CONSERVATION AND ECOLOGY OF BREEDING LANDBIRDS IN A RIPARIAN RESTORATION CONTEXT

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By

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The undersigned, appointed by the Dean of the Graduate School, have examined the dissertation entitled:

CONSERVATION AND ECOLOGY OF BREEDING LANDBIRDS IN A
RIPARIAN RESTORATION CONTEXT

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A candidate for the degree of Doctor of Philosophy,

And hereby certify that in their opinion it is worthy of acceptance.

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Professor Frank R. Thompson, III

This dissertation is dedicated to my mentors, who have devoted their lives to bird

conservation and inspired many along the way:

Dr. John Faaborg, Geoffrey R Geupel, and Dr. Steven G. Herman,

to my friend, Jim DeStaebler, who shared with me several years

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ABSTRACT

While $14 to $15 billion have been invested in 37, 000+ river restoration projects across North America since 1990, only 10% are currently monitored for biological function, although habitat restoration is a stated goal of many such projects. My work seeks to examine factors that affect landbird demographics in the context of floodplain forest restoration on a large, regulated river in an agricultural valley. Using infrared, time-lapse video equipment, I identified nest predation by agriculture-associated predators as a primary source of nest mortality in the Sacramento River Valley, California. Then, using 10 years of empirical nest, vegetation, and hydrology data, combined with GIS land cover data, I compared multiple competing *a priori* hypotheses to explain nest predation on two open-cup nesting bird species, one resident (Spotted Towhee *[Pipilo maculatus]*) and one migrant (Black-headed Grosbeak [*Pheucticus melanocephalus]),* using an AIC model-selection approach. I then predicted nest survival rates under varying ecological conditions, based on the best-supported models. Nest mortality rates on restoration and mature remnant forest sites did not differ for either species examined, indicating that restoration sites are functioning at least as well as forest sites as breeding habitat, in terms of nest predation. Results for the Spotted Towhee, a resident open-cup nesting species, indicate that nest predation, in addition to nest parasitism, by the Brown-headed Cowbird (*Molothrus ater*) may be a critical limiting factor for this population. Results for the Black-headed Grosbeak indicate that flood timing influences nest predation, as nest predation rates are lower when the median flood date is closer to the onset of nesting. These results suggest that spring floods, historically driven by snow pack melt from the

mountain ranges of northern California, but now regulated by Shasta Dam, may play an important role in regulating small mammalian nest predator populations. Overall, this study suggests the importance of horticultural habitat restoration combined with naturalization of the river flow regime and reconnection of the river with the floodplain to the persistence and restoration of songbird populations in California's Central Valley.

CHAPTER 1

AN ECOSYSTEM PERSPECTIVE ON THE CONSERVATION AND RESTORATION OF CALIFORNIA'S CENTRAL VALLEY AVIFAUNA

Stacy L. Small

Importance of riparian habitat to birds. Western North America's riparian zones provide critical refuge for landbirds in all stages of their annual cycle (DeSante and George 1994). Over 50% of riparian species breed "primarily or exclusively" in deciduous riparian communities (Tewksbury et al. 2002), and many more use riparian zones for some part of the year.   In spring and summer, these areas provide abundant food resources and nesting cover for breeding birds and their young; in spring, fall, and winter they serve as critical migration stopover, dispersal, and wintering sites (Gaines 1977, Humple and Geupel 2002). The special value of riparian habitat may be attributed to several of its features -- the presence of water, the complex structure of its vegetation, and abundant food -- insects and berries, especially (Gaines 1977, Ohmart 1994).

Riparian habitat is scarce in the American West, constituting less than 1% of the total landscape; however, riparian forests support more species of breeding birds than any other terrestrial community in the West (Ohmart and Anderson 1986, Knopf et al. 1988), and many studies have shown that diversity and density of breeding birds is higher in riparian compared to upland zones (Tewksbury et al. 2002 and references therein). However, this is not to deny the importance of adjacent upland zones, as quality upland habitat provides important supplementary resources for

breeding and post-breeding adult riparian birds and juvenile birds produced in adjacent riparian zones (Szaro and Jakle 1985, White et al. 2005) and for birds on migration (Carlisle et al. 2004).

Riparian habitat on the Central Valley's large rivers. The Sacramento River, California's largest river, flows southward through the Central Valley, draining approximately 67, 728 km^2 of northern California; its drainage basin includes the southern Cascade Mountains (Shasta and Lassen Peaks), western slope of the northern Sierra Nevada, and the northern Coast Range. The San Joaquin River flows northward through the Central Valley and drains approximately 41, 129 km^2, including the western slope of the southern Sierra Nevada and the southern Coast Range; these two large, meandering single-channel rivers meet to form the Sacramento/San Joaquin Delta on San Francisco Bay (Mount 1995). Through massive human land conversion for agriculture, aided by major flood control and water regulation projects, riparian forests in the Central Valley have been reduced to relatively small patches embedded in matrix of agriculture and grasslands; an estimated 5% of riparian habitat remains (Katibah 1984), and surface water flows are drastically manipulated for agricultural and urban use (Mount 1995).

Before European colonization that stemmed from the gold rush of the 19th century, the floodplain forests of the large, meandering Sacramento and San Joaquin Rivers offered a vast and complex habitat mosaic of emergent wetland and riparian forests of various types and age classes in an otherwise arid and relatively inhospitable landscape (Katibah 1984). Central Valley riparian forest is a dynamic vegetation complex that is continually re-shaped by river processes (Mount 1995). River meander is a principal process that facilitates the regeneration of woody riparian vegetation (Johnson 1998), and in this broad, flat valley, river channels historically migrated widely across the floodplains in response to bank erosion and sediment deposition. Erosion of

outer channel banks on river bends created exposed "cut banks" and toppled riparian vegetation into the water; sediments that eroded from the banks were deposited downstream on point bars, where cottonwood and willow seedlings germinated to form strips of nascent forest. Where channel movement was recent, floodplains were dominated by Fremont cottonwoods (*Populus fremontii*) and willows (*Salix* spp.); it could take as little as 50 years to proceed from point bar seedlings to established forest on a mature floodplain (McGill 1979). Farther from the active channel, where the river had historically meandered, the forest was dominated by Valley oak (*Quercus lobata*) and Blue Elderberry (*Sambucus mexicanus*). Where the river channel had been cut off by avulsion, ox-bow lakes and ponds and dead-end sloughs supported permanent and seasonal wetland communities that were lined by swamps of Buttonbush (*Cephalanthus occidentalis*), willow, White alder (*Alnus rhombifolia*), and Oregon ash (*Fraxinus latifolia*) (Thompson 1961).

On point bars, plant community succession typically progressed from gravel bar through willow scrub, cottonwood-willow forest, mixed riparian forest, and Valley oak forest, increasing in elevation, dryness, and distance from channel as sediment accumulated and the active channel shifted away from the original point bar (McGill 1979). On old channels and oxbow lakes, vegetation typically progressed through wetland and swamp phases and either continually cycled through these stages or eventually developed into the forest types described above (Cepello 1991).

In a historically unprecedented flood control and land "reclamation" effort, large dams were constructed in the mid-20th century -- Friant Dam on the San Joaquin River in 1942 and Shasta Dam on the Sacramento in 1945 (Mount 1995); rapid land conversion to agriculture ensued

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below the dams, resulting in massive habitat loss from land clearing and vegetation death from water flow regulation (Askins 2000, Postel and Richter 2003). Current water management practices disrupt the process of ecological succession upon which riparian forests and their avifauna depend; large dams slow channel migration rate and hamper native vegetation recruitment (Friedman et al. 1998); banks stabilized with rip-rap interfere with bank erosion and sedimentation processes (Mount 1995); levees separate the main channel from the floodplain, disrupting the flood regime of wetlands, floodplain terraces and oxbow lakes (Ward and Stanford 1995, Kondolf 1998); sediment regulation by dams interferes with sediment transport and deposition (Kondolf 1998).

Of particular concern to the overall survival of riparian forests in the Central Valley is the massive disruption of habitat succession resulting from water flow regulation (Poff et al. 1997). The altered hydrograph that results from current water regulation practices interferes with native plant seedling recruitment and survival on point bars (Mahoney and Rood 1998). Plant species dispersal is adapted to the historic hydrograph; seed release is timed to coincide with optimal hydrologic conditions for root growth. Cottonwoods and willows release seeds during the spring receding limb of the hydrograph; seeds that lodge on exposed, damp point bars grow roots that follow the water table during its summer draw-down. Sycamores, alders and ash release seeds in the fall, prior to the average peak water flow. River flows that are kept artificially high during the summer for agricultural irrigation and abruptly cut in the fall may alternately drown or desiccate seedlings, or prevent proper root growth. Such alteration of flood regimes also has implications for regulation of terrestrial mammal and riparian bird populations (Chapter 4).

Status of Central Valley riparian avifauna. Approximately sixty-seven bird species are currently known to nest and raise young in Sacramento Valley's riparian forest (Gaines 1977), and 125 species have been documented using Sacramento and San Joaquin riparian zones on migration (Humple and Geupel 2002); many species over winter in these riparian areas (PRBO unpubl. data) , but much less is known about this period. Lowland riparian forest and its unique features are critical riparian bird habitat, but many species also inhabit the Valley Oak woodlands on the upper floodplain terraces year-round, including Acorn Woodpecker (*Melanerpes formicivorus*), Oak Titmouse (*Baeolophus ridgwayi*), White-breasted Nuthatch (*Sitta carolinensis*), California Towhee (*Pipilo crissalis*) (Zak 2002). Therefore, lower and upper floodplain habitats, including cottonwood-willow forest, emergent marsh, willow scrub, and Valley Oak woodlands are some of California's most critical bird habitat for conservation.

Belding (1890) and Grinnell and Miller (1944) offer early distributional records of birds in the Central Valley; re-visiting many of Grinnell's historic Sacramento Valley riparian study sites, Gaines (1977) documented high densities of breeding land birds in cottonwood-willow forest, but reported that twelve species had declined or disappeared from these sites in just a few decades. Four species -- Least Bell's Vireo (*Vireo bellii pusillus*), Willow Flycatcher (*Empidonax traillii*), Warbling Vireo (*Vireo gilvus*), and Bald Eagle (*Haliaeetus leucocephalus*) -- were no longer breeding in the Sacramento Valley. At the time of these surveys, no breeding pairs of the Least Bell's Vireo had been reported in twenty years. However, recent reports indicate that this species is recolonizing restoration sites in the heavily degraded San Joaquin Valley (Wood et al. *in prep*).

Habitat loss and degradation are the primary threats to western riparian avifauna (Ohmart 1994); DeSante and George (1994) cited destruction of riparian habitat as a primary cause of overall land bird declines in western North America in the past century, while noting concurrent increases in bird species associated with humans and agriculture, such as Brown-headed Cowbird and American Crow (*Corvus brachyrhynchos*).

While remnant riparian forest harbors some of the last breeding bird populations in the Central Valley (RHJV 2004), and three western subspecies breed only in the valleys of California -- Least Bell's Vireo, Red-shouldered Hawk [*Buteo lineatus elegans*], and Blue Grosbeak [*Guiraca caerula salicaria*]), many historic breeding populations are now regionally extirpated or severely depleted; several species have been recognized as threatened or endangered. The federally-endangered Least Bell's Vireo is now extirpated from the San Joaquin and Sacramento Rivers, as are breeding Willow Flycatchers. On the other hand, a major population of one California-endangered species, the Yellow-billed Cuckoo (*Coccyzus americanus*) still breeds on the Sacramento River, as do two California-threatened bird species, Bank Swallow (*Riparia riparia*) and Swainson's Hawk (*Buteo swainsoni*) (the latter also nests in the San Joaquin Valley).

As early as the late 1970's, Laymon (1981) noted very low numbers of nesting Yellow Warblers (*Dendroica petechia*) on the Sacramento River at Red Bluff. Surveys on four wildlife refuges -- Sacramento, Delevan, Colusa, and Sutter -- in the Sacramento Valley between 1986 and 1993 showed a declining trend for 17 species and confirmed the absence or very low numbers of several riparian species, including Least Bell's Vireo, Yellow Warbler, Song Sparrow (*Melospiza melodia*), and Warbling Vireo (Gilmer et al. 1998). In the Sacramento Valley, the Song Sparrow is now mostly restricted to the managed wetland areas connected with the Butte

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Sink region, while only a few scattered pairs of Yellow Warblers nest along the main stem in established riparian forest remnants (Small, pers. obs.). Most recently, the Lazuli Bunting (*Passerina amoena*), which nests in forest clearings and edges and experience high rates of nest parasitism and predation (Gardali et al. 1998), is exhibiting population declines along the Sacramento River (Gardali et al. 2006).

The species most affected by habitat loss and modification are mainly migratory riparian specialists that are either: a) small-bodied, or b) area-sensitive (i.e. require large territories for acquiring food to raise young); all of these, excluding Bank Swallow, are open-cup nesting species. Open-cup nesters are more vulnerable overall to nest predation and cowbird parasitism; small-bodied birds suffer greater hardship from parasitism, as they may raise fewer of their own young alongside cowbird nestlings (Faaborg 2002). The extant breeding species selected as study species for this project, Spotted Towhee and Black-headed Grosbeak, are larger than the typical cowbird host and can raise one or more of their own young alongside a cowbird nestling. Area-sensitive species such as the Yellow-billed Cuckoo require larger territories to gather food for their young and may not persist as self-sustaining populations where habitat has been dramatically reduced (Laymon and Halterman 1987).

This work seeks to investigate specific factors at multiple scales that influence reproduction of extant bird populations in a riparian restoration context and by doing so, give indications as to why some riparian bird species have already been extirpated from the region and what may be done to restore the Central Valley riparian bird community.

Threats to Central Valley riparian avifauna. The suite of threatened, endangered, and locally extirpated species represents a range of habitat requirements that covers all age classes of riparian habitat, including cut banks, wetlands, willow scrub, shrubby understory, mature and regenerating forests, and isolated senescent trees; declines of these species, regardless of their listing status, reflect major threats to overall riparian ecosystem function resulting from disrupted biotic and abiotic processes. The main potential stressors to Central Valley riparian avifauna are habitat loss from land clearing and disrupted habitat succession, conversion of the surrounding landscape to agriculture and the associated increase in nest predators and parasites, and alteration of river flows that deviate dramatically from historic hydrographs.

