolved but that do not convey completely to the changed conditions within the SC invaded areas. In some cases, this may lead the birds to select habitats that may be deficient in certain important elements. In other cases they may select unsuitable habitat because better sites are unavailable.

Site selection. The sw WIFL appears to be attracted to a given location or site, an area of from one to a few hundred hectares, by such site characteristics as nearness to water, dense vegetation at heights of from 2 or 3 m to 10 m, in moderate to broad floodplains (strips only a few trees wide are unsuitable), with adequate perching sites, and with an abundance of food insects. The total amount of shrub-tree vegetation in riparian areas within the range of the sw WIFL appears to have actually increased during the period of its decline. Its decline must then be related to habitat quality rather than quantity. The most obvious change in quality is the invasion of the native plant communities by SC. Site fidelity may partially explain why the sw WIFL now nests in SC in some areas. The birds probably originally nested in willows at these locations and after SC invaded they simply began nesting in it rather than move to a different location.

If SC provided good habitat, then we would expect sw WIFL populations to be increasing and that it might extend its range into newly infested SC areas. Instead, it apparently has not been able to adapt completely to SC dominated breeding areas; previous breeding populations along the SC dominated lower Colorado and lower Gila rivers have been extirpated, and recent populations along the SC-dominated upper Verde River of Arizona have been almost lost. Breeding populations have expanded into one new area, the Grand Canyon, that is SC dominated; however, this area acts as a biological sink with a negative reproductive rate, but probably because of cowbird parasitism. The sw WIFL still does not breed in the vast monotypic SC stands on the Pecos or the Virgin rivers, unless native vegetation grows nearby, even though migrants pass through the Pecos area annually.

Nearness to water. Both willows and SC grow along streambanks near water. Willows can grow only with a higher water table, and thus must grow near water. SC has a deep root system and can grow further from the water's edge. However, other factors often allow SC to outcompete willows that grow adjacent to water. Both SC and willows can withstand partial submersion and survive overbank flooding for several months. The sw WIFL generally will nest in areas where the trees are in flood waters a few feet deep as at Lake Mead (Sferra *et al.* 1997), Topock Marsh (C. Smith, Personal commu., 1997), and along the middle Rio Grande (Ahlers 1997), along the Virgin River (McKernan and Braden 1999), or in areas of wet but not flooded soil. Along the middle Rio Grande of New Mexico, the floods of the late 1980's washed out or drowned SC near the river, which then revegetated with willows; the sw WIFL then began nesting in the willows but not in the SC which remained further from the water.

The sw WIFL surveyors frequently have noted that nesting occurred only near free water. Johnson *et al.* (1999) developed a hypothesis that free water in the river channel during all or most of the breeding season, but especially during May and June, is a minimum requirement for nesting; overbank flooding of the nest site may also be important to encourage nesting. On the Rio Grande of New Mexico (Johnson *et al.* 1999), the river channel was completely dry for 100 days during the 1996 breeding season at San Marcial and a total of only 1 nest was built by 4 pairs of flycatchers in 9 territories. At one site there, 3 birds established territories during May but then abandoned them during June and early July; the river was dry during this period. In normal years when water was present in the channel during all or most of the breeding season (1994, 1995), 5 mated pairs built 5 nests. During 1997 (another normal year), 7 males established territories but only 2 attracted mates, these 2 pairs built 2 nests.

A shortage of females appeared to be the major cause for the few nests. Presence of water could be a direct factor in site selection and suitability for the females or absence of water could be an indirect factor by producing lower humidity, lower insect food availability, or higher temperatures (as on the Lower Colorado River). SC could be a contributing cause of this mortality because its great use of water would increase the drying up of the river. In extensive stands of monotypic SC on the lower Colorado, Gila and Pecos rivers, where the sw WIFL does not breed, much of the habitat is xeric and lacks seasonal inundation, caused by river regulation, pumping and diversion, and evapotranspiration by the dense SC stands.

Food insects. The sw WIFL could be attracted to a SC site by the great number of adult pollen and nectar feeding insects present at the time of site selection but later might be adversely affected because the immature stages of these insects, or other types of insects, were not present. At Roosevelt Lake in 1996, the 12 nests with 29 eggs found in mixed vegetation stands on the Tonto Creek inflow (all nests in SC) produced 16 fledglings, while 14 nests also with 29 eggs found in monotypic SC stands on the Salt River inflow (also all in SC) produced only 4 fledglings (Sferra *et al.* 1997). Nest productivity has been lower at the Salt River inflow than at Tonto Creek during every year surveyed (1994 to 1998) (Greenwald 1998, Paradzick *et al.* 1999). This might indicate a shortage of some critical type of food in monotypic SC stands, such as caterpillars (Drost *et al.* 1998), as discussed previously. Even at the Salt River inflow, mesquite and other native plants grow abundantly adjacent to the SC stands in rangelands at 50 to 100 m and further inland from the river, where a greater variety of insects would be available. At Topock Marsh, a large area of near monotypic SC, surveyors have not reported on the proximity of the nests (all of which are in SC) to surviving patches of willows and other non-SC vegetation.

Nest Tree Selection

The sw WIFL appears to be opportunistic in the selection of the nest tree at a given site; it probably selects whichever tree appears to it superior in some characteristic such as canopy density, branch structure, or size, even though other nearby plants also might be within the range of suitability.

Canopy density. The sw WIFL prefers vegetation with 90 to 95% canopy density; both willows and SC can supply this requirement. However, Sferra *et al.* (1997) noted that once SC approached 50% of the composition of the stand, on the lower San Pedro River, the sw WIFL nested only in it, even though sufficient willows were still present. Personal observations by one of us (DeLoach) at the Tonto Creek inlet of Roosevelt Lake indicated that the willows at that site did not have as dense a canopy as the SC, and that the SC now had occupied the more favorable areas where the willow would be expected to grow; all nests were in SC here. It would appear that once SC reaches a density of ca. 50% of the stand, the effect of this competition reduces the favorability of the remaining willows, in this case by reducing canopy density. The nesting birds may have simply selected the most dense trees.

Branch structure. Much observational data indicates that the sw WIFL is strongly attracted to nest in SC trees, even though apparently suitable willows grow nearby, and even though only scattered, unvigorous SC trees are surrounded by thickets of willows in very good condition. The attractive trait appears to be a single stimulus, the branching structure of SC, which is essentially ideal for nest placement. The sw WIFL prefers to nest in a branch with several small, vertical stems originating near a point so that the nest may be attached in the crotch (Sogge 1997, personal commu.). Both SC and the native nest trees provide this structure, but many small vertical branches coming off a limb are a major feature of SC structure. In many cases, a SC tree may have a branch structure superior to an adjacent willow tree, so is selected for the nest. The stimulus is so strong that Richman (personal commu., 2000) suggested that it appeared to be a classical case of a "super stimulus" in which the one stimulus overrides other factors that may be less than ideal, or even detrimental. This results in a "fatal attraction" of the sw WIFL for SC, and increased mortality and lower reproductive success in SC than in the native breeding habitat. A similar situation was recently reported in which the American robin (*Turdus migratorius*) has begun nesting heavily in the exotic, invasive honeysuckle (*Lonicera maackii*) where it suffers much higher predation and lower reproductive rate than in its native nest trees (Schmidt and Whelan 1999).

At several sites, surveyors have observed nests in a lone SC tree growing among dense, well structured willow stands. Examples are at the lower San Pedro River (Paradzick, personal commu. 1997) and at San Marcial on the middle Rio Grande (Mehlhop 1999, personal commu.). In an unusual case, one sw WIFL pair even nested in a dead SC tree in the willow stand at San Marcial (Maynard 1994). At Mesquite South on the Virgin River, NV, 4 nests were found in SC and only 1 in coyote willow in a community with a Goodding willow/cottonwood dominated overstory and a SC/coyote willow understory (McKernan and Braden 1999). One flycatcher nest was found on the Bosque del Apache NWR on the middle Rio Grande in New Mexico, in 1996, and it was located in a lone SC tree within a dense patch of coyote willow that was even-aged with occasional larger SC or cottonwood trees scattered throughout (Cooper 1997).

These cases sometimes are cited as implying the great value of SC to the sw WIFL. We do not believe this to be true. At San Marcial, the birds nested in both willows and SC, showing that both were acceptable. Nevertheless, they chose the tree in which that particular characteristic was *most* acceptable; in several cases this was SC. The occurrence of a nest in a lone SC tree surrounded by large thickets of willows in which nests also occur, fails to argue that SC is important to the bird at that site. We suggest that if SC trees were not available at such sites, the sw WIFL would nest just as frequently as now in the willow/SC habitat. The converse of this also has been reported: W.C. Hunter and B. Soloman (both personal commu. 1997) stated that on the lower Colorado River the sw WIFL often is associated with the few willow or cottonwood trees remaining in largely monotypic SC stands, perhaps in this case for the cooler microclimate and/or the greater diversity of food insects present.

Reproductive Success

Reproductive success is key to understanding the decline and, hopefully, the eventual increase of sw WIFL populations. The effort of many of the surveys often has concentrated in locating and counting adult populations and on the fate of the eggs laid, which is of value for determining the specific mortality factors. Unfortunately, all the data needed for calculation of reproductive success, especially fledglings produced per female (or per male-female pair) during the breeding season, or all the data needed to associate reproductive success with habitat type and nest substrate (willows compared with SC), have not always been reported. Also, mortality of the fledglings until their migration to overwintering areas in Central America, a much more difficult undertaking, apparently never has been measured. We here review the available data from this point of view.

Surveys during 1996 to 1998 along the lower Colorado River and along the Virgin River and other tributaries in southern Nevada, provide data on reproductive success in different types of vegetation and along an elevational-temperature gradient. Reproductive success was greater in sites with native willow habitat, or in sites with mixed willow/SC habitat, than in sites with monotypic or dominant SC habitat, during all 3 years.

During 1996, nesting was confirmed at only 2 of the 34 sites surveyed (McKernan 1997). At the Topock Marsh site, three 100-acre study blocks were located on the Havasu National Wildlife Refuge (140 m elevation) within an area of 5,000 acres of 90% SC with 10% black willow in isolated stands within the SC, adjacent to the marsh and vast areas of standing water; the sites were 60% flooded in May to 10% flooded in July. The 3 pairs of adult sw WIFL found here produced 1 nest, 2 eggs, 2 nestlings, and 1 fledgling, or 0.33 fledglings per pair. The Lake Mead Delta site was an area of 1000 acres (240 acres surveyed), of 92% willows, 5% SC and 3% cottonwood, 85 to 100% inundated to 3 ft. deep, at 365 m elevation; 5 pairs produced 6 nests, 16 eggs, 9 nestlings, and 6 fledglings, or 1.2 fledglings per pair, or a nesting success 3.6 times greater than at Topock Marsh.

In 1997, the lower Colorado River surveys were expanded to include 76 sites; importantly, 11 sites were added at 4 locations northward along the Virgin River drainages (elevation 340 to 550 m) in southern Nevada (McKernan and Braden, 1998). At Topock Marsh, 12 pairs at 2 of the 6 sites produced 9 nests and 10 fledglings for an average of 0.83 fledglings per pair; only 1 nest was predated and 1 parasitized. At 3 of the 11 Virgin River sites (Virgin River Delta #1, Morman Mesa and Mesquite South) 11 pairs produced 15 fledglings, or 1.36 per pair or 1.6 times more than at Topock Marsh. At Virgin River

Delta #1 (monotypic black willow), 6 pairs produced 14 nests and 9 fledglings, or 1.5 per pair, even though 12 of the nests were partially parasitized, predated or abandoned. The site was completely and continuously inundated to an average depth of 15 ft. At Morman Mesa (50% coyote willow, 30% black willow and 20% SC), 2 pairs produced 3 nests and 4 fledglings, or 2.0 per pair. At mesquite South, (30% black willow overstory and 20% coyote willow and 50% SC understory), 3 pairs produced 5 nests and 2 fledglings, or 0.67 per pair, even though all 5 nests were partially parasitized, predated or abandoned. Nesting success might have been even greater at the Virgin River sites except for the high rate of predation, parasitism and nest abandonment, which was low at Topock Marsh.