Habitat loss. Habitat loss has both direct and indirect effects on bird populations. Drastic habitat modification on the scale observed in the Central Valley directly eliminates unique features to which species have adapted. For example, the Bank Swallow relies upon cut banks on meandering rivers to excavate nest cavities that occur in dense colonies of 5-3,000 pairs (Garrison 2002). Least Bell's Vireos rely upon dense riparian under story (Kus 2002) and Willow Flycatchers rely upon willow thickets and other deciduous riparian trees and shrubs (Craig and Williams 1998), while Swainson's Hawks (*Buteo Swainsoni*) depend upon tall mature trees for nest sites (Woodbridge 1998). Song Sparrows, Common Yellowthroats (*Geothlypis trichas*), and Yellow-breasted Chats (*Icteria virens*) nest in dense, low vegetation characteristic of wetlands and streamside habitats (Guzy and Ritchison 1999, Eckerle and Thompson 2001, Arcese et al. 2002), while Yellow-billed Cuckoos use large patches of regenerating cottonwood-willow forest with moderate-sized trees in the Sacramento Valley (Laymon 1998). All of these features have been compromised in the Central Valley by dams, land conversion, water flow regulation, and bank stabilization projects.

The conversion of floodplain to agriculture may also create conditions favorable to nest predators, resulting in higher nest mortality through increased nest predation (Bayne 1997, Donovan et al. 1997, Rodewald and Yahner 2001, Burhans et al. 2002, Chalfoun et al. 2002). Using time-lapse infrared video, Small (2005) has shown that predation is the primary cause of nest mortality on a ground-nesting songbird species, the Spotted Towhee, along the Sacramento River, and that many nest predators along the Sacramento River are species associated with humans and agriculture, including raccoon, rodents, cowbirds, and jays (Chapter 2). At the local, nest-site scale, certain microhabitat features, such as nest cover and concealment from predators, may influence nest success to some extent (Budnik et al. 2002), but this has proven difficult to substantiate in other regions (Burhans and Thompson 1998).

Riparian areas surrounded by agriculture and grasslands are population centers for Brown-headed Cowbirds in California, where they typically lay their eggs in riparian birds' nests and forage in adjacent agricultural fields and grasslands. Such activity can substantially reduce productivity of the host birds by reducing clutch size and the number of host young that can be raised simultaneously to the cowbird young (Robinson et al. 1995).

Grazing in the riparian zone. No published figures are available on the full extent of spring/summer cattle grazing in Central Valley riparian zones, but grazing does occur during this critical growth period, when it has the most severe impact on riparian vegetation (Tewksbury et al. 2002, Small, pers. obs.). Spring and summer grazing in the riparian zone damages vegetation and causes bank erosion (Saab et al. 1995). In a study of western riparian systems, Tewksbury et al. (2002) showed that avian abundance and richness, especially deciduous forest specialists, were lower at grazed locations. Furthermore, Brown-headed Cowbird activity has been

associated with cattle feedlots in another western riparian system, the Bitterroot Valley in Montana (Tewksbury et al. 1998). In the San Pedro Riparian National Conservation Area in Arizona, elimination of grazing in the riparian zone facilitated vegetation re-growth, resulting in more rich and abundant bird life; of particular note were the re-establishment of under story nesters, such as Common Yellowthroat, Song Sparrow, and Yellow-breasted Chat (Kreuper 1993).

Invasive vegetation. Finally, in the Central Valley, invasive plant species compete widely for space and water with native riparian vegetation and present challenges for native understory restoration, in particular Giant Reed (*Arrundo donax*), *Tamarix* sp., Star Thistle (*Centaurea solstitialis*), Bermuda Grass (*Cynodon dactylon*), and Johnson Grass (*Sorghum halepense*), which may rapidly colonize a site as a monoculture and outcompete the native understory vegetation (Small pers. obs.).

Restoration potential of riparian avifauna. A long-term vision for restoring the Central Valley's riparian bird communities should encompass re-colonization by extirpated species as well as reversing the declines of once common riparian breeders, with the ultimate goal of establishing self-sustaining populations. Current restoration efforts are already benefiting the Central Valley's extant riparian bird populations. Diversity of riparian-associated land birds on restoration sites has increased with time since planting in the Sacramento Valley (Golet et al. 2003) and Small and Gardali (in prep.) have shown that Sacramento Valley supports a source population of Black-headed Grosbeaks, a migratory riparian-associated species that breeds in forest remnants and restoration sites. Many breeding birds have colonized Sacramento River riparian restoration sites within ten years of planting, including Common Yellowthroat, Lazuli Bunting, Spotted Towhee, Black-chinned Hummingbird, American Goldfinch, Yellow-billed

Cuckoo, Downy Woodpecker, and Oak Titmouse (PRBO unpubl. data), and many more species use these sites on migration (Humple and Geupel 2002). Several riparian species are showing positive abundance trends on Sacramento Valley restoration sites (Gardali et al. 2006).

The conservation potential of the following threatened or endangered species may depend upon large-scale habitat restoration and re-establishment of riparian ecosystem processes:

Least Bell's Vireo. The federally-endangered Least Bell's Vireo once bred throughout California's riparian systems; its dramatic population declines were driven primarily by habitat loss and nest parasitism by the Brown-headed Cowbird (Kus 1999). It had been extirpated from the Central Valley, which was once a large part of its historic range (Ballard et al. 2003a) until 2005, when a pair established a successful breeding territory on a 3-year-old restoration site in the San Joaquin Valley (Wood et al. 2005).

Its current distribution is still primarily restricted to counties in southern California, but it has been expanding northward into its historic range since federal listing in 1986 and subsequent restoration efforts (Kus 2002). Restoration potential for this species is high; adults colonized restoration sites that were adjacent to natural riparian forest and which offered the appropriate habitat structure -- dense shrubs at the 0-2 meter level for nesting and a dense, layered canopy for foraging (Kus 2001). Furthermore, Least Bell's Vireos nesting on restoration sites show reproductive success equivalent to that on natural riparian sites (Kus 2001). Cowbird control has given a short-term boost to productivity, but landscape level solutions that restore breeding habitat and reduce cowbird foraging habitat are recommended (Kus 1999).

Western Yellow-billed Cuckoo. The California-endangered Yellow-billed Cuckoo has declined tremendously as a result of floodplain clearing throughout the west and is still experiencing local declines in the Sacramento Valley, which hosts one of two persistent breeding populations in California (the other is on the South Fork Kern River). Less than 40 pairs were detected along the Sacramento River on surveys conducted in the mid-1980's (Laymon 1998). This species is associated with regenerating cottonwood-willow forest and breeds in large patches of this forest type. It typically nests in willows and forages in cottonwoods; nests are often concealed with vines or tall herbaceous vegetation. Its diet consists of large insects and tree frogs; during wet years with much flooding, it may partially rely on upper floodplain terraces for foraging, as larvae of its major prey items, katydids and sphinx moth, winter underground. The Yellow-billed Cuckoo should benefit from large-scale reforestation, restoration of habitat succession processes, and elimination of grazing in the riparian under story (Laymon and Halterman 1987). Restoration potential for this species is especially high; on the South Fork Kern River, breeding Yellow-billed Cuckoos have colonized 125 hectares of restored cottonwood-willow habitat (Laymon 1998). In the Sacramento Valley, single pairs of cuckoos have been observed nesting on habitat restoration sites after 8-10 growing seasons (Small pers. obs).

Bank Swallow. Roughly 100 breeding colonies of the California-threatened Bank Swallow (*Riparia riparia*) are distributed throughout northern and central California. This species relies upon vertical cut banks with friable soil to excavate nest burrows. The two major population centers for this species are the Sacramento and Feather Rivers and their tributaries; half of the state's population occurs on the Sacramento River. The primary threat to this species is bank stabilization with rip-rap that prohibits bank erosion, especially prevalent on the lower

Sacramento River (Garrison 1998). Establishment and preservation of meander belts that permit bank erosion processes would benefit this species.

Swainson's Hawk. The California-threatened Swainson's Hawk breeds in riparian areas in the Sacramento and northern San Joaquin Valleys. While not a riparian-obligate bird, this species nests in tall riparian trees in this region and forages in the surrounding landscape, over grasslands, fallow fields, and row crops. The Central Valley represents one of two major California population centers for the Swainson's Hawk, the Great Basin being the other. Pesticide-induced mortality on the migration and wintering grounds has been high for this species, but it is also threatened by loss of quality nesting and foraging habitat in California (Woodbridge 1998).

Willow Flycatcher. The federally-endangered Southwestern Willow Flycatcher (*Empidonax traillii extimus*) is likely the subspecies that once occurred in the Central Valley. This species uses dense streamside vegetation for nesting, including willow thickets and many other riparian shrub and tree species. Habitat loss, grazing disturbance, and cowbird parasitism have driven the declines of this riparian obligate species (Craig and Williams 1998).

Conservation principles for restoring Central Valley riparian habitat. In response to bird population declines, I offer the following conservation principles for restoring Central Valley riparian habitat and bird communities:

1) Take a multi-species approach to conservation planning. As described above, many declining or extirpated species rely on some unique feature of riparian habitat, and many have suffered

from the direct and indirect effects of habitat loss and landscape modification. When juxtaposed, the diverse habitat requirements of these individual species compose a picture of a healthy river system with its abiotic and biotic processes intact. Therefore, a single-species conservation approach that focuses on preserving one feature of the system, like exposed bank, or canopy cover, or tall mature trees, will inevitably fail to address the overall function of the system. On the other hand, restoration approaches that seek to simultaneously restore processes such as meander, point bar and cut bank formation, water table drawdown, floodplain reconnection, and native plant recruitment and survival, will likely benefit multiple species by maintaining the full complement of seral vegetation. In such a modified system as California's Central Valley, this cannot happen without major planning and human and mechanical intervention (Alpert et al. 1999), but the concept of restoring processes, both abiotic and biotic, is certainly necessary and should be identified as a core objective of regional conservation programs (Askins 2000). The Riparian Habitat Joint Venture of California Partners In Flight have produced a multi-species riparian bird conservation plan that highlights the needs of officially "listed" and common riparian birds in California; this plan may serve as a model of multi-species conservation planning (RHJV 2004).

2) Apply a process-based approach to restoration. A process-based, ecosystem management approach that addresses the needs of an array of riparian-associated species will best restore function to the ecosystem (Kondolf 1998, Askins 2000), with the benefit of preserving locally and regionally declining bird species. We must apply long-term and broad-scale vision to restoration and think in terms of restoring habitat function that will produce a range of riparian habitat types, from emergent wetlands to young cottonwood-willow forests, willow scrub, and upper terrace communities like Valley Oak Woodland and Oak Savannah; this requires a

combination of mechanical and process-based techniques (Griggs 1993, Hunter et al. 1999). The following broad goals focus on restoring ecosystem function while benefiting the maximum number of species. Ultimately, they would facilitate riparian plant community succession by sustaining all seral stages of riparian forest (Griggs 1993): 1. Restore stream flow patterns to those compatible with recruitment and survival of cottonwoods and willows (Mahoney and Rood 1998) and regulation of small mammal populations (Chapter 4), 2. Preserve and/or restore river meander and resultant geomorphological features (Buer et al. 1989, Johnson 1992), 3. Reconnect the main river channel with the floodplain (Ward and Stanford 1995), 4. Restore floodplain topography (Askins 2000), 5. Increase overall deciduous forest cover (semi-open tall canopy with shrub patches; DeSante and George 1994, Tewksbury et al. 2002), 6. Promote native under story growth for shrub nesting species (Kus 1998), 7. Preserve and restore habitat at all floodplain elevations, from point bars to drier upper terraces (Laymon 1998), 8. Concentrate reforestation projects adjacent to "natural" habitat (Laymon 1998, Kus 2002), 9. Eliminate grazing in riparian zones during growing season (Saab et al. 1995).

3) Integrate long-term ecological research, monitoring, and management. The same long-term vision applied to restoration efforts must apply to research and monitoring of restoration projects. Bernhardt et al. (2005) reported that few (≤10%) of 37, 000+ river and stream restoration projects are monitored for biological function, even though habitat improvement is a commonly stated objective of such projects. To measure restoration success requires long-term, large-scale demographic monitoring of productivity and survival of target populations, as well as research designed to test the effects of mechanical restoration, flood regime, and landscape context on avian demography (DeSante and George 1994, Smallwood 2001, Donovan et al. 2002).

Restoration, monitoring, and research should be coordinated within an adaptive management framework in which results are applied to management and further tested using population data.

We should consistently support population monitoring programs that evaluate source-sink dynamics and relate them to habitat composition and configuration; this requires long-term data sets on annual productivity, survival, and dispersal (Donovan et al. 2002). We should also maintain baseline surveys to measure population trends as restoration progresses (Gardali et al. 2006).

Summary. Many riparian bird species that are common elsewhere are declining, threatened, or extirpated from California's largest rivers. The greatest threats to riparian avifauna are loss and degradation of habitat from agricultural conversion and disrupted hydrologic regime, which has potentially contributed to increased nest predation and parasitism, as the following chapters will explore. However, the conservation potential of California's Central Valley riparian avifauna is high. Its rehabilitation will require restoration of river processes that facilitate habitat succession and regulate predator populations, supplemented by mechanical restoration techniques. These processes include river meander, natural flow regime, and connection of the main river channel with the floodplains. Increasing overall forest cover and restoring the biotic features characteristic of the Central Valley's historic riparian forests should also benefit a wide array of species. Conservation goals should encompass the re-establishment of a full complement of riparian bird species, with an emphasis on locally extirpated and declining species. Success can ultimately be measured by the presence of self-sustaining populations of these birds, which will require both long-term demographic monitoring and replicated experiments testing the effectiveness of restoration techniques.