At Lake Mead Delta, only 3 pairs were found, which produced 3 nests and 4 fledglings, or 1.33 fledglings/pair; the vegetation at this site continued to deteriorate from last year because of flooding from Lake Mead, now averaging 15 ft. deep. At Muddy River Delta (60% black willow and cottonwood overstory and 40% SC understory), 2 pairs produced 2 nests but the site was not well surveyed thereafter so nesting success was unknown (McKernan and Braden 1998).

During 1998, the lower Colorado River surveys were expanded to 110 sites at 10 locations (McKernan and Braden 1999). At Topock Marsh, 17 pairs produced an estimated 16 fledglings in SC and 4 pairs produced an estimated 4 fledglings in willows, or 0.94 fledglings per pair in SC and 1.00 per pair in willows. Twice as many fledglings were produced in willows as expected, since willows constituted only 10% of the vegetation but contained 20% of the fledglings.

The Pahranagat NWR site (85 mi. N of Las Vegas), was an area of 70% black willows, 20% cottonwoods and 10% cattails, inundated up to 6 ft. deep for half the field season: 8 pairs produced 20 fledglings, or 2.50 per pair, or 2.66 times more than those in SC at Topock Marsh.

The best comparison of nesting success in SC vs. willow was among the 11 sites in the Virgin River area, all at higher elevations (360 to 550 m) and each site with a choice of suitable SC or willows. At the 3 main sites where reproduction was recorded (Virgin River Delta #4, Mormon Mesa, and Mesquite South), 11 fledglings were produced in willows and only 1 in SC; nesting success (fledglings per pair) was 1.51 in willow and 0.27 in SC, or 5.6 times greater in willow. At the Virgin River Delta site #4, 3 pairs produced 2 fledglings (0.67 per pair), all in monotypic sapling black willow at the northwest end of the site. Vegetation composition changed gradually to mixed willow/SC in the middle of the site and to nearly monotypic SC at southeastern end. The site was inundated from Lake Mead. At Morman Mesa site #1, 4 pairs in willows produced 9 fledglings (2.25 per pair) and 2 pairs in SC produced 1 fledgling. The vegetation consisted of variable amounts of intermediate to mature black willow overstory with an understory of coyote willow and SC or of early to mid-successional monotypic stands of coyote willow and/or SC; the site was fully inundated during late spring and early summer and intermittently thereafter. At Mesquite South (30% black willow, 20% coyote willow, 50% SC, at 480 m elevation), 2 pairs produced 7 nests, 6 in SC and 1 in willow (pairs in each vegetation type were not given, so we distributed this as 1.71 pairs in SC and 0.29 in willows) but no fledglings were recorded. Vegetation consisted of black willow (with an occasional cottonwood) overstory and mixed SC and coyote willow understory, surrounded by continuous forests of SC on 3 sides. This site is within the banks of the Virgin River but was only intermittently flooded from irrigated agricultural fields. At Muddy River Delta, 2 pairs produced 2 nests but fledged no young.

No reproduction by the sw WIFL was detected south of Topock Marsh during any of the surveys; 2 or 3 nests were found but no eggs, nestlings or fledglings were found. During 1996, 9 sites were surveyed at Topock Gorge, Lake Havasu and the Bill Williams River (138-170 m elevation) and 19 sites from Ehrenberg southward to the Gila River (40 to 80 m elevation) (McKernan 1997). During 1997, 12 sites were surveyed from Topock Gorge to Hall Island and 28 sites from Ehrenberg south to the Gila River (McKernan and Braden 1998). During 1998, 54 sites were surveyed from Topock Gorge south to Gadsden (McKernan and Braden 1999). This is a large area, surveyors cannot cover it all, and the possibility of reproduction cannot be completely ruled out. Nevertheless, after surveying 122 sites during the 3 years, we may assume that successful reproduction at least is minimal, or that breeding populations may have been extirpated south of Topock Marsh. This agrees with the hypothesis of Hunter (1987) that this lowest-elevational area is too hot for successful reproduction by the sw WIFL (discussed previously). On the other hand, if high temperatures caused egg mortality, we might expect dead eggs to be found in the nests, and they were not (McKernan and Braden 1999); however, the females also might sense that temperatures are too high and leave or not lay eggs.

In Arizona, the most direct comparison of nesting success was at Roosevelt Lake, between the Tonto Creek inflow (mixed vegetation but large SC dominant) and the Salt River inflow (monotypic, large SC). Nesting success was greater at Tonto Creek every year from 1994 to 1997 (average 1.43 fledglings per adult pair) than at the Salt River inflow (average 0.72 per pair), or 2.0 times greater in mixed vegetation than in monotypic saltcedar (data compiled by Greenwald 1998). Nesting success also has been consistently higher at the small montane sites (Greer and Alpine) where no SC is present and nesting is mostly in Geyer's willow; here, 2.6 fledglings per pair were produced in 1998; this was 1.3 times more than at 11 mid-elevation sites, 3 sites with "some" SC present and 8 with SC "dominant" (both with 2.0 fledglings per pair) (Paradzick *et al.* 1999). Among these mid-elevation Arizona locations, nesting success often has been variable and not readily associable with the level of SC dominance. In California, nesting success in native vegetation varied from 0.97 to 2.0 fledglings per pair at 2 major sites (San Luis Rey and South Fork Kern River) from 1994 to 1997. At 8 sites along the Rio Grande, NM during 1996, 0.57 fledglings per pair were produced at 3 sites "dominated" by SC, and 0.33 per pair at 4 sites with "some" SC (data compiled by Greenwald 1998). Nesting success from the California and New Mexico data overall appears low, perhaps in part because this was not a major emphasis during these surveys.

Our analysis of these data must be viewed with some caution. Numerous factors influence the measurement of nesting success in addition to site characteristics (whose influence also is not well understood) including the skill of the surveyors, accessibility of the site, surrounding agricultural lands, and elevation and temperature. Also, all information needed for our analysis was not always recorded in the reports. Nevertheless, the amount of data now at hand strongly indicates that nesting success is greater in the native willow habitat than in near monotypic SC habitat. We do not find information from the data in the reports of McKernan (1997) and McKernan and Braden (1998 and 1999) to support their conclusion that nesting success is greater in SC. Even though the birds may choose SC as a nesting substrate in some situations, as also suggested by McKernan and Braden (1999), this choice may not always be to their reproductive advantage. Also, the survey reports are preliminary and may not necessarily be the authors' final conclusions. Nevertheless, their preliminary conclusions appear to strongly influence FWS policy regarding the needs for recovery of the sw WIFL and the influence that biological control of SC might have on that. We here present other logical explanations for the decline of the sw WIFL and for its observed behavior and response to the recently changed environmental conditions, including the SC invasion, that more closely agree with the observed field situations. We anticipate that future surveys will provide data to clarify sw WIFL behavior and the effects of SC in the ecosystem.

Lack of Functional Equivalency between SC and C/W for the sw WIFL

Stromberg (1998) compared "functional equivalency" of cottonwood/willow and saltcedar stands along the small, unregulated, middle San Pedro River of southeastern AZ. The 5 x 20 m study plots were with highly variable woody stem densities between plots, and located at approximately equal distances from the river. The 20 cottonwood plots consisted of woody plants with a mean age of 18 (range 1-66) years, 12 m high, 319 (4 to 692) stems/100m^2, 44% seepwillow, 17% cottonwood, 10% willow, 6% *Clematis*, and 18% SC. The 26 SC plots contained woody plants of mean age 22 (range 4-43) years, 7 m high, 174 (15 to 333) stems/100m^2, 70% SC, 10% seepwillow and 6% burroweed.

She compared 30 soil, geomorphological, and vegetation structural traits. Mean values for 22 of the traits did not vary between the SC and cottonwood plots. Eleven traits varied either in mean values or temporal trends. Of the 13 traits construed as indicators of riparian ecosystem functions, mean values and temporal patterns for 6 were similar between C/W and SC - sedimentation rate, soil silt content, wetland indicator score, organic matter, stand density, and light availability. However, calculated functional equivalency indexes were similar only for 4 factors. Two of the different traits, herbaceous species richness and native herbaceous cover, both desirable traits, were higher in SC.

Soil salinity and depth to water table were similar between SC and C/W, as would be expected along a small unregulated, frequently flooding river, and with plots at approximately equal distances from the channel. The traits that might affect animal populations were not measured, for the most part. However, 3 factors were construed as relating to animal habitat; the computed functional equivalency index for light availability was equal for SC and C/W but those for canopy height and stand density were lower for SC. Stromberg (1998) included only soil and community type data in her analysis. Functional type data or information on physiological ecology, such as leaf area, plant water potential, photosynthesis, stress tolerance, and root:shoot ratios were not used.

Based on these data, Stromberg (1998) concluded that SC can serve as an ecologically important functional analog to the "displaced" native species along reaches that have become too dry to support native trees. This presumably refers to equivalent stand structure - i.e., woody vegetation of similar height and density, and equivalent associated plant species, although she did not specify which traits were analagous. This conclusion is abundantly supported by many observations along Southwestern streams; SC has in fact replaced large areas of C/W, seepwillow, arrowweed and other native vegetation. However, the SC and C/W stands really are not very structurally equivalent: the SC thickets have less horizontal and vertical structural diversity both within stands and between stands than does C/W (Lovich and DeGouvernain 1998), they usually have less species diversity within stands, and are far from functionally equivalent in wildlife habitat quality (Anderson and Ohmart 1984). Only abiotic factors were examined that might influence plant community characteristics. Ellis (1995) found that dense stands of SC along the middle Rio Grande, NM differed structurally from mature cottonwood forests. Also, associated species are often not similar between SC and C/W stands, especially in the later stages of SC takeover, when soil salinity is high, soil moisture is low, and species composition approaches 100% SC as along the Virgin River (Smith *et al.* 1998).

Stromberg's (1998) assertion that, relative to C/W, SC appeared to be enhancing biodiversity of understory herbaceous species, also is supported by her data (61 species present in the SC plots, and 36 in the C/W plots). However, percent cover of all herbaceous species was low. A total of 73 herbaceous species were found in all plots together but only 6 species with greater than 1% cover, the 2 most abundant with 6% and 11%; all 6 species with greater than 1% cover were in the SC plots. Herbaceous species richness only averaged 1.25 species/m^2 in the C/W and 1.5/m^2 in the SC plots. A total of 22 woody species also were recorded from the plots, including SC, cottonwoods and willows, 15 species in the C/W and 18 species in the SC plots. Only 5 species had more than 5 stems per 100m^2. This low species richness and low % cover would be expected in dense stands of either C/W or SC. However, stand density for both SC and C/W plots was quite variable, with standard deviations equaling the means in both the SC and C/W plots. Therefore, some plots must have had very few C/W or SC plants, and thus the opportunity for much greater herbaceous cover and number of species; why this was not reflected by greater species richness and percent cover is not clear.

On the other side of this controversy, Smith *et al.* (1998), Busch and Smith (1995) and Cleverly *et al.* (1997) reported data indicating major differences in functional equivalency between C/W and SC. Their studies measured true functional traits and found significant differences between SC and cottonwood/willow in leaf sodium content, water potential, osmotic potential, stomatal conductance (cottonwood only), leaf carbon isotope ratio (an indicator of the source of water used, i.e. surface or groundwater), photosynthetic rate (willow only), sap flow, and width of growth rings. The much higher sodium content in leaves of SC mean that it can operate at much lower osmotic potential and has the capability for reaching lower total plant water potentials. The lower carbon isotope ratios of SC leaf tissue suggest that it operates at significantly higher water use efficiency than does C/W.

Their studies of functional ecology along the lower Colorado River revealed that SC has greater stress tolerance (drought and salinity) than C/W and that SC is a facultative phreatophyte whereas cottonwoods and willows are obligate phreatophytes. Removal of SC from around willow trees improved water relations and growth of the willows, indicating potentially strong competitive effects between SC and willows (Busch and Smith 1995). SC also showed much more efficient recovery from fire than did cottonwoods and willows which contributes to an even greater dominance by SC in riparian communities following fire (Busch and Smith 1993, Busch and Smith 1995). The higher water use efficiency of SC is counter to the notion of SC as a "water spender"; in fact, leaf-level stomatal conductance and branch-level sap flow are comparable between SC and C/W on a leaf-area basis. However, whole plant sap flow and transpiration rates are higher in SC because it maintains a higher leaf area per unit of sapwood and per unit area of soil surface than does C/W. The higher water use efficiency in SC also suggests tighter stomatal control, thus limiting water loss during dry conditions and confirming the findings of J.E. Anderson (1982). These experiments explain how SC has only a moderate peak transpiration rate (compared with C/W) on a leaf area basis but a very high rate on a stand basis.