CHAPTER 2

MORTALITY FACTORS AND PREDATORS OF SPOTTED TOWHEE NESTS IN THE SACRAMENTO VALLEY, CALIFORNIA

Stacy L. Small

ABSTRACT

Nest predation was the main nest mortality factor for Spotted Towhees (*Pipilo maculatus*) along the Sacramento River, California, during 1993 -2003, followed by cowbird parasitism. From 2001 to 2003, I monitored 161 Spotted Towhee nests and filmed 24 nests using miniature infrared video cameras to identify predators. Daily survival rate was 0.928 for this period. I detected no difference in nest survival between the incubation and nestling stages. Nests with cameras had marginally higher survival rates than those without. I filmed nine nest predation events in 2002 and 2003. Eight of these were upon nestlings, while one was upon eggs. Predators were birds, mammals, and a snake, including Red-shouldered Hawk (*Buteo lineatus*), Brown-headed Cowbird (*Molothrus ater*), Western Scrub-Jay (*Aphelocoma californica*), raccoon (*Procyon lotor*), black or Norway rat (*Rattus* sp.), two unidentified rodents, and a racer (*Coluber constrictor*). Many of these predators are associated with agriculture and/or human habitation. I documented two multi-predator events. In both instances, a diurnal partial predation by a bird was completed by a nocturnal rodent predator. Two predation events occurred at the very end of the nestling period. I advise investigators engaged in nest success studies to consider the possibility of partial predation that may reduce a female's overall reproductive output and note that a nest should only be considered successful when direct evidence of fledglings is observed

near the nest. I recommend more detailed studies of nest predator composition and the

compound effects of Brown-headed Cowbird nest parasitism and "infanticide."

INTRODUCTION

Predation is a primary cause of nest failure for many open-cup nesting birds (Ricklefs 1969,

Martin 1992). Nest predators may include birds, mammals, snakes, and ants (Thompson et al.

1999, Morrison and Bolger 2002a, Renfrew and Ribic 2003, Stake and Cimprich 2003, Peterson

et al. 2004), and most documented nest predators are food generalists that prey upon nests

opportunistically. Dominant nest predators may differ among habitats (Thompson and Burhans

2003), and the role of these predators may vary with time or ecological conditions at multiple

spatial scales (Donovan et al. 1997, Lahti 2001, Chalfoun et al. 2002). Understanding the

mechanisms that limit avian reproductive success requires identification of the specific nest

predators that cause nest mortality. Nest survival models tested in the absence of such

knowledge may lack important ecological information about the specific factors contributing to

nest mortality. Even if only a small sample of actual predators can be positively identified, this

information may go a long way toward developing appropriate nest survival models (Thompson

and Burhans 2003).

Identification of nest predators is challenging and, until recently, has been based on indirect or

anecdotal evidence. Direct human observations of nest predation events may be made, but only

rarely. Other studies have used indirect methods to examine nest mortality; such methods

include documenting nest condition following depredation (Best 1978), recording dental or bill

marks of predators using plasticene eggs placed in artificial nests (Major 1991), surveying

potential predator populations and correlating results with nest success (Patten and Bolger 2003),

and doing predator removal experiments (Schmidt et al. 2001).

Indirect methods of predator identification, however, may be unreliable. Inter- and intraspecific

variation in predator behavior at the nest means that identification based on condition of the

depredated nest may be misleading (Lariviere 1999, Pietz and Granfors 2000, Liebezeit and

George 2003, Thompson and Burhans 2003). Surveys of potential predator populations may not

reveal which species actually act as the dominant nest predators in an area (Peterson et al. 2004),

and nest predator experiments that rely upon artificial nests may attract different predators than

do real nests (Thompson and Burhans 2004). Overall, photo identification of nest predators is

more reliable than indirect methods, because predator identity and timing of predation is more

certain (Cutler and Swann 1999).

My objectives were to calculate nest survival rates, to determine the primary nest mortality

factors for an open-cup nesting passerine in the Sacramento Valley, and to identify nest predators

on ground and shrub nests. I used time-lapse, infrared micro-video cameras to document predator

identities and timing of predation events.

METHODS

Nest survival. Nest survival data were obtained by locating and monitoring nests following the

methods of Martin and Geupel (1993). My field assistants and I used parental behavior cues,

systematic searches, and adult flushes to locate nests. We minimized disturbance to the nest site

during nest checks by taking multiple paths to the nest and checking nests from a distance,

whenever possible, and avoiding nest checks when corvids were present. Nests were located

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during the 1993-2003 breeding seasons on five remnant riparian forest and five restoration sites on the Sacramento River National Wildlife Refuge in Butte, Colusa, Glenn, and Tehama Counties, California (near 39° 40' N, 121° 57' W). These sites are primarily mixed riparian forest habitat surrounded by agriculture (orchards, row crops, and rice fields). Nest searching began in late April, early in the Spotted Towhee breeding season, and lasted until breeding activity declined in late July. Nests were located on the ground and in shrubs, trees, tall forbs, and river and forest debris; nest height ($N = 280$) ranged from 0 to 500 cm (35.06 ± 3.1 [mean ± 1SE]). We determined nest fate by checking nest contents every 1 - 4 d (rarely more than 4). I categorized a nest as "successful" if it fledged at least one towhee young, based upon direct observations of fledglings or parental care activities close to the nest.

I calculated daily nest survival probabilities and 95% confidence intervals, following (Mayfield 1975) and (Johnson 1979). Duration of the nesting cycle was based upon my data: 2 d laying, 11 d incubation, and 9 d nestling. I computed daily nest mortality by dividing the total number of nests that failed by the total number of exposure days, defined as days during which nests were observed active. I used the Last Active-B criteria for exposure-period termination (Manolis et al. 2000); for nests with uncertain outcomes, I defined termination as the last date the nest was observed active. For nests with known fates, I defined termination as the midpoint between the last day the nest was observed active and the first day it was observed inactive (rounded to 0.5 day). Before calculating nest survival for the period 2001-2003 (the years I monitored nest predators), I checked for confidence interval overlap to examine whether nest survival differed among years.

Nest mortality factors. To compare the relative impact of different nest mortality factors for Spotted Towhees on the Sacramento River in 1993-2003, I calculated separate daily nest mortality rates and 95% confidence intervals for each of five primary nest mortality factors that I identified during this time period: predation, Brown-headed Cowbird (*Molothrus ater*) parasitism, human activity, abandonment for unknown reasons, and flooding. I categorized nests as "failed due to predation" if all viable host contents disappeared from the nest before host eggs hatched or before host young were developed enough to fledge, or if the female deserted the nest after some (but not all) contents were observed missing. I categorized nests as "failed due to cowbird parasitism" if: 1) the host parent deserted a nest following cowbird parasitism, 2) only cowbird eggs hatched, or 3) the nest fledged only cowbird young. I categorized nests that were deserted with only host contents as "abandoned," nests that failed as a result of nest cameras or other human disturbance as "failed due to human activities," and nests that were submerged in spring floods as "failed due to flooding." I pooled data across years in this summary analysis because I am not doing a hypothesis test, but simply a descriptive comparison of confidence intervals; limited annual sample sizes for the different mortality factors preclude statistical testing for a year effect in this case.

Video cameras. To document nest predation events in 2001-2003, I used four infrared, time-lapse video systems; two were assigned to riparian forest nest plots and two to restoration plots. One system was manufactured by Sandpiper Technologies, California, and three were manufactured by Fuhrman Diversified, Texas. The Sandpiper micro-camera dimensions were 4.763 x 4.763 x 7.620-cm, and the Fuhrman micro-camera dimensions were 3.175 x 3.175 x 6.033-cm; all camera units were outfitted with infrared diodes at the factory. Cameras were attached to jointed mounting arms connected to a 1.905-cm diameter aluminum pole that was

sunk into the ground; the pole was wrapped with dark brown or camouflage duct tape, available at hunting supply stores. The camera unit was adjusted to film nest contents from a distance of approximately 0.5-m. Cameras were attached by cable to a 24-hour time lapse video camera recorder (VCR) in a waterproof case that filmed at a speed of 4 frames per second. The VCR was placed 25-50 m from the nest to reduce human visits to the nest site, except for occasional camera adjustments.

Videotapes were changed daily, and deep-cycle marine batteries that powered the system were changed every other day. Whenever possible, nest contents were checked remotely, using a handheld video monitor that plugged into the VCR. Nests were videotaped around-the-clock until they either fledged or failed. The camera system was then moved to another active nest site on the same plot, preferably the one that was earliest in the nest cycle.

To minimize disturbance to the nest site and ensure against abandonment by the parent birds, in 2003 I implemented techniques described by Stake and Cimprich (2003), including a 2-3 d acclimation period to allow the parent birds to get used to the camera on territory, without placing it right at the nest. During this period, the camera was moved closer to the nest by 1-2 m per day. On the day that videotaping began, the camera was set at approximately 0.5 m from the nest; nests were viewed remotely through a hand-held video monitor and moved back if the female had not returned to the nest within 30 min. Videotaping was started during the incubation stage when possible ($N = 17$), although in some cases it was started during the nestling stage ($N = 7$). Cameras were never placed at nests during nest building or egg laying, in order to avoid disturbance during this sensitive period of nest site establishment.

RESULTS

Nest survival. From 2001 to 2003, my field assistants and I located and monitored 161 Spotted Towhee nests along the Sacramento River; 24 of these nests were filmed with video cameras. Cameras were deployed near 6 additional nests that were not filmed. Daily nest survival rate was 0.928 ([95% CI: 0.912 to 0.943], $N = 1076.5$ days, 138 nests) for this period.

Daily nest survival did not differ among the three years, 2001 (0.940 [95% CI: 0.917 to 0.963], $N = 415$ days, 48 nests), 2002 (0.927 [95% CI: 0.898 to 0.956], $N = 314$ days, 41 nests), and 2003 (0.941 [95% CI: 0.915 to 0.966], $N = 336$ days, 39 nests); confidence intervals overlapped among all three years.

Nest survival did not differ between the incubation stage (0.924 [95% CI: 0.903 to 0.945], $N = 618$ days, 103 nests) and the nestling stage (0.932 [95% CI: 0.909 to 0.955], $N = 458$ days, 86 nests). Nest survival where cameras were deployed (0.950 [95% CI: 0.925 to 0.974], $N = 317$ days, 29 nests) was marginally higher than where no cameras were deployed (0.918 [95% CI: 0.899 to 0.938], $N = 759.5$ days, 109 nests), with slight confidence interval overlap. Six nests were deserted in response to cameras; most incidents occurred early in the breeding season. Preventative measures implemented in 2003 eliminated the desertion problem.

Nest mortality factors. Between 1993 and 2003, 265 Spotted Towhee nests were monitored along the Sacramento River, including the 161 nests discussed above. Sixty-three percent of the nests were located using parental behavior cues, 29% were found by flushing, 5% were found through systematic searches of likely nest sites, and 4% were found by luck. One hundred fifty-five nests failed; 131 of those were depredated, 16 failed due to Brown-headed Cowbird

parasitism, 6 failed due to human activity (nest cameras), 2 were abandoned for unknown reasons, and one failed as a result of flooding. The cowbird parasitism rate was 38%; 60% of parasitized nests contained more than one cowbird egg. Mean number of cowbird eggs in parasitized nests was 1.96 ± 0.09 (range 1 to 4, $N = 101$ parasitized nests).

The daily nest predation rate (0.068 [95% CI: 0.056 to 0.080], $N = 1933.5$ days, 222 nests; Figure 1) was 4.5 times higher than cowbird-related nest mortality rates (0.015 [95% CI: 0.007 to 0.023], $N = 1081.5$ days, 107 nests), with non-overlapping confidence intervals. The cowbird-related nest mortality rate was similar to the nest mortality rate from human activity (.006 [95% CI: .002 to .010], $N = 1017$ days, 97 nests) and was higher than the nest mortality rates from abandonment (.002 [95% CI: .000 to .004], $N = 983$ days, 93 nests) and flooding (.001 [95% CI: -.001 to .003], $N = 975.5$ days, 92 nests).

Nest predators. I obtained 4,155 h of video footage of 24 active Spotted Towhee nests over three years. Nine predation events were videotaped; four in 2002 and five in 2003 (Table 1). Eight of these predations were upon nestlings, rather than eggs. Predators were birds, mammals, and a snake. Bird predators were Red-shouldered Hawk (*Buteo lineatus*), Brown-headed Cowbird, and Western Scrub-Jay (*Aphelocoma californica*). Mammal predators were raccoon (*Procyon lotor*), black or Norway rat (*Rattus* sp.), plus two unidentified rodents. The one snake predation event involved a racer (*Coluber constrictor*). Both the snake and the rat depredated nests within 24 h of the predicted fledge date. Infrared images of nest predation events are depicted in Figure 2.

I documented two cases of multi-predator events. In both cases, a nocturnal rodent predation event followed a diurnal predation by a bird at the same nest. In the first case, a hawk depredated two towhee young during the day, and an unidentified rodent depredated the remaining cowbird nestling that night. In the second case, a female cowbird pecked and tossed a towhee nestling from an unparasitized nest, and another unidentified rodent visited and consumed the remaining two towhee young five days later, at night. The other five depredations involved single predators.

DISCUSSION

Nest survival of the Spotted Towhee in the Sacramento Valley during 2001-2003 was similar to that at another northern California riparian site, Clear Creek (Shasta County; 40°30' N, 122° W) in 1999-2003 (0.922 [95% CI: .859 to .949], N = 370 days, 44 nests; PRBO Conservation Science unpubl. data). I identified nest predation as the primary nest mortality factor for this species on my study sites, followed by cowbird parasitism. While cowbird parasitism remains a secondary mortality factor, as many parasitized nests still fledge at least one host young, it should be noted that the parasitism rate for this species on my study sites (38%) far exceeded those of early reports (Baumann 1959, Davis 1960, Friedmann 1963), and that a majority of parasitism cases (60%) are multiple parasitism events, which could result in lower annual fecundity without changing nest survival results. Also, I now have video documentation of an adult cowbird removing a Spotted Towhee nestling from a nest, which further confounds the effects of nest parasites and predators on productivity.

I filmed a diverse array of nest predators that included birds, mammals, and a snake. No one predator appeared to be dominant, although three rodent predation events were documented, two

of which followed partial nest predations by birds. Both nocturnal and diurnal predators visited nests, suggesting that predators use a variety of cues to find nests. These may include parental and nestling behavior cues during the day and olfactory or visual cues during the day or night. Time of day differed among nest predator taxa; mammals depredated nests at night, birds and one snake depredated nests during the day. Other studies report both nocturnal (most mammalian nest predators and some snakes) and diurnal (birds and many snakes) predators (e.g., Renfrew and Ribic 2003, Stake and Cimprich 2003, Peterson et al. 2004).