On a floodplain basis, then, SC would use more water than native vegetation because SC transpires at a very high rate per unit of soil surface and also because it usually occupies a larger area of soil surface across the bottomlands (because of its facultative phreatophytic character and its deep root system).

Smith *et al.* (1998) and Devitt *et al.* (1997) reported that *Tamarix* is able to recover quickly from either a removal of the water table or depletion of soil water from the upper profile for several weeks during hot summer months, confirming earlier studies by USDI-BOR (1973). During the first year of growth, SC allocates almost entirely to root growth, resulting in a plant only 0.1 m high but with a root system 2 m deep. This confers a great competitive advantage in an environment where spring floods are followed by a rapidly declining water table during the first year, thus allowing rapid above-ground growth prior to canopy closure in subsequent years (Smith *et al.* 1998).

The studies reported by Smith *et al.* (1998) along the Virgin River in southern NV (one of the most unregulated rivers in the southwest), explain how the major LACK of functional equivalency between C/W and SC results in the observed takeover by SC of mixed successional stands through time. Young stands (less than 10 years old) in their study areas contained a mixture of SC, arrowweed, coyote willow, and screwbean mesquite. As the stands aged, the native willow and screwbean decreased in relative dominance first, due to the habitat becoming increasingly desiccated and saline. The halophytic shrub arrowweed (also native), persisted as a co-dominant with SC the longest. After 50 to 60 years, the floodplain contained a 100% cover of SC.

The concept of functional equivalency *sensu stricto*, developed by Stromberg (1998) is shown to lack the robustness necessary to explain the observable dominance of SC in riparian systems much different from the middle San Pedro River. Even here, the data do not well support the contention that SC will not increase in the future and come to dominate that river system, though such is more likely on other river systems. The lower Virgin River, also unregulated, was taken over by near 100% SC stands during the past 50 to 60 years.

The concept of functional equivalency of SC and native plant communities *sensu stricto* has been extended in recent years by various workers to include ecological goods and services in support of animal communities, including the sw WIFL (Brown and Trosset 1989, Anderson 1998). This extension of the concept goes far beyond supporting data of Stromberg (1998), Ellis (1995) or any other data we could find. Stromberg (1998) did not address the maintenance of faunal diversity, a variable that should be considered in a comprehensive functional equivalency comparison. She attempted to extend the concept in this direction by citing Ellis (1995) who found that dense S/C stands provided for many (but not all) of the habitat requirements for migrating and breeding birds along the middle Rio Grande, NM.

The extension of the concept seems to have been promoted in spite of much evidence to the contrary: that bird species diversity and density is substantially lower in SC than in native plant communities, that sw WIFL reproductive success is lower in SC, and that SC does not provide the types of fruits or seeds required by frugivores or granivores, and provides a greatly reduced diversity of the insects required by insectivorous birds and other animals, that its foliage is less palatable, that it provides little habitat for cavity dwelling species, and the propensity for wildfires in SC not only destroys the native willow/cottonwood forests but burn substantial populations of nesting sw WIFL and probably of other birds. Also, good circumstantial evidence indicates that SC provides inadequate protection from lethal high summer temperatures in some areas (that may be responsible for the extirpation of the sw WIFL from much of its former breeding grounds on the lower

Colorado and lower Gila Rivers), that it probably contributes to drying out of surface water habitats required by the flycatcher, that it probably provides less protection from cowbird parasitism and possibly from predation of nests than do the native willow thickets, and that it probably exacerbates nearly every known or suspected mortality factor of the sw willow flycatcher. The concept does not consider the obvious correlation that the sw WIFL has declined over the past 50 years as SC has displaced or replaced its native breeding habitat. In fact, SC may be acting as a negative flycatcher sink, attracting birds to nest but not providing adequate food or other resources and protections (reviewed by DeLoach and Tracy 1997).

The concept that SC and C/W provide equivalent habitat for the sw WIFL also impedes the understanding of ecosystem degradation and the decline of many species, including the sw WIFL, and the open examination of other information and other concepts. It has led investigators to ignore or discount major factors influencing the sw WIFL. The concepts are so widely accepted within some groups that researchers are even led to draw the opposite conclusions from that shown by their own data. This erroneous information then leads flycatcher biologists to use nesting success as a major argument for the value of SC to the flycatcher. If not changed, this concept that SC is beneficial to the sw WIFL, and the construction of management plans around this concept, may lead to continued decline of the sw WIFL and other species.

Discussion

We have reviewed the published literature and agency reports, and we here present hypotheses that may help to explain the many synergistic ecological interactions between 1) SC and the physical environment and between SC and the native plant community that have led to the present degradation of these native riparian plant communities of the West, and 2) between SC and the various mortality factors that affect animal populations at various trophic levels that have led to the decline in populations of many species, including the sw WIFL.

Effects of SC on the plant community. One school of thought, that we call the “anthropogenic-abiotic paradigm”, holds that the invasion and continued dominance of SC was caused by prior anthropogenic and mostly abiotic modifications of riparian ecosystems such as the construction of large dams, channelization and diversion of streams, pumping of groundwater, and includes livestock overgrazing and phreatophyte control programs. These modifications have altered hydrologic regimes, interrupted the regenerative cycle of native plants, lowered water tables, allowed soil salinity and wildfire frequency to increase, and directly killed native plant communities. This paradigm teaches that SC only passively invaded after the native plant communities already had died or were weakened - it then simply “replaced” the native vegetation. SC is seen to be inherently “more aggressive” and “better adapted” to the present altered conditions than is the native vegetation and to have become an immutably fixed, dominant component of western riparian ecosystems. If SC is controlled, the native vegetation still cannot recover unless the anthropogenic-abiotic changes are reversed, which entail great economic and social costs. We agree that all the abiotic and anthropogenic factors are important, but that the paradigm is incomplete and does not correctly explain what has occurred with the SC invasion nor does it correctly project the effects of potential biological control of SC.