I documented several avian predators, including Red-shouldered Hawk, Western Scrub-Jay, and Brown-headed Cowbird. Other investigators have filmed hawks depredating passerine nests, including Broad-winged Hawk (*Buteo platypterus*; (Picman and Schriml 1994, Thompson et al. 1999), Northern Harrier (*Circus cyaneus*; Pietz and Granfors 2000) and accipiters (McCallum and Hannon 2001). In addition to filming a Brown-headed Cowbird removing a towhee nestling from an unparasitized nest, I also found dead, pecked nestlings in or scattered around several other towhee nests. As these nests were not filmed, they were categorized as depredated by unknown predators; however, the pattern appears to fit that of the cowbird-induced "infanticide" (Elliott 1999) I documented on video. Granfors et al. (2001) videotaped 132 nests and documented 7 instances of Brown-headed Cowbirds destroying eggs or nestlings; some of these attacks were made upon unparasitized nests. Other investigators have documented female Brown-headed Cowbirds removing nestlings from passerine nests (Tate 1967, Stake and Cimprich 2003); hypotheses put forth for this behavior include forced re-nesting in order to increase parasitism opportunities for the cowbird (Arcese et al. 1996, Elliott 1999) or food competition with neighboring host nests (Granfors et al. 2001).

I documented only one snake predation event, in which a racer made three trips to the nest, removing one nestling each trip, despite attacks by the parent birds. While Patten and Bolger (2003) found that snake abundance predicts nest failure of ground-nesting Spotted Towhees in Southern California coastal scrub, and Morrison and Bolger (2002) filmed a high proportion (90%) of snake predations upon ground nests of Rufous-crowned Sparrows (*Aimophila ruficeps*), snakes did not appear to be dominant nest predators in this riparian system.

In two cases, multiple predators visited and depredated the same nest. In both, a diurnal partial predation by a bird was completed by a nocturnal rodent predator. Stake and Cimprich (2003) report a similar incident in which partial predation by a cowbird was followed by snake predation at the same nest, and Thompson and Burhans (2004) also report multi-predator events. Other recent nest camera studies report partial predation events as well (Liebezeit and George 2003, Renfrew and Ribic 2003).

I found that placing cameras at or near nests did not increase nest predation rates; in fact, nest survival was marginally higher where cameras were deployed. Other investigators have tested for a "camera effect" and found no (Thompson et al. 1999, Renfrew and Ribic 2003, Stake and Cimprich 2003, Thompson and Burhans 2003, Peterson et al. 2004) or minimal effect (Renfrew and Ribic 2003). If measures described by Stake and Cimprich (2003) to prevent nest desertion are followed, this method proves to be an effective, low-impact method for monitoring nest predation of Spotted Towhees and other open-cup nesting passerines.

Understanding nest predator-prey relationships requires knowing the ecology of the primary nest predator species (Lariviere 1999). Both behavior and habitat use of specific nest predators

should be considered when developing and testing hypotheses about nest mortality. Most of the nest predators I videotaped along the Sacramento River are highly associated with agriculture and/or human habitation, specifically Western Scrub-jay (Curry et al. 2002), Brown-headed Cowbird (Elliott 1999, Tewksbury et al. 1999), raccoon (Heske et al. 1999), and *Rattus* spp. (Long 2003).

Nest predation by *Rattus* species may be of particular concern in the Sacramento Valley. Small mammal surveys, in conjunction with continued nest predator monitoring, would help to determine the relative abundance of exotic rodents and their impact on breeding songbirds, and to determine whether population control of exotic rodent species is warranted.

Investigators should consider predation very late in the nest cycle to be a possibility when determining the outcome of nests that closely approached fledging. A nest should only be considered successful where fledglings or parental care activities are directly observed near the nest after the presumed fledge date; otherwise, nest outcome should be declared "uncertain." Also, the possibility of partial nest predation, which may reduce the overall reproductive output of female birds, should be considered in future studies of nest success.

More detailed studies of nest predator composition, using video at real, active nests, could potentially reveal patterns of nest predation between sites and habitats. Furthermore, the compound effects of cowbird "infanticide" and parasitism should be more thoroughly investigated. Although labor-intensive, nest monitoring programs that combine both human observations and video camera surveillance yield the highest quality data on avian reproductive

success and will alert managers to the specific mechanisms contributing to nest mortality that may influence avian population trends.

CHAPTER 3

SPOTTED TOWHEE (*Pipilo maculatus*) POPULATION DYNAMICS IN A RIPARIAN RESTORATION CONTEXT

Stacy L. Small, Frank R. Thompson, III, Geoffrey R. Geupel, and John Faaborg

ABSTRACT

Nest predation was the primary cause of nest mortality for Spotted Towhees along the Sacramento River, California, during 1993 -2003, followed by cowbird parasitism. Most nest predators documented during this period, including the Brown-headed Cowbird, rodents, and raccoon, were associated with agriculture and human habitation. We investigated factors at multiple scales that potentially influence nest predation risk in the region, within the context of large-scale riparian habitat restoration. We used the logistic-exposure method and AIC model selection procedure to compare predator search, predator abundance, restoration, and seasonal effects hypotheses. Our models contained covariates that represented nest activity, nest site, restoration, landscape composition (per cent agriculture within 50 and 500 meter radii around nest), flood and seasonal effects, as well as a random effect of plot and year. Our best supported models contained the covariates "cowbird young" and "date." Model-based estimates of nest survival for nests with cowbird young compared to nests without cowbird young showed that nests with cowbird young had a much higher survival rate (0.732, 95 % CI: 0.475, 1.116) than those without (0.040, 95% CI: 0.005, 0.279). Model-based estimates of nest survival throughout the breeding season indicate a within-season decline in nest survival. Nest survival increased only marginally with nest concealment, but its post-hoc inclusion improved the top models. These models were proposed under the "nest activity" hypothesis, but because of the unexpected

positive effect of "cowbird young", this hypothesis was not supported. Of the covariates in the top model, "cowbird young" had the strongest effect, with an odds ratio of 11.01 (95% CI: 3.16, 38.41). All supported models contained the variable "cowbird young," which was the only covariate with a large effect size. In contrast to our prediction, nest survival increased with cowbird young in the nest, implicating cowbirds in nest predation activities. To assess the population status of this species, we calculated lambda, the finite rate of population increase, using a model that incorporated model-based nest success estimates for parasitized (.052) and unparasitized (.758) nests, double brooding, the observed cowbird parasitism rate for this species (38%), number of young fledged from successful parasitized (.372) and unparasitized (1.3) nests, apparent adult survival (.245) and a range of potential juvenile survival values (0.000 – 0.664) estimated as percentages (0-100%) of adult survival. Resulting lambda values (.245-.329) did not approach the replacement level of 1, indicating that this population is not self-sustaining. We recommend large-scale riparian habitat restoration in the surrounding floodplain landscape to reduce nest predation and parasitism pressures.

INTRODUCTION

Conservation of riparian bird populations inhabiting North America's large river floodplains may depend upon major habitat restoration efforts conducted at the landscape scale (Askins 2000). Birds can serve as excellent bio-indicators of riparian area function (Rich 2002), but to evaluate restoration success in terms of habitat quality requires demographic studies at the appropriate scale for species that depend upon this habitat (Smallwood 2001). However, in a recent synthesis of 37, 099 U.S. river restoration projects, Bernhardt et al. (2005) reported that few

(≤10%) are monitored for biological function, even though habitat improvement is a commonly stated objective of such projects.

The Sacramento River, California's largest river system, has undergone massive riparian habitat loss over the past century, primarily a result of agricultural conversion and water regulation (Hunter et al. 1999), contributing to regional bird population declines and local extirpations of open-cup nesting birds. Floodplain habitat restoration has been conducted in the Sacramento Valley for nearly 15 years, with the objective of increasing and improving habitat function for riparian and aquatic life (Golet et al. 2003). We sought to evaluate large-scale riparian restoration efforts in the Sacramento Valley in terms of nest survival. To do so, we conducted a multi-scale analysis of risk factors for nest predation on Spotted Towhees (*Pipilo maculatus*), taking an information-theoretic model selection approach (Burnham and Anderson 2002). We compared a set of *a priori* candidate models proposed to explain variation in nest predation in a riparian restoration context over a ten-year period (1994-2003), then predicted nest survival under varying ecological conditions, based upon our best approximating models.

Nest predation has been identified as the primary source of nest failure for most passerines (Ricklefs 1969, Martin 1992, Martin 1993) and for Spotted Towhees on our study sites (Small 2005). The congeneric Eastern Towhee (*Pipilo erythropthalmus*) is declining in New England, where daily nest success is low due to high nest predation (Krementz and Powell 2000). Nest predation not only has implications for fledging success, but for recruitment of yearlings and long-term population regulation (Sherry and Holmes 1992).

Nest predation dynamics may operate at multiple scales (Donovan et al. 1997, Thompson et al. 2002), so we considered habitat variables at several scales (Table 2): local (nest site; 5 m), territory (50 m), and patch (500 m), measured as radii around observed nests, as well as landscape-level flood effects and temporal effects. We compared six working hypotheses to explain variation in Spotted Towhee nest predation in the Sacramento Valley, in the context of floodplain restoration: 1) "restoration," 2) "temporal," 3)"nest concealment," 4) "nest activity," 5) "agriculture," and 6) "flood effects," represented by 44 total candidate models total (Table 3).

In general, functional (behavioral) predator responses occur at local and patch scales, while numeric (predator abundance) responses occur at the landscape scale (Chalfoun et al. 2002). Our "restoration", "temporal effects", "nest concealment" and "nest activity" hypotheses may be considered "predator search" hypotheses, as they primarily address the functional response of a predator's ability to locate the nest, while our "agriculture" and "flood effects" hypotheses may be considered "predator abundance" hypotheses, as they address a numeric response to large scale phenomena.

Our study species, Spotted Towhee, is a ground- and shrub-nesting songbird that is resident in California, but migratory in other parts of the western United States (Greenlaw 1996). It is an excellent indicator species for restoration success on the Sacramento River, as it breeds in low substrate on both mature riparian forest and restoration sites, colonizing restoration sites within several years after planting. While predation has been identified as the primary nest mortality factor for this species on our sites (Small 2005), cowbird parasitism pressure is unusually high here compared to previous anecdotal reports for this species (Greenlaw 1996). In 1993-2003,

38% of Spotted Towhee nests observed on our sites were parasitized, and 60% of those cases were multiple parasitisms (Small 2005).

Candidate models. All candidate models were run with and without the following covariates: stage (eggs or young), date, and a stage x date interaction term. Also, all models included a random effects variable, "plot-year," as a study design element to account for potential spatial autocorrelation.

Restoration effect. The candidate models representing the "restoration effect" hypothesis included combinations of the following covariates: habitat type (restoration or riparian forest) and per cent agriculture in surrounding landscape (500 m radii around nests), as well as nest stage, calendar date, and a date x stage interaction term. We predicted that nest survival for this species would be higher on restoration sites. In general, predators may be less familiar with territories on newer sites and, as habitat structure changes annually on an early successional riparian site, predators must learn territories and potential nest sites anew each year. Also, compared to mature riparian study sites, the understory habitat of the restoration sites was shrubbier with more diversely structured, low, dense vegetation, offering more potential towhee nest sites and presenting a greater nest searching challenge to potential predators, in accordance with the "many nest-site" hypothesis of Martin and Roper (1988).

Temporal effects. The candidate models representing the temporal effects hypothesis included combinations of the following covariates: calendar date, nest stage, and a date x stage interaction term. Temporal variation, within and between breeding seasons, may produce demographic patterns akin to the spatial variation described by source-sink models (Burhans et al. 2002).

Calendar date may describe patterns of predator activity or abundance, and year may capture effects not explicitly described by other models, as predator populations may vary with multiple interacting factors from year to year, including agricultural harvests, flood regime, and precipitation. Other investigators found that year was an important factor explaining nest predation (Burhans et al. 2002, Morrison and Bolger 2002b, Nur et al. 2004). We predicted that nests later in the season and those in the nestling cycle would have lower nest survival, as predators may cue into nest activities and learn bird territories over the season (functional predator response).

Nest concealment. The candidate models representing the nest concealment hypothesis included combinations of the following covariates: per cent nest concealment and nest height, as well as nest stage, calendar date, and a date x stage interaction term. We predicted that nest survival would increase with nest cover, as greater nest concealment may hinder predator's visual search efforts and reduce number of "opportunistic" nest predations. Budnick et al. (2002) found that nest concealment and cover affects nest predation, although others (Burhans and Thompson 1998) failed to detect such an effect. Brown (1997) found that predation by birds correlated with nest exposure, but predation by Black Rats (*Rattus rattus*) was equal at exposed and concealed nests. Howlett and Stutchbury (1996) found no effect of vegetation cover at the nest on predation rates of a ground-nesting bird, the Hooded Warbler (*Wilsonia citrina*), suggesting that opportunistic foraging by non-specialist predators had the greatest impact on that species. In another study, nest concealment was paradoxically higher in years of heavier nest predation (Forstmeier and Weiss 2004). We also predicted that nest survival would decrease with nest height (Budnik et al. 2002, Burhans et al. 2002, Patten and Bolger 2003), as the bulky Spotted

Towhee nest typically becomes more visible from below when the nest is suspended in vegetation rather than embedded in ground vegetation or litter.

Nest activity. The candidate models representing the "nest activity" hypothesis included the following covariates: nest stage, cowbird young and nest concealment, as well as calendar date, and a date x stage interaction term. The "nest activity" hypothesis predicts that increased activity around the nest, associated with parental care and nestling begging, would attract the attention of nest predators, resulting in higher nest mortality. Both nestling begging (Haskell 1994) and parental activity (Budnik et al. 2002) have been shown to increase nest predation risk. The nest activity hypothesis also predicts that nests with cowbird young, which may beg loudly and persistently, would have higher predation rates (Dearborn 1999), as would more exposed nest sites that provide less concealment of parental activities.