A second concept, developed by Stromberg (1998), states that SC can act as a functional analog of C/W in areas that have become too desiccated and/or too saline for C/W to grow, apparently referring to stand structure. This concept, *sensu stricto*, applies only to the plant community and its relation to the physical environment, and does not consider effects on animal communities. This concept seems to apply to the condition on the middle San Pedro River of southeastern Arizona where it was developed. This is a small, unregulated river, with natural hydrologic cycles and floods that leach out salts and limit wildfire frequency; the area is not dominated by SC, although SC has invaded. However, this concept is inadequate to explain the observed dramatic invasion of SC along many regulated and, especially, along unregulated streams. Experiments by Smith *et al.* (1998) and his students demonstrate that many functional responses of SC and C/W are not equivalent and can account for the frequently observed ability of SC to rapidly establish, to compete directly and strongly with C/W, and to interact with many abiotic factors through feed-forward mechanisms to increase its own competitive advantage, and over time to convert mixed native plant communities into stands of 100% SC (Busch and Smith (1993, 1995; Cleverly *et al.* 1997; Sala *et al.* 1996; Devit *et al.* 1997).

Both of these concepts either seriously underestimate the role of saltcedar in the degradation of riparian ecosystems and lead to a sense of hopelessness that SC's dominance can be reversed or to a sense that SC is not damaging to natural ecosystems. These concepts lead to very expensive programs to restore natural hydrologic cycles and geomorphologic conditions on one hand or to reliance on "passive recovery" without reducing the "aggressiveness" of SC. Both types of programs are of unproven efficacy in controlling SC, of unproven acceptance by the sw WIFL, and do nothing to control SC outside the small area where these treatments can be applied.

We propose a modification of this largely abiotic paradigm by introducing the concept of biotic factors, primarily 1) the potential for herbivorus insects of SC alone (now mostly lacking in North America) to significantly reduce the abundance of SC, 2) the ability of SC to compete directly with the native plant community, and 3) the ability of SC to interact with the abiotic environment and with the anthropogenic changes in a dynamic manner that increases its own competitive advantage. We have reviewed numerous examples where SC has invaded areas not affected by anthropogenic changes, and where the native vegetation returned naturally and rapidly without manual revegetation, demonstrating that in these areas SC has "displaced" the native plants through direct and indirect competition.

Under our modified paradigm, the so called "greater aggressiveness" and "better adaptation" of SC to the modified ecosystems is seen to consist in large degree to the lack of insect herbivores that damage the plant. Biological control has been successful against several other serious, invading exotic weeds that also appeared more aggressive and better adapted and dominated native plant communities. In fact, the introduction of only one or a few highly host specific natural enemies (usually insects or plant pathogens) from the homeland of the weeds rapidly and safely controlled these weeds in the invaded area, and reduced them to non-aggressive, non-damaging, members of the plant community. Such control has been obtained with at least 10 serious exotic, invasive weeds in North America, with many other weeds in other countries, and control of several more such weeds is in progress. We regard this as documented proof that biotic factors are important determinants of plant abundance. We suggest that conservation biologists and plant ecologists consider the effects of the numerous past successful projects on biological control of invasive, exotic weeds as a guide to construct paradigms that include biotic factors as major determinants of plant abundance and to understand that biological control can be used successfully to manage problems such as the SC invasion.

Effects of SC on declining animal populations, especially of the sw WIFL. The decline of the sw WIFL, as is the decline of many other birds, fishes and some mammals, reptiles, other animals and some plants, is correlated with the invasion of SC and also with the construction of large dams and other human modifications of riparian ecosystems, and with the invasion of native cowbirds into the southwest. All these factors have undoubtedly been of major importance, and all interact.

Our review indicates that SC has the ability to interact through its dominance of the native plant community to seriously degrade wildlife habitat quality. In the case of the sw WIFL, SC influences the bird's behavioral responses, and can interact with many of its mortality factors to exacerbate their negative effects. Although we reviewed these effects only for the sw WIFL, the same principles and many of the same factors probably also impact several other declining or T&E species in western riparian ecosystems infested with SC. When they encounter an invasive, exotic plant species, animals commonly remain associated with the native plants with which they evolved and on which they depend for food, a place to live, and for protection from climatic extremes and natural enemies. It would appear to be counterintuitive for an animal to forsake the native plants with which it evolved and to preferentially select an invasive, exotic plant so different as SC in which to live and breed. Yet, the superficial observations of the sw WIFL at some sites in Arizona indicate that it is preferentially selecting exotic saltcedar in lieu of its native willow breeding habitat. Our review examines this situation.

SC is an exotic invader that is drastically different from, and not closely related to, any native North American plants. The native animals did not evolve with it, and are not adapted to it. They cannot utilize its tiny fruits and seeds, can feed but little on its rather unpalatable foliage, and it does not provide cavities or nesting structure needed by many species. SC thickets have low horizontal and vertical structural diversity, low species diversity including diversity of the insects that many birds and other insectivores require for food, and do not provide sufficient protection from natural enemies, fires or climatic extremes. Although SC-invaded areas appear lush and green, they actually are ecological deserts. The more specialized animals, especially insects, birds, some reptiles, and many desert fish species are the most unable to utilize SC and are the most negatively affected by the changed environmental conditions that SC produces. Some native animal species, including the sw WIFL, obtain some benefit from SC but, overall, less than they would obtain from the native plant communities. However, the bottom line is clear: populations of the sw WIFL and several other T&E species have been declining for at least the past 50 years, as SC has increased and as native plant communities have decreased. We found several causes for the sw WIFL decline that are, or may be, related to SC, through an examination of the many reports of the bird's behavior, reproduction, and survival in response to SC *vs.* its response to the native plant community. We have presented hypotheses that explain how SC could negatively affect the sw WIFL at each stage of its breeding cycle. These factors alone could account for all of the observed population decline but other factors, such as unfavorable conditions of overwintering areas, may yet be discovered.

Our review indicates that SC negatively affects habitat quality and nest site suitability by reducing the horizontal and vertical structural and species diversity of the plant community, by reducing the abundance and quality of suitable native nest trees, and by reducing the presence of free water and the diversity and abundance of food insects present. We show how SC could interact to increase the negative effects of nearly all the known or proposed mortality factors of the sw WIFL. We show how SC can attract the sw WIFL to nest in it by certain superior characteristics but then fails to provide for all the bird's needs through its lack of certain critical resources. We suggest that this behavior is caused by a single "super stimulus", the superior branching structure of SC for nest placement. This stimulus is so powerful that the sw WIFL chooses to nest in SC in spite of the fact that other resources and protections are deficient in SC, resulting in lower reproductive success. This concept has not been considered heretofore as an explanation of sw WIFL behavior. The behavior, in effect, amounts to a "fatal attraction" of the sw WIFL for SC.