Agriculture effects. The candidate models representing the agriculture effects hypothesis contained combinations of the following covariates: "per cent agriculture" in surrounding landscape (50 and 500 m radii around nests) and agricultural edge density (50 m radii around nest), as well as calendar date, nest stage, and a date x stage interaction term. We predicted that nest predation would increase with more agriculture in the surrounding landscape. Most nest predators videotaped on our sites are associated with agriculture (Small 2005). Human-altered riparian landscapes may support higher densities of nest predators, parasites, and exotic species (Saab 1999). Corvids may increase in landscapes fragmented by agriculture, leading to increased nest predation (Andren 1992). Similarly, agriculture supports higher densities of raccoons, and ground nests may be especially vulnerable to raccoon predation (Schmidt 2003). Finally, non-native rodents are associated with agriculture (Ballard et al. 2003b), which may

drive up nest predation rates in forest patches (Bayne and Hobson 1998). Rats are well known to

be efficient nest predators that have the potential to threaten bird populations (Brown 1997,

VanderWerf and Smith 2002).

Flood effects. The candidate models representing the flood effects hypothesis contained

combinations of the following hydrology covariates, measured annually: 1) flood duration

(maximum and median length, in hours, of high flow pulses), 2) flood intensity (mean discharge

per flood event, measured as cubic feet per second [cfs]), and 3) flood timing (median Julian date

of high flow pulses) recorded at nearest bridge gauges. We also compared hydrology models that

included habitat type, calendar date, nest stage, and a date x stage interaction term.

Our flood hypotheses predict that nest survival would increase with longer and more intense

floods annually, as well as floods nearer to the breeding season. We hypothesized that floods

would reduce rodent populations by reducing adult numbers and depressing reproductive success

(numeric predator response). Schmidt and Ostfeld (2003) showed that nest mortality of another

shrub- and ground-nesting species, Veery (*Catharus fuscescens*), increases with small mammal

density.

METHODS

Study area. We located and monitored active Spotted Towhee nests on five nest plots – two

restoration plots and three mature forest plots -- from 1994 through 2003 on the Sacramento

River National Wildlife Refuge in Butte, Colusa, Glenn, and Tehama Counties, California (39°

40' N, 121° 57' W). Plots were 16-20 ha in size and located within the 1-2 year floodplain of the

Sacramento River. These sites are primarily mixed riparian forest surrounded by agriculture. Mature forest and riparian restoration plots were interspersed and at least 1 km apart, arrayed along approximately 60 river miles. Restoration sites had been planted with a mix of native riparian shrubs and trees, using horticultural techniques described by Alpert et al. (1999). Forest gaps on the restoration sites were occupied by native Mugwort (*Artemesia douglasiana)* in some locations and invasive herbaceous plants in others, including Johnson Grass (*Sorghum halepense*), Bermuda Grass (*Cynodon dactylon*), and Perennial Pepperweed (*Lepidium latifolium*). Mature forests were primarily Fremont Cottonwood (*Populus fremontii*) /willow mix, with a mid-story of CA Wild Grape (*Vitis californica*), Blue Elderberry (*Sambucus mexicana*), and Box Elder (*Acer negundo*). Open gaps were primarily occupied by Mugwort, Himalayan Blackberry (*Rubus discolor*), or willow scrub. Scattered patches of woody river debris could be found throughout the forest floor.

Nest data. Nest data were obtained by locating and monitoring nests, following the methods of Martin and Geupel (1993). Nests were located using parental behavior cues, systematic searches, and adult flushes to locate nests. We minimized disturbance to the nest site during nest checks by taking multiple paths to the nest, checking nests from a distance, whenever possible, and avoiding nest checks when corvids were present. Nest searching began in late April, early in the Spotted Towhee breeding season, and lasted until breeding activity severely declined in late July. Nests were located in diverse substrates, including leaf litter and grass on the ground, also in shrubs, trees, tall forbs, and woody river debris. We determined nest fate by checking nest contents every 1 - 4 days (rarely more than 4). We categorized a nest as "successful" if was not depredated, based upon direct observations of fledglings or parental care activities close to the nest. Nestlings were counted upon each nest check, and the number of young (host young and/or

cowbirds) present in the nest upon the final active nest check was considered the number of young fledged.

After the nest fledged or failed, we measured nest height from the ground and estimated per cent concealment from 6 directions -- above, below, and side in the four cardinal directions -- from 1 m distance. Concealment estimates were averaged to create a single "nest concealment" variable. Nest locations were noted on nest plot maps and recorded with a Garmin GPS unit in the years 2000 and beyond. GPS locations were checked against hard copy maps and points were corrected in one year by adjusting manually approximately 10 m due west in the year 2002. Nest locations for years previous to 2000 were added manually to the GIS layer as point data, based on hard copy maps.

Landscape data. Landscape data were obtained using Fragstats 2.0 (McGarigal and Marks 1994), with a cell size of 5 m, based upon California Department of Water Resources GIS coverage, from 1998 and 1999. Cover type was classified as riparian forest, agriculture, or other (Figure 5).

Hydrology data. Hydrology parameters were calculated using USGS hourly discharge data taken from three river gauges at bridge stations nearest our study sites (north to south): Vina-Woodson Bridge, Hamilton City, and Colusa (Table 4). Where hourly data points were missing, values were substituted by taking the mean of the readings immediately before and after the missing data points.

We defined the threshold for a high pulse event to be the rate of flow at which the river connects with the floodplain on our study sites. Flood stage for our study sites, located within 1-2 year floodplain, was estimated to be 50, 000 cfs, based on field notes of high water events and corresponding discharge readings at nearest bridges, as well as hydrologic modeling conducted as part of the Army Corps Hamilton City Comprehensive Study (G. Lemon, DWR, personal communication).

We calculated flood metrics for the winter/spring flood season starting from October 1 and ending with the last floods of the season, typically ending by mid-June of the following calendar year. We related these flood metrics to the overlapping spring/summer breeding season (Figure 3). Figure 4 shows Sacramento River hydrographs for the study period.

Analytical methods. We employed an AIC model selection approach in our analysis (Burnham and Anderson 2002). This approach is based in likelihood and information theory and is conducted in a "weight of evidence" context. It allows for ranking of multiple competing hypotheses based on criteria known as "Akaike weights." Akaike weights are based on a formula that incorporates likelihood estimators plus a penalty for number of parameters in the model, thereby encouraging model parsimony. This approach allows the investigator to not only choose a "best approximating model" but also to evaluate the relative strength of each model (Anderson et al. 2000).

To obtain our likelihood estimator, we used the "logistic-exposure" method (Shaffer 2004). This method uses a modified logit-link function that accounts for "exposure period" or the number of days a nest was under observation. One nest check interval was counted as an observation. We

used PROC NLMIXED (SAS Institute 2000, Rotella et al. 2004), which allowed us to incorporate a random effect of "plot-year" as a study design element. Our binomial response variable was "survive," which indicated that the nest was not depredated during a given nest check interval. Before proceeding to rank models, we tested whether our global model, containing all covariates, differed from the null hypothesis.

Then, we estimated period nest survival rates within a range of ecological conditions, based on our model with the most support. To do so, we employed the "estimate" statement in SAS (SAS Institute 2000) and used the observed range of values for the covariate of interest, while holding the other covariates in the model constant at their sample mean or, in the case of calendar date, sample median (Shaffer and Thompson In Press). Before predicting nest survival based on our top model, we tested the fit of this model to the data, using the Hosmer-Lemeshow goodness-of-fit test (Hosmer and Lemeshow 1989).

To estimate population growth rates, we used a one stage, female-only model described by Donovan and Thompson (2001) to estimate fecundity and calculate lambda, the finite rate of population increase, based on productivity and survival parameters. The model accounts for double brooding and number of nest attempts, and we modified it to incorporate the different fledging rates for parasitized and unparasitized nests. We used empirical data to compute all model inputs except juvenile survival, for which we calculated a range of values, based on percentages (0-100%) of adult survival. We used local adult survival estimates for the Spotted Towhee in the Sacramento Valley for the period 1995-2000, reported by Gardali and Nur (2006). We incorporated three nest attempts to account for double-brooding and regular re-nesting attempts after nest failures, and we used model-based estimates of nest survival for

parasitized and unparasitzed nests, obtained following methods described by (Shaffer and Thompson In Press).

RESULTS

Our results are based on a sample of 208 nests, located and monitored between 1994 and 2003. Descriptive statistics for model covariates follow. Mean nest height was 36.37 ± 3.81 cm and ranged from 0 to 500 cm. Mean per cent nest concealment was 68.89 ± 1.45 per cent, and ranged from 8.33 to 100 per cent. Median calendar date for nest initiation was June 7. Mean flood duration was 133 ± 12.18 hours and mean river discharge per flood event was 65, 202 ± 341 cfs. Median high water date was May 10.

The model with the greatest weight of evidence ($w_i = 0.690$) included the covariates "cowbird young," "date," and "nest concealment" (Table 5). Our model-based estimate of daily nest survival was 0.941 ± 0.022 (95% CI: 0.898, 0.984), based on this model. The model-based estimate of period nest survival was 0.262 (95% CI: 0.094, 0.706), using a total nest period length of 22 days.

The second-best model ($w_i = 0.154$) contained these same covariates, plus the covariate "stage" and a "stage x date" interaction term. All supported models contained a combination of these five covariates, and the covariate "cowbird young" appeared in every supported model. Based on the Hosmer-Lemeshow goodness-of-fit test, our top model did fit the data (chi-sq = 4.531, $P = 0.806$).

Model-based estimates of nest survival for nests with cowbird young compared to nests without cowbird young showed that nests with cowbird young had a much higher survival rate (0.732, 95 % CI: 0.475, 1.116) than those without (0.040, 95% CI: 0.005, 0.279; Figure 6). Model-based estimates of nest survival throughout the breeding season indicate a within-season decline in nest survival (Figure 7). Nest survival increased only marginally with nest concealment (Figure 8), but its post-hoc inclusion improved the top models. These models were proposed under the "nest activity" hypothesis, but because of the unexpected positive effect of "cowbird young", this hypothesis was not supported.

Of the covariates in the top model, "cowbird young" had the strongest effect, with an odds ratio of 11.01 (95% CI: 3.16, 38.41). The effect direction of cowbird young was positive, opposite the predicted direction. The effects of the other two covariates in the top model were in the predicted direction, but minimal. The covariate "calendar date" had an odds ratio of .993 (95% CI: 0.987, 0.999), with the predicted negative effect. The covariate "nest concealment" had an odds ratio of 1.012 (95% CI: 1.002, 1.021), with the predicted positive effect (Table 6).

Of non-depredated nests, parasitized nests fledged far fewer host young overall (.744 per nest; 95% CI: 0.458, 1.029; n = 73) than unparasitized nests (2.603; 95% CI: 2.312, 2.893; n = 39; Figure 9).

Lambda, the finite rate of population growth, ranged from 0.245 to 0.329, based on period nest success rates of non-parasitized nests (0.052) and parasitized nests (0.758), an observed cowbird parasitism rate of 38% during the period 1994-2003 (Small 2005), female young fledged per

successful nest from unparasitized (1.302) and parasitized (0.372) nests (assuming half of fledglings are female), and a range of juvenile survival values calculated as percentages (0-100%) of Spotted Towhee apparent adult survival -- 0.245 for the period of 1995-2000 in the Sacramento River Valley (Gardali and Nur 2006).

DISCUSSION

Our best-supported nest predation models were those that contained the covariates "cowbird young" and "calendar date," with a random effect of "plot-year". Nest predation increased slightly as the season progressed. Other investigators have detected seasonal effects in nest predation rates; Burhans et al. (2002) detected a mid-summer peak in nest predation, as did Nur et al. (2004).

No agriculture or flood effects were detected for this species. There was no detectable difference between restoration and forest sites in nest predation rates, indicating that restoration sites are functioning as well as forest sites as breeding habitat, in terms of nest predation. Twedt et al. (2001) similarly found that Eastern Towhee nest success did not differ between bottomland forests and cottonwood plantations in the Mississippi Valley, but that average daily nest survival of 19 species combined was higher in remnant mature forests.

The effect size of nest concealment alone was small, but its *post-hoc* inclusion improved the top model; other studies have indicated some effect of nest concealment on nest predation and parasitism (Burhans and Thompson 1998, Budnik et al. 2002, McLaren and Sealy 2003) and Martin et al. (2000) showed that nest predation increases in the nestling stage, when nest site quality is taken into account.

In contrast to our prediction, nest survival increased with cowbird young in the nest. All supported models contained the variable cowbird young, which had a positive effect on nest survival and was the only covariate with a large effect size; the odds ratio for parasitized nests to escape nest predation was 10.82, compared with unparasitized nests. Dearborn (1999) found that cowbird begging in Indigo Bunting (*Passerina cyanea*) nests increased nest predation risk; therefore, we expected to see higher nest predation rates in nests with cowbird young. In contrast, we found that Spotted Towhee nests containing cowbird young suffered lower predation rates than those that did not.

Differential body size between our study species and buntings may partially account for these contrasting results; Spotted Towhees weigh 33-49 g (Greenlaw 1996), while Indigo Buntings weigh only 12-18 g (Payne 1992). Cowbird begging intensity has been shown to represent honest signaling, being driven by hunger levels (Hauber and Ramsey 2003, Lichtenstein and Dearborn 2004). Cowbird nestlings may tend to be more satiated and therefore beg less intensely in a nest of the relatively large-bodied Spotted Towhee, which can provision a cowbird nestling and one of its own young; of non-depredated towhee nests, parasitized nests produced 0.74 towhee young (95% CI: 0.46-1.03, n=39) compared to 2.60 towhee young from unparasitized nests (95% CI: 2.31-2.89, n=73). However, differential body size does not explain the substantially higher nest predation rates of unparasitized nests.

We propose two alternate explanations for this unexpected result: 1) a key predator is discriminating between nests that contain cowbird young and those that do not and selectively preying upon those that do not; or 2) parasitized nests are being preferentially defended by adults

with an interest in their outcome. For the first explanation to hold, the predator must have the ability to discern cowbird from host young and have an investment in the survival of cowbird young or, conversely, an interest in the failure of unparasitized nests.

Arcese et al. (1996) also reported higher predation rates on unparasitized nests in a population of Song Sparrows (*Melospiza melodia*) on Mandarte Island, British Columbia. They also reported decreased Song Sparrow nest mortality in the absence of cowbirds and proposed the "forced re-nesting" hypothesis, suggesting that cowbirds depredate unparasitized nests to create new nesting opportunities.

Our second proposed explanation suggests that Brown-headed Cowbirds defend nests which they have parasitized. While there are numerous published records of cowbirds killing nestlings of host species (reviewed in Granfors et al. (2001) and captured in video footage from our own study sites [Small 2005]), we are aware of no evidence of adult cowbirds defending host nests against predators.

In the highly agricultural Sacramento Valley, where several smaller-bodied cowbird hosts had been locally extirpated by the end of the 20th century (Gardali et al. 1998), quality host nests may be at a premium and potentially limiting for Brown-headed Cowbirds. Many of the extant host species are not ideal hosts, in that they are: 1) larger than cowbirds (Black-headed Grosbeak [*Pheucticus melanocephalus*]), 2) primarily seed-eaters (House Finch [*Carpodacus mexicanus*] and American Goldfinch [*Carduelis tristis*]), 3) cavity nesters (Oak Titmouse [*Baeolophus inornatus*]; Small pers. obs.), 4) sparsely distributed (Common Yellowthroat [*Geothlypis*

trichas], Yellow-breasted Chat [*Icteria virens*]) or otherwise ineffective hosts (Lazuli Bunting [*Passerina amoena*]; Gardali et al. 1998).

Higher predation rates on unparasitized Spotted Towhee nests in a population with high cowbird pressure (38% parasitism rate, 60% multiple parasitisms; Small 2005) and where effective host species are few lend support to Arcese et al.'s (1996) "forced re-nesting" hypothesis. Our results also corroborate those of a Brown-headed Cowbird removal experiment that resulted in lower nest predation in the Fraser River Delta (Smith et al. 2003).

On our study sites, an increase in nest predation over the breeding season may be partially explained by avian predators, including cowbirds, learning territories over the season. The asynchronous breeding periods of Brown-headed Cowbirds and Spotted Towhees may further contribute to this pattern, as cowbirds do not begin egg-laying until several weeks into towhee breeding season. Alternately, competition for food resources could explain higher predation rates on unparasitized nests (reviewed in Granfors et al. 2001); future investigations should test for food limitation in this population.

Spotted Towhee nests in the Sacramento Valley are parasitized at a rate higher than historically reported for this species (Greenlaw 1996), potentially resulting in reduced annual productivity, as parasitized nests may fledge some, but fewer, host young. The relatively large body size of towhees, compared to most of the regionally extirpated host species, may be one of the reasons this species persists as a breeder in the Sacramento River Valley. In this region, where several open-cup nesters have already been extirpated, cowbird activity in the form of both nest

parasitism and predation may be reducing towhee reproductive success through multiple mechanisms.

The apparent adult survival rate for the Sacramento Valley Spotted Towhee population during the period 1995-2000 is low, compared to rates reported for resident and partial migrant species (20-58%) (Greenberg 1980). Low survival rates and poor reproductive success result in lambda values modeled that do not approach 1. This population is apparently not reproducing at replacement levels and is likely being sustained by immigration from outside.

However, this species' regional persistence and its ability to produce some young on both restoration and mature forest sites affords managers an opportunity to improve the prognosis for this and possibly other open-cup nesting species that have suffered the impacts of habitat loss and degradation and associated nest predation and parasitism in the Sacramento Valley over the past half century. Knowledge of specific limiting factors should facilitate regional bird population recovery.

Our results show higher predation rates on unparasitized nests and nests active later in the breeding season, suggesting that cowbirds are acting as key predators on Spotted Towhee nests in this agricultural region, where cowbirds are abundant and host availability is potentially limiting. This indicates that Brown-headed Cowbirds may have been an important limiting factor for declining passerine populations in the Sacramento Valley during the 20th century, compounding the effects of habitat loss and population reduction. To more specifically determine the role of Brown-headed Cowbirds in regional population declines, experimental cowbird control may be warranted.

However, while experimental cowbird control may give us more a more precise and detailed understanding of cowbird impacts, we are not recommending cowbird control as a mitigation measure at this point. Management for the productivity and re-establishment of breeding bird populations, especially open-cup nesters, should remain focused on restoration of the riparian landscape, with the long-term goal of continually increasing the proportion of riparian to agricultural habitat. This approach provides the benefit of increasing available nesting habitat while decreasing foraging habitat for cowbirds and other nest predators.

Cowbird pressures are secondary to the most critical avian conservation threat on North American floodplains, namely anthropogenic habitat change and loss (DeSante and George 1994, Askins 2000, Rothstein and Peer 2005). The arrival of the cowbird in the Sacramento Valley in the 1930's (Neff 1931) coincided with the onset of agricultural conversion in the region. Agriculture-dominated landscapes tend to sustain cowbird populations, where host nests are available adjacent to prime foraging sites (Goguen and Matthews 1999). Such is the case in the Sacramento Valley, where riparian floodplain forests have been largely converted to agriculture, and extant breeding riparian birds have been exposed to nest predation and cowbird parasitism in riparian forest remnants.

Landscape-scale solutions to cowbird and other predator impacts in the western U.S. have been proposed by DeSante and George (1994), Tewksbury et al. (2002), and Rothstein and Peer (2005). There is general agreement that the ultimate solution to riparian bird population declines is to increase the proportion of riparian habitat relative to agriculture in degraded landscapes such as the Sacramento Valley. Our results show that restoration sites function as breeding

habitat, with nest survival comparable to mature forest sites and some young being produced. Increasing the amount of available habitat should ultimately benefit breeding bird populations by providing more nest sites and reducing predator/parasite pressure.

CHAPTER 4

FLOOD TIMING AFFECTS NEST PREDATION IN A RIPARIAN-BREEDING

POPULATION OF BLACK-HEADED GROSBEAKS (*Pheucticus melanocephalus*)

Stacy L. Small, Frank R. Thompson, III, David Galat, Geoffrey R. Geupel, John Faaborg

ABSTRACT

Habitat restoration projects are often designed to improve conditions for breeding populations of

birds and other taxa, yet it has been recently reported that fewer than 10% of such projects are

monitored for biological function. Demographic data linked to ecosystem processes are

critically needed for effective restoration and conservation planning. Recently developed

analytical techniques allow for modeling of avian nest survival using categorical and continuous

covariates, time-dependent covariates, and random effects. In an effort to evaluate conditions

for a breeding population of a riparian-associated species in a habitat restoration context, we

modeled nest survival of the Black-headed Grosbeak in relation to biotic and abiotic factors,

including behavior, cowbird parasitism, microhabitat, landscape composition, and flood regime,

using the logistic-exposure method and an AIC model selection approach. Our best-supported

model was median flood date, representing the "flood effects" hypothesis ($w_i = .296$;

odds ratio = 1.009; 95% CI: 1.002, 1.014). The effect direction was positive for this covariate,

indicating a reduction of nest predation with more spring flooding, toward the start of breeding

season. Our results demonstrate a link between flood timing and terrestrial bird population

dynamics, indicating that naturalization of the flow regime to more closely approximate pre-dam

hydrographs should be a primary strategy for protecting and restoring floodplain forests in the Central Valley of California and the breeding bird populations that depend upon them.

INTRODUCTION

In the arid western U.S., riparian zones support the richest avifuana of any habitat type (Knopf et al. 1988) and in California, riparian floodplains support the richest fauna of any ecosystem (Griggs 1993). Most of California's largest rivers, which flow through the agricultural regions of the Great Central Valley, have been severely altered for the benefit of crop irrigation and water diversion to the state's largest cities, many of which occur in arid climates (Mount 1995).

Ecosystem processes of the Sacramento River, California's largest river system, have been seriously degraded by the construction of Shasta Dam in the 1940's and subsequent river regulation that has disrupted the natural river flow regime and facilitated irrigated agriculture, entailing such land use practices as floodplain leveling, deforestation, and disconnection of the river and floodplain (Mount 1995, Postel and Richter 2003).

These phenomena have resulted in cumulative impacts of riparian habitat loss and degradation, with serious implications for the persistence of riparian bird populations in the region. Along with agricultural conversion came outbreaks of nest predator species such as Black and Norway rats (*Rattus* spp.; Brooks and Barnes (1972)) and the expansion of Brown-headed Cowbirds, which were first reported in the Valley in the 1930s (Neff 1931) but have since become abundant (Laymon 1987, Gardali et al. 1998). Also, medium-sized mammalian nest predators associated with agriculture and human development, such as raccoons and opossums, are abundant on remnant woodlots throughout the Sacramento Valley (Souza 1995).

Restoration of large river floodplain forests in California and elsewhere throughout North America may be critical to the persistence of breeding riparian bird populations (Askins 2000). Large-scale floodplain restoration efforts have been underway in the Sacramento River Valley since 1990 (Griggs 1993, Alpert et al. 1999, Hunter et al. 1999, Golet et al. 2003). Along large, regulated rivers, two primary means of floodplain restoration are: 1) horticultural methods, using mechanical agricultural techniques for planting and irrigation (Alpert et al. 1999), and 2) naturalization of the river flow regime to correspond more closely with the river's historic hydrograph, along with which its aquatic and terrestrial systems evolved (Hunter et al. 1999, Postel and Richter 2003).

Although the need to link animal demographics to restoration efforts at appropriate scales has been recognized (Smallwood 2001), fewer than 10% of 3,000+ river restoration projects in North America evaluate biological response to river restoration (Bernhardt et al. 2005). While several investigators have examined bird community response and abundance patterns on riparian and wetland restoration sites (Ratti et al. 2001, Gardali et al. 2006), few have examined long-term avian demographics within a floodplain riparian restoration context. Long-term monitoring of nest survival over a large geographic scale is challenging and labor-intensive, but for understanding bird population response to ecological restoration, it is one of the most relevant population parameters.

We sought to evaluate factors affecting nest survival of a riparian-associated Neotropical migrant songbird, the Black-headed Grosbeak (*Pheucticus melanocephalus*), breeding in the Sacramento River Valley, California, in the context of large-scale habitat restoration efforts. We examined

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whether horticultural restoration, hydrologic regime, landscape context, local nest site features,

behavior, and/or temporal factors played a role in nest survival of this open-cup nesting species,

which breeds on both restoration and remnant forest sites in the valley.

Candidate models. Using an information-theoretic AIC model-selection approach (Burnham

and Anderson 2002), we compared multiple working hypotheses to explain variation in nest

predation in this system, a primary cause of open-cup nest mortality on our study sites (Small

2005) and elsewhere (Ricklefs 1969, Martin 1992, Martin 1993).

Descriptions of the covariates included in our candidate models may be found in Table 2.

Candidate models describing competing hypotheses for Black-headed Grosbeak nest survival are

outlined in Table 7. All models were run with and without the following covariates: stage (eggs

or young), date, and a stage x date interaction term. Also, all models included a random effects

variable, "plot-year," as a study design element to account for potential spatial autocorrelation.

Restoration effect. The candidate models representing the "restoration effect" hypothesis

included combinations of the following variables: "habitat type" (restoration or riparian forest)

and "per cent agriculture" in surrounding landscape (500 m radii around nests), as well as "nest

stage," "calendar date," and a date x stage interaction term. We predicted that nest survival for

this species would be higher on restoration sites. In general, predators may be less familiar with

territories on newer sites and, as habitat structure changes annually on an early successional

riparian site, predators must learn territories and potential nest sites anew each year. Also,

compared to mature riparian study sites, the mid-story habitat of the restoration sites was

shrubbier and more dense, offering more potential grosbeak nest sites and presenting a greater

nest search challenge to potential predators, in accordance with the "many nest-site" hypothesis of Martin and Roper (1988).

Temporal effects. The candidate models representing the temporal effects hypothesis included combinations of the following variables: "calendar date," "nest stage," and a date x stage interaction term. Temporal variation, within and between breeding seasons, may produce demographic patterns akin to the spatial variation described by source-sink models (Burhans et al. 2002). Calendar date may describe patterns of predator activity or abundance, and year may capture effects not explicitly described by other models, as predator populations may vary with multiple interacting factors from year to year, including agricultural harvests, flood regime, and precipitation. We predicted that nests later in the season and those in the nestling period would have lower nest survival, as predators may cue into nest activities and learn bird territories over the season, a functional predator response. Other investigators have detected seasonal effects in nest predation rates; Burhans et al. (2002) detected a mid-summer peak in nest predation, as did Nur et al. (2004).

Nest concealment. The candidate models representing the nest concealment hypothesis included combinations of the following variables: "per cent nest concealment" and "nest height," as well as "nest stage," "calendar date," and a date x stage interaction term. We predicted that nest survival would increase with nest cover, as greater nest concealment may hinder predator's visual search efforts and reduce number of "opportunistic" nest predations. Budnick et al. (2002) found that nest predation decreases with nest concealment and cover, although others (Burhans and Thompson 1998) failed to detect such an effect. Brown (1997) found that predation by birds correlated with nest exposure, but predation by Black Rats (*Rattus rattus*) was equal at exposed

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and concealed nests. In another study, nest concealment was paradoxically higher in years of

heavier nest predation (Forstmeier and Weiss 2004). We also predicted that nest survival would

increase with nest height (Budnik et al. 2002, Burhans et al. 2002), as grosbeak nests higher in

the canopy may be less accessible or visible to terrestrial predators.

Nest activity. The candidate models representing the "nest activity" hypothesis address adult and

offspring behavior at the nest and included the following variables: "nest stage," "cowbird

young" and "nest concealment", as well as "calendar date", and a date x stage interaction term.

The "nest activity" hypothesis predicts that increased activity around the nest, associated with

parental care and nestling begging, would attract the attention of nest predators, resulting in

higher nest mortality. Both nestling begging (Haskell 1994) and parental activity (Martin et al.

2000) have been shown to increase nest predation risk. We included the variable nest

concealment in one of the nest activity models, as concealment may function in combination

with behavior at the nest to make it more or less detectable to predators (Weidinger 2002).

Agriculture effects. The candidate models representing the agriculture effects hypothesis

contained combinations of the following variables: "per cent agriculture" in surrounding

landscape (50 and 500 m radii around nests) and "agricultural edge density" (50 m radii around

nest), as well as calendar date, nest stage, and a date x stage interaction term. We predicted that

nest predation would increase with more agriculture in the surrounding landscape. Most nest

predators videotaped on our sites are associated with agriculture (Small 2005). Human-altered

riparian landscapes may support higher densities of nest predators, parasites, and exotic species

(Saab 1999). Corvids may increase in landscapes fragmented by agriculture, leading to

increased nest predation (Andren 1992). Similarly, agriculture supports higher densities of

raccoons, and ground nests may be especially vulnerable to raccoon predation (Schmidt 2003).