Functional equivalency. The concept of functional equivalency of SC and C/W, as originally developed, applied only to plant community relationships with the physical environment. However, it has been extended recently to include equivalency of SC and C/W in providing habitat and ecological goods and services to animal communities, including the sw WIFL. This extension is without experimental or observational support and is contrary to nearly all field observations. We suggest that SC and C/W are not equivalent habitat for animal populations, that SC is not beneficial to wildlife, and that in fact it is harmful to most species, including the sw WIFL.

The two concepts of the anthropogenic-abiotic paradigm and the functional equivalency of SC and C/W deny the obvious, that SC has invaded and dominates both regulated and unregulated streams, and that populations on many plant and animal species have declined precipitously as the dominance of SC has increased. SC is an extremely important part of the downward spiral of habitat quality on both regulated and unregulated streams. It is a major factor, perhaps the major factor, in the decline of many species of birds, mammals, reptiles, fish and plants, including many T&E species and the sw WIFL.

The continued acceptance of these inappropriate or incomplete concepts creates a sense of complacency regarding the SC invasion. This is likely to form the basis of management policies that will be ineffective in restoring native plant and animal populations and that may actually perpetuate their continuing decline, possibly even to extinction in some cases.

The information we have gathered, and the paradigm we present, indicates that an invasive exotic that comes to dominate an ecosystem and that brings about a substantial decrease or deterioration of the native plant community may provide some benefits to some species but overall will not be advantageous to the natural ecosystem and probably not to most of the native species in it. If allowed to persist or to further increase, some exotic weeds may well cause the extinction of native species that have been declining since the exotics began to dominate (Sawhill 1999). In Australia, over 50 plant species are considered endangered because introduced weeds out-compete them (Bell 1983, Leigh *et al.* 1983). In Germany, 89 of 589 rare plants are declining as a result of herbicide applications to control weeds (Sukopp and Trautmann 1981). Removal of large dams seems unlikely in the near future. However, modification of the channelized streams and/or the allowance of controlled flooding along riparian corridors would largely correct the adverse abiotic effects but methods must be developed that minimize negative economic and social consequences.

Ecological effects of controlling SC. Barrows (1998) proposed that two factors should be clear before land managers embark on an exotic species control program: 1) does the exotic negatively impact native species, and 2) is control possible and feasible?

We, along with Barrows answer emphatically yes to both questions, as regards saltcedar. We have cited many examples of the harm caused to native plant and animal species by the SC invasion and we believe that biological control clearly is capable of controlling SC. Controlling SC would produce great benefits and, as we have discussed, would produce positive interactions at various trophic levels throughout the ecosystem. Control of SC has been attempted on a large scale by broadcast herbicidal treatments, bulldozing or other mass mechanical methods, and by hand methods. Broadcast herbicidal and mechanical methods are broad spectrum controls and are very damaging to the native plant communities, whose protection was the object of control in the first place. Hand methods, (usually cutting and stump treatment with herbicides, or sometimes of pulling seedlings by hand) do not damage native plants but are highly labor intensive. All are very expensive and all require periodic retreatment to prevent or control reinfestations.

The principal concerns that until now have impeded the application of biological control of SC are that 1) some areas may have been so degraded by anthropogenic ecosystem changes (mainly high soil salinity and low watertables) that the native vegetation cannot recover after control, 2) that control will proceed so quickly that the native trees (willows and cottonwoods) will not be able to recover in time, leaving a period of a few years in which insufficient habitat is available to sustain sw WIFL breeding populations, and 3) a philosophical objection to introducing any foreign organisms whatsoever, including biological control agents, despite the fact that the riparian areas presently are severely degraded by non-native vegetation, including SC and that these exotic invaders continue to rapidly expand their area of infestation and their damage to native ecosystems.

The arguments presented here predict that most areas infested by SC are likely to revegetate naturally and rapidly after biological control, although some areas may be too altered for this to occur without human intervention. Field experience in manually clearing SC along numerous small streams and springs, and even on the most degraded area of all, the lower Colorado River floodplains, and the natural revegetation by willows and the continued persistence of this vegetation for many years after floods along major rivers, all demonstrate that natural revegetation is probable in many areas. Hand control mimics the effects of biological control and can predict its effects, at least in major part. All of the present nesting areas of the sw WIFL appear to be suitable for natural revegetation, as indicated by the presence of at least some willows now growing there. The only exception may be the Salt River inflow to Roosevelt Lake (which also may not be too saline); however, Roosevelt Lake already has been given up as sw WIFL breeding habitat in order to raise the level of the lake, which is the water reservoir for the city of Phoenix.

We do not doubt that some areas now may be too saline, or depth to watertable too great, to allow the natural return of C/W if SC is reduced in density and cover by biological control. However, the several statements in the literature implying that most SC infested areas along regulated streams are irrecoverable are undocumented and, we believe, of much less extent than implied. We also acknowledge that occasional controlled flooding, or of raising water tables along downcut streams by constructing frequent, low dams, or by other methods, would be beneficial to vegetation recovery in areas where natural revegetation under present conditions is unlikely. Much of the area unsuitable for C/W is suitable for other native plants such as honey, velvet and screwbean mesquites and quailbush, which are also of benefit to many wildlife species.

The speed of biological control and the rapidity of the recovery of trees suitable for sw WIFL nesting is not completely clear. The experimental releases now approved and underway are designed to measure these factors. Other similar leaf beetles used for biological control of weeds have dispersed slowly, unless through massive human redistribution. The large, woody nature of SC and its well known resiliency to damage indicates that attack by the biological control agents over a period of several years will be required to kill a medium-sized or large plant, although seedlings might be killed the first year. The effect would be a gradual thinning and reduction in canopy cover and size of plants which would allow for recovery of native plants concurrent with control of SC, and a repression of its further spread. This change is expected to occur over a period of several years at any one site, and with little or no overall decrease in vegetation or wildlife habitat. The limited and carefully monitored experimental releases of biocontrol insects are all at great distances from where the sw WIFL nests in SC. This will allow several years in which to initiate manual revegetation at sw WIFL breeding areas, if needed.