Finally, non-native rodents are associated with agriculture (Long 2003), which may drive up nest

predation rates in forest patches (Bayne and Hobson 1998). Rats are well known to be efficient

nest predators that have the potential to threaten bird populations (Brown 1997, VanderWerf and

Smith 2002).

Flood effects. The candidate models representing the flood effects hypothesis contained

combinations of the following hydrology variables, measured annually: 1) flood duration

(maximum and median length, in hours, of high flow pulses); 2) flood intensity (mean discharge

per flood event, measured as cubic feet per second [cfs]); and 3) flood timing (median Julian date

of high flow pulses) recorded at nearest bridge gauges. We also compared hydrology models that

included "habitat type," "calendar date," "nest stage," and a date x stage interaction term.

The flood hypotheses predicted that nest survival would increase with longer and more intense

floods annually, as well as floods nearer to the breeding season. We hypothesized that floods

would reduce rodent populations by reducing adult numbers and depressing reproductive

success, a numeric predator response. Schmidt and Ostfeld (2003) showed that nest mortality of

another open-cup nesting species, the Veery (*Catharus fuscescens*), increases with small

mammal density. We included the variable "habitat type" in several of our flood effects models,

predicting that early successional habitat would potentially provide less shelter for small

mammals in floods than mature riparian forest. Williams and Ratnaswamy (2001) found that

following a brief flood on the lower Missouri River floodplain, *Peromyscus* species captures

were lower in young, regenerating forest than in mature floodplain forest.

METHODS

Study area. We located and monitored active Black-headed Grosbeak nests on five nest plots – two restoration plots and three mature forest plots -- from 1994 through 2003 on the Sacramento River National Wildlife Refuge in Butte, Colusa, Glenn, and Tehama Counties, California (39° 40' N, 121° 57' W). Plots were 16-20 ha in size and located within the 1-2 year floodplain of the Sacramento River. These sites are primarily mixed riparian forest surrounded by agriculture. Mature forest and riparian restoration plots were interspersed and at least 1 km apart, arrayed along approximately 60 river miles. Restoration sites had been planted with a mix of native riparian shrubs and trees, using horticultural techniques described by Alpert et al. (1999). Black-headed Grosbeaks nested on restoration sites within five years of planting, in dense Arroyo Willow (*Salix lasiolepsis*), Box Elder (*Acer negundo*), and Blue Elderberry (*Sambucus mexicana*) shrubs. Mature forests were primarily Fremont Cottonwood (*Populus fremontii*)/willow mix, with a midstory of California Wild Grape (*Vitis californica*), Blue Elderberry, and Box Elder. Grosbeaks nested in the mid-story shrubs listed above, in addition to mature Fremont Cottonwoods and Black Willows (*Salix goodingii*).

Nest data. Nest data were obtained by locating and monitoring nests, following the methods of Martin and Geupel (1993). Nests were located using parental behavior cues, systematic searches, and adult flushes to locate nests. We minimized disturbance to the nest site during nest checks by spending minimum time at the nest site, checking nests from a distance when possible, and avoiding nest checks when Western Scrub-jays (*Aphelocoma californica*) were present. Nest searching began in May, with the onset of Black-headed Grosbeak nest building, and lasted until breeding activity severely declined in late July. We determined nest fate by checking nest contents every 1 - 4 days (rarely more than 4). Nests contents were checked with a mirror pole, a

wide angle bicycle mirror mounted on an extendable pole. Higher nests were checked using an 11 ft. aluminum tripod ladder, in combination with the mirror pole. We categorized a nest as "successful" if it was not depredated, based upon direct observations of fledglings or parental care activities close to the nest. Nestlings were counted upon each nest check, and the number of young (host young and/or cowbirds) present in the nest upon the final active nest check was considered the number of young fledged.

After the nest fledged or failed, we estimated nest height from the ground using an extendable pole, and visually estimated per cent concealment from 6 directions -- above, below, and side in the four cardinal directions -- from 1 m distance (Martin et al. 1997) . Concealment estimates were averaged to create a single "nest concealment" variable. Nest locations were noted on nest plot maps and recorded with a Garmin GPS unit in the years 2000 and beyond. GPS nest locations were checked against hard copy field maps and points were corrected in one year by adjusting manually approximately 10 m due west in the year 2002. Nest locations for years previous to 2000 were added manually to the GIS layer as point data, based on hard copy field maps.

Landscape data. Landscape data were obtained using Fragstats 2.0 (McGarigal and Marks 1994), with a cell size of 5 m, based upon California Department of Water Resources GIS coverage, from 1998 and 1999. Cover type was classified as "riparian forest" (restoration and mature forest combined), "agriculture", or "other" (mostly urban/suburban or foothill grasslands) (Figure 5).

Hydrology data. Hydrology parameters were calculated using USGS hourly discharge data taken from three river gauges at bridge stations nearest our study sites (north to south): Vina-Woodson Bridge, Hamilton City, and Colusa (Table 4). Where hourly data points were missing, values were substituted by taking the mean of the readings immediately before and after the missing data points.

We defined the threshold for a high pulse event to be the rate of flow at which the river connects with the floodplain on our study sites. Flood stage for our study sites, located within 1-2 year floodplain, was estimated to be 50, 000 cfs, based on field notes of high water events and corresponding discharge readings at nearest bridges, as well as hydrologic modeling conducted as part of the Army Corps Hamilton City Comprehensive Study (G. Lemon, DWR, personal communication).

We calculated flood metrics for the winter/spring flood season starting from October 1 and ending with the last floods of the season, typically ending by mid-June of the following calendar year. We related these flood metrics to the overlapping spring/summer breeding season (Figure 3). Figure 4 depicts Sacramento River hydrographs for the study period.

Analytical methods. We employed an AIC model selection approach in our analysis (Burnham and Anderson 2002). This approach is based in likelihood and information theory and is conducted in a "weight of evidence" context. It allows for ranking of multiple competing hypotheses based on criteria known as "Akaike weights." Akaike weights are based on a formula that incorporates likelihood estimators plus a penalty for number of parameters in the model, thereby encouraging model parsimony. This approach allows the investigator to not only choose

a "best approximating model" but also to evaluate the relative strength of each model (Anderson and Cooper 2000).

To obtain our likelihood estimator, we used the "logistic-exposure" method (Shaffer 2004). This method uses a modified logit-link function that accounts for "exposure period" or the number of days a nest was under observation. One nest check interval was counted as an observation. We used PROC NLMIXED (SAS Institute 2000, (Rotella et al. 2004), which allowed us to incorporate a random effect of "plot-year" as a study design element. Our binomial response variable was "survive," which indicated that the nest was not depredated during a given nest check interval.

Then, we estimated period nest survival rates within a range of ecological conditions, based on our model with the most support. To do so, we employed the "estimate" statement in SAS (SAS Institute 2000) and used the observed range of values for the covariate of interest, while holding the other covariates in the model constant at their sample mean (Shaffer and Thompson In Press). Before calculating our model-based nest survival estimates, we tested the fit of the top candidate model, using the Hosmer-Lemeshow goodness-of-fit test (Hosmer and Lemeshow 1989).

RESULTS

We located and monitored 294 active Black-headed Grosbeak nests from 1994 through 2003 on the Sacramento River National Wildlife Refuge. Mean nest height was 368.16 ± 9.95 cm and ranged from 100 to 900 cm. Mean per cent nest concealment was 59 ± 4.71 per cent and ranged from 5 to 100 per cent. Median calendar date for nest initiation was June 13.   Mean flood

duration was 125.43 ± 11.29 hours and mean river discharge per flood event was 62, 589 ± 789

cfs. Median high water date was May 20.

Our best-supported model was median flood date, representing the "flood effects" hypothesis

(Table 8), as indicated by the weight of evidence score (wi = .296) and odds ratio (1.009, 95%

CI: 1.002, 1.014). The effect direction was positive for this covariate, indicating a reduction of

nest predation with more spring flooding, toward the start of breeding season (Table 9). Median

flood date was the only model for which the 95% confidence interval did not contain 1. Based

on the Hosmer-Lemeshow goodness-of-fit test, our top model did fit the data (chi-sq = 14.833, P

= 0.062).

Our model-based estimate of daily nest survival was 0.963 ± 0.003 (95% CI: 0.957, 0.9670),

based on this model. Estimated period nest survival was .422 ± 0.000 (95% CI: 0.361, 0.494),

using a total nest period length of 23 days.

Predicted nest survival in relation to flood timing (Figure 10) shows an increase in nest survival

as the median flood date approaches spring and the onset of breeding season. Three other flood

models did not converge, so they were not included in the ranking.

The other models with some support were per cent agriculture in the landscape (500 m scale),

representing the "agriculture effects" hypotheses and nestling stage, representing the "nest

activity" hypothesis (Table 8). The effect size was not large for any of the supported models,

with odds ratios close to 1. The effect directions for percent agriculture (500 m radius) and

nestling stage were positive, opposite of the predicted direction, so our "agriculture" and "nest

activity" effects hypotheses were not supported. Finally, there was no observed difference in nest survival between restoration and mature forest sites, and no temporal effects were detected.

DISCUSSION

We compared candidate models that represented six competing hypothesis to explain nest predation along the Sacramento River, in the context of a large-scale riparian restoration project. These hypotheses were: 1) restoration, 2) flood, 3) agriculture, 4) nest concealment, 5) nest activity, and 6) temporal effects. Our best-supported model contained the variable "median flood date" representing the "flood effects" hypothesis. Our results suggest that spring flooding, approaching the start of Black-headed Grosbeak breeding season, is associated with lower nest predation, indicating that flood regime may be linked to avian nest survival through fluctuating predator populations.

We observed no difference in nest survival between restoration and mature forest sites, indicating that restoration sites are performing at least as well as remnant forest sites in terms of nest predation. We observed marginal agriculture and nest stage effects, but not in the predicted direction, so there was no support for the agriculture and nest activity hypotheses.

Griggs (1993) vividly described effects of occasional major floods on rodent populations in the middle Sacramento Valley. Extensive floods may reduce rodent populations for several years, facilitating riparian vegetation regeneration. Conversely, he described rodent population booms following several years without extensive flooding, inhibiting sapling growth through extensive herbivory. An early natural history paper from northern California makes explicit descriptive connections between flood events and rodent population cycles (Grinnell 1939). In regards to

terrestrial rodent population cycles, Grinnell remarked "...this flood factor loom[s] in my mind as superimportant in accounting not only for the observed boundaries of geographic ranges of species and races, but also perhaps the most potent causative factor of observed fluctuations in population numbers." Similarly, Hoslett (1961) described mass mortality, approaching local extirpation, of small mammals during intense spring flooding that inundated the broad floodplains of the Upper Iowa River in the March 1936. In a review of the effect of river regulation on birds and mammals, Nilsson and Dynesius (1994) called for more rigorous study of how river regulation affects reproduction of riparian species and more recent studies link flooding with rodent and small mammal mortality (Andersen et al. 2000).

Spring flood peaks on the Sacramento River, historically generated by melting snow packs in the mountains of northern California, have been leveled out by large dam construction and operation upstream from our study sites (Mount 1995). Our results demonstrate a link between flood timing and terrestrial bird population dynamics, indicating that naturalization of the flow regime to more closely approximate pre-dam hydrographs and reconnection of the river and floodplain, in combination with large-scale, horticultural-based restoration, should be a primary strategies for protecting and restoring floodplain forests in the Central Valley of California and the breeding bird populations that depend upon them.

APPENDIX A: TABLES

Table 1. Date, time, predator species and nest contents (Y=young, E=eggs) for predation events filmed at Spotted Towhee nests along the Sacramento River, California, USA, 2002-2003.

Nest	Date	Time	Predator	Nest contents
1	19 June 2002	14:26	Red-shouldered Hawk [a]	Y
1	19 June 2002	22:14	unidentified rodent [a]	Y
2	13 July 2002	06:53	unidentified predator [b]	E
3	27 July 2002	11:35	Western Scrub-Jay	Y
4	15 June 2003	04:02	raccoon	Y
5	4 July 2003	12:22	racer[c]	Y
5	---	12:30	---	---
5	---	14:40	---	---
6	6 July 2003	08:41	Brown-headed Cowbird [a, d]	Y
6	11 July 2003	04:20	unidentified rodent [a]	Y
7	18 July 2003	01:34	*Rattus* sp.	Y&E

Table 2. Covariates included in nest survival models, abbreviations, and definitions (with predicted effect directions).

Covariate	Abbr.	Definition
Intercept		
Nestlings	NStg	Nestling stage (-)
Calendar date	Date	Julian date (-)
Cowbird young	CowY	Nest contains cowbird young (-); towhee only
Restoration site	HabR	Habitat type = riparian restoration (+)
Nest height	NHt	Nest height from ground: towhee (-), grosbeak (+)
Nest concealment	NCon	Nest concealment at 1 m radius, averaged 6 ocular estimates (+)
Flood duration	FDur	Mean duration of annual flood events (+)
Flood intensity	FInt	Mean flow (cfs) of annual flood events (+)
Flood timing	FTim	Median flood date, annually (+)
Per cent agriculture 50m	Ag50	Amount of agriculture in 50 m radii around observed nests (-)
Agricultural edge density 50m	AgED50	Meters of agricultural edge within 50 m radii of observed nests (-)
Per cent agriculture 500m	Ag500	Amount of agriculture in 500 m radii around observed nests (-)
Nest stage x calendar date	NStg x Date	Interaction term, nest stage and calendar date
Plot-year	μ	Random effect of Plot and Year

Table 3. Working hypotheses and candidate models for Spotted Towhee nest survival along the Sacramento River, 1994-2003. μ represents random effect of "plot-year."