The observation that the sw WIFL is now using SC, together with incomplete scientific knowledge and theory to understand the causes or consequences of this, lead to a great reluctance by endangered species workers to take action against SC. Incredibly, some regulatory actions even approach calling for protection of SC as beneficial habitat for the sw WIFL and other T&E species. This attitude is fed by what we see as incorrect concepts derived from incomplete paradigms, discussed previously. These concepts seem to obscure the view that the SC invasion is the predominant biotic change apparent in western riparian ecosystems and therefore that it is a primary suspect in the decline of the sw WIFL, along with declining populations of many other animal species. This attitude impedes the open examination of the many methods in which SC may interact with abiotic and biotic factors to degrade the habitat of the sw WIFL and other declining species and through which it may interact with behavioral patterns or mortality factors to reduce sw WIFL reproduction and survival.

A well justified fear of invasive exotic organisms, but a tendency to place beneficial biocontrol agents in the same category, as well as a spate of recent sensationalist and biased articles in the popular and even the scientific press that are inaccurate and represent an unfounded anti-biological control point of view, all create a skepticism among environmental workers about using biological control, especially where endangered species are involved. The philosophical opposition to introducing foreign biological control agents is not scientifically justified. This type of opposition comes mostly from those unfamiliar with the process and unfamiliar with the great benefits obtained and the safety of biological control in its use against some 40 weed species in North America (Nechols *et al.* 1995, Rees *et al.* 1996), another 22 species in Hawaii (Funasaki *et al.* 1988), and many others in other countries (Julien and Griffiths 1999). The skepticism regarding biological control is caused by confusing the harmful cases of introduced organisms such as kudzu or the nutria (neither introduced by biological control workers) with the safe introduction of weed biological control agents, and by accepting incomplete hypotheses and paradigms for understanding the ecological relationships and projecting the effects of biological control. The long, successful and safe record of biological control of weeds should dispel most doubts in the process, especially in view of the careful testing, selection, use of only highly host specific control agents, and the many regulatory safeguards involved (Coulson 1992, DeLoach 1997, McFadyen 1998).

The concerns related to the present project are understandable: the sw WIFL is critically endangered, it now nests mostly in SC in several major breeding areas in Arizona (but entirely or mostly in native plants in neighboring states), and, if successful and if introduced directly into or near the sw WIFL breeding areas (such no doubt would require special approvals), biological control would eventually reduce the size and density of these SC nest trees. However, these concerns are dispelled by an examination of the conditions in the field and the ecological relationships involved. The analysis we present here attempts to explain the pervasive and insidious harm done by SC to the native plant community and to the sw WIFL and other declining or T&E species. A better understanding of these relationships leads to the conclusion that the sw WIFL is endangered in large measure because of the SC invasion. Its recovery will be assisted by the gradual, highly host specific effects of the control insects in reducing SC stands and with the concurrent increase in stands of willows, cottonwoods and other native plants.

Our best guide to evaluate the consequences of the proposed biological control program of SC is to observe the consequences of past programs that controlled other invasive, exotic weeds of natural areas, such as St. Johnswort, tansy ragwort, puncturevine, musk thistle, alligatorweed, waterhyacinth, waterlettuce, leafy spurge, and the new promising programs on purple loosestrife and melaleuca. Introduced foreign insects already are being used on many natural wildlife refuges and national parks to control several exotic invading weeds. Almost any action entails some small risks. However, in this case the risks of no action appear far greater, and indeed are what we have been observing in western riparian ecosystems for several years now - the destruction of these ecosystems by exotic, invading plants and the decline of many native species toward extirpation or extinction.

The observable invasion and dominance by SC in western riparian ecosystems, and the concurrent decline in many animal species, several to the point of becoming threatened or endangered, has produced a call from the public, by wildlife refuge and park managers, and by ecologists and environmentalists to control this weed. Many environmental organizations now have a strong interest in controlling SC in natural areas, including on national wildlife refuges. SC also produces substantial negative impacts on water supplies for municipalities and agriculture, and it reduces recreational values. Agricultural and municipal agencies represent a powerful force to proceed with SC control by whatever methods are effective, including broadcast herbicidal and/or mechanical controls. Such large scale programs are now underway along the Pecos River of TX and NM because of the delay in implementing biological control. However, these methods are broad spectrum, kill many or all plant species in addition to SC, and may be harmful to native ecosystems.

We believe that biological control offers a viable choice to conventional controls, that is effective, efficient, and within acceptable risk levels to wildlife and to the sw WIFL, and that it will allow recovery of the invaded ecosystems and of the individual threatened species within them without harming the native plant communities and dependent animal communities. However, full recovery still will require changes in the physical environment in some areas, such as allowing controlled flooding.

The application of biological control currently is being restrained until reasonable assurance can be given that it will not harm the natural ecosystem, especially the declining and T&E species, and most especially the sw WIFL that now utilizes SC extensively in Arizona. Successful management decisions to bring about the recovery of sw WIFL populations, various programs to control SC, and specifically, the biological control program, all depend on an understanding of the factors that affect sw WIFL populations.

We suggest here an alternate paradigm for understanding the determinants of SC abundance that more closely explains the observable ecosystem degradation. We offer several hypotheses which together constitute a new paradigm for understanding the causative role that SC may play, both directly and through interactions with abiotic factors, in the observed decline in many animal species, including T&E species. Our hypotheses are based on data or on observations reported by various workers and by logical considerations of possible causitive pathways. Our hypotheses and proposals are based on science, and all are falsifiable, which distinguishes science from dogma. Some may turn out to be incorrect, or to need modification, but all can be proved or disproved by future research. A thorough understanding of these concepts is important in making correct management decisions, including the decision to proceed with biological control or the decision to do nothing to control saltcedar. We believe a decision to use biological control will lead to ecosystem recovery and to recovery of many of the declining and T&E species, including the sw WIFL. We believe a decision to do nothing will result in the continuing deterioration of native riparian ecosystems that has been ongoing during the past several decades.

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