Model	Survive =
Global	NStg, Date, NStg X Date, CowY, NHt, NCon, HabR, Ag50, AgED50,Ag500, FDur, FInt, FTim, μ
Restoration	HabR, Ag500, NStg, Date, NStg X Date, μ
	HabR, μ
	HabR, Ag500, μ
	HabR, NStg, μ
	HabR, Date, μ
	HabR, Ag500, NStg μ
	HabR, Ag500, NStg, Date, μ
Temporal	NStg, Date, NStg X Date, μ
	Date, μ
Nest concealment	NCon, NHt, NStg, Date, NStg x Date, μ
	NCon, μ
	NHt, μ
	NCon, NHt, μ
	NCon, NHt, NStg, μ
	NCon, NHt, Date, μ
	NCon, NHt, NStg, Date, μ
Nest activity	NStg, CowY, NCon, Date, NStg X Date, μ
	NStg μ
	CowY, μ
	NStg, CowY, μ
	NStg, Date, μ
	CowY, Date, μ
	NStg, CowY, Date, μ
	CowY, NCon, Date, μ
	NStg, CowY, Date, NStg x Date, μ
Agriculture	Ag50, AgED50,Ag500, NStg, Date, NStg x Date μ
	Ag50, μ
	AgED50, μ
	Ag500, μ
	Ag50, Ag500, μ
	Ag50, AgED50,Ag500, μ
	Ag50, AgED50,Ag500, NStg, μ

Table 3 (cont'd). Working hypotheses and candidate models for Spotted Towhee nest survival along the Sacramento River, 1994-2003. μ represents random effect of "plot-year."

Model	Survive =
Flood effects	FDur, FInt, FTim, HabR, NStg, Date, NStg x Date, μ
	FDur, μ
	FInt, μ
	FTim, μ
	FDur, FInt, FTim, μ
	FDur, FInt, FTim, HabR, μ
	FDur, FInt, FTim, HabR, NStg, Date, μ
Null	μ

Table 4. Nest plot distances from nearest river gauge locations at bridge stations along the Sacramento River, CA.

Bridge Station	County	Latitude	Longitude	Study Site	Habitat Type	Distance to Bridge (km)
Vina-Woodson	Tehama	39.9170° N	122.1000° W	Kopta Slough	Restoration	3.22
				Flynn	Remnant Forest	22.53
Hamilton City	Glenn	39.7520° N	121.9940°W	Phelan Island	Restoration	8.05
				Capay /Kaiser	Remnant Forest	12.87
Colusa	Colusa	39.2140° N	121.9990 ° W	Sul Norte	Remnant Forest	6.44

Table 5. All supported models for Spotted Towhee nest survival in the Sacramento Valley, CA, 1994-2003. Number of observations, number of parameters (*K*), AIC values, and weight of evidence (*w_i*).

Model	n	K	-2logL	AICc	Δ AICc	w_i
Cow yng, date, conceal	1118	5	722.829	732.858	0.000	0.690
Cow yng, date, conceal, stage, d x s	1118	7	721.801	735.855	2.999	0.154
Cow yng, date	1118	4	728.938	736.958	4.099	0.089
Cow yng, date, stage	1118	5	728.844	738.873	6.014	0.034
Cow yng, date, stage, d x s	1118	6	728.130	740.170	7.312	0.018
Cow yng	1118	3	735.249	741.260	8.402	0.010
Cow yng, stage	1118	4	735.094	743.114	10.255	0.004

Table 6. Effect sizes and direction, odds ratios and 95% confidence intervals for covariates in best approximating model for Spotted Towhee nest survival along the Sacramento River, CA, 1994-2003.

Parameter	Estimate	Odds ratio	Odds ratio 95% CI
Cowbird young	2.399	11.01	3.16, 38.41
Date	-0.007	0.993	0.987, 0.999
Concealment	0.012	1.012	1.002, 1.021

Table 7. Working hypotheses and candidate models for Black-headed Grosbeak nest survival in the Sacramento valley, 1994-2003. μ represents random effect of "plot-year."

Model	Survive =
Global	NStg, Date, NStg X Date, NHt, NCon, HabR, Ag50, AgED50,Ag500, FDur, FInt, FTim, μ
Restoration	HabR, Ag500, NStg, Date, NStg X Date, μ
	HabR, μ
	HabR, Ag500, μ
	HabR, NStg, μ
	HabR, Date, μ
	HabR, Ag500, NStg μ
	HabR, Ag500, NStg, Date, μ
Temporal	NStg, Date, NStg X Date, μ
	Date, μ
Nest concealment	NCon, NHt, Date, NStg x Date, μ
	NCon, μ
	NHt, μ
	NCon, NHt, μ
	NCon, NHt, NStg, μ
	NCon, NHt, Date, μ
	NCon, NHt, NStg, Date, μ
Nest activity	NStg, Date, NStg X Date, μ
	NStg μ
	NStg, Date, μ
Agriculture	Ag50, AgED50,Ag500, NStg, Date, NStg x Date μ
	Ag50, μ
	AgED50, μ
	Ag500, μ
	Ag50, Ag500, μ
	Ag50, AgED50,Ag500, μ
	Ag50, AgED50,Ag500, NStg, μ
	Ag50, AgED50,Ag500, Date, μ

Table 7 (cont'd). Working hypotheses and candidate models for Black-headed Grosbeak nest survival in the Sacramento valley, 1994-2003. μ represents random effect of "plot-year" (cont'd).

Model	Survive =
Flood effects	FDur, FInt, FTim, HabR, NStg, Date, NStg x Date, μ
	FDur, μ
	FInt, μ
	FTim, μ
	FDur, FInt, FTim, μ
	FDur, FInt, FTim, HabR, μ
	FDur, FInt, FTim, HabR, NStg, Date, μ
Null	μ

Table 8. Best supported models for Black-headed Grosbeak nest survival in the Sacramento Valley, CA, 1994-2003.   Number of observations, number of parameters (K), AIC values, and weight of evidence (w_i).

Model	n	K	-2logL	AICc	Δ AICc	w_i
Median flood date	1723	3	1016.45	1022.46	0.00	.296
% ag, 500 m	1723	3	1018.90	1024.91	2.45	.087
Nestling stage	1723	3	1020.19	1026.19	3.74	.046
Null	1723	2	1026.19	1026.19	3.93	.042

Table 9. Effect sizes and direction, odds ratios and 95% confidence intervals for covariates in best approximating model for Black-headed Grosbeak nest survival in the Sacramento Valley, CA, 1994-2003.

Parameter	Estimate	Odds ratio	Odds ratio 95% CI
Median flood date	0.008	1.008	1.002, 1.014
% ag, 500 m	0.010	1.009	0.999, 1.021
Nestling stage	0.251	1.285	0.912, 1.811

APPENDIX B: FIGURES
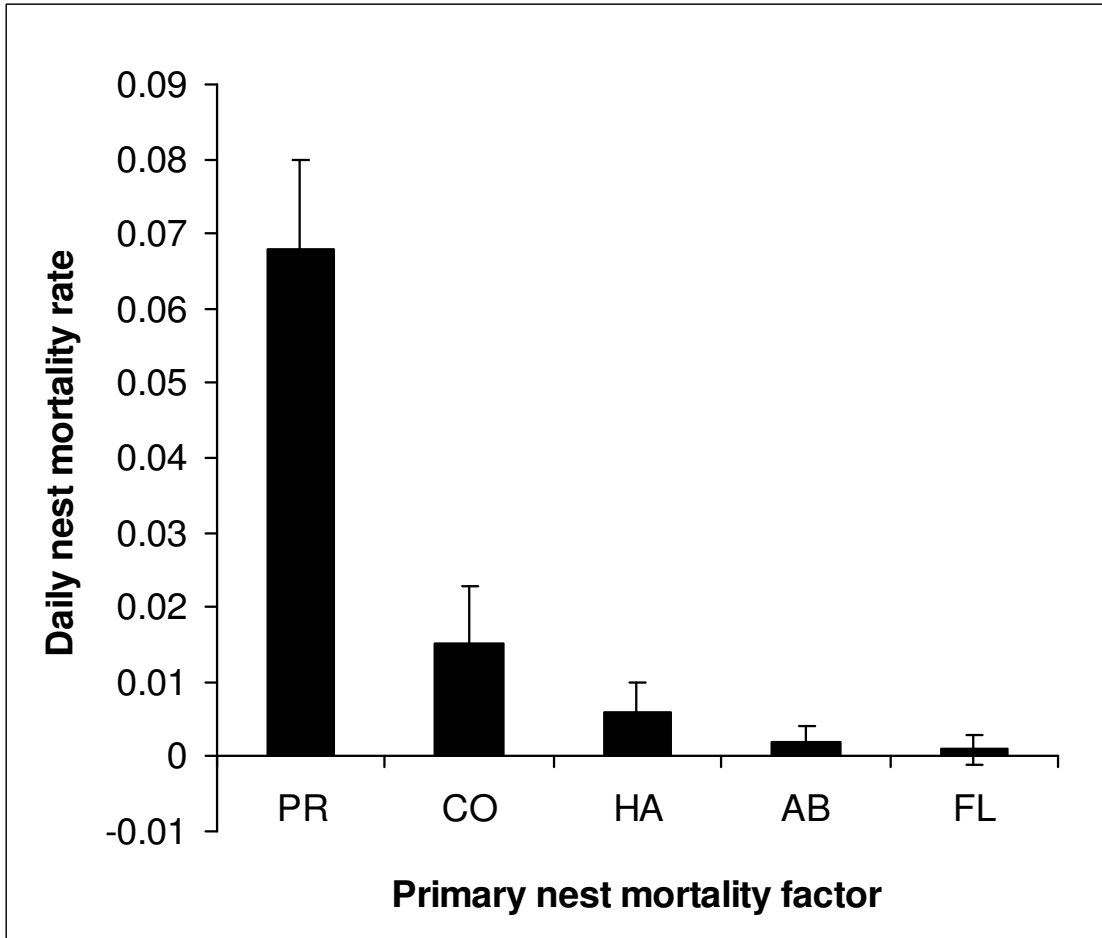
Figure 1. Daily nest mortality rates and 95 % confidence intervals by primary nest mortality factor -- predation (PR), Brown-headed Cowbird parasitism (CO), human activity (HA), abandonment (AB), and flooding (FL) -- for Spotted Towhees along the Sacramento River, California, USA, 1993-2003 (nest sample size above bars). Exposure days for each category were PR = 1933.5, CO = 1081.5, HA = 1017, AB = 983, FL = 975.5.
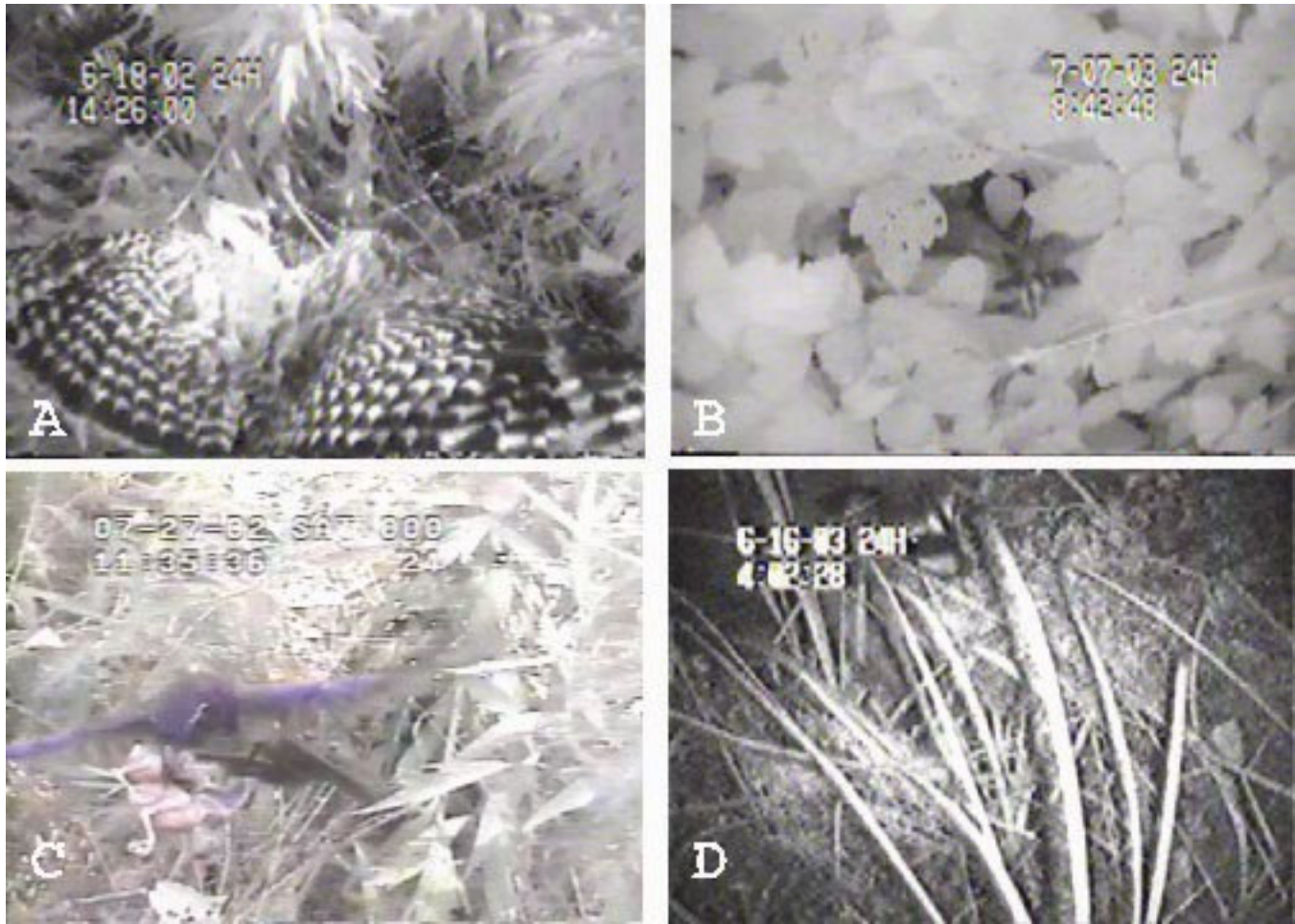
Figure 2. Videotaped images of Spotted Towhee nest predation events along the Sacramento River, California, USA: A) a Red-shouldered Hawk depredates two nestlings, B) a Brown-headed Cowbird female flings a nestling from an unparasitized nest, C) a Western Scrub-Jay departs from a nest with a nestling in its bill, D) a raccoon consumes two nestlings at the nest.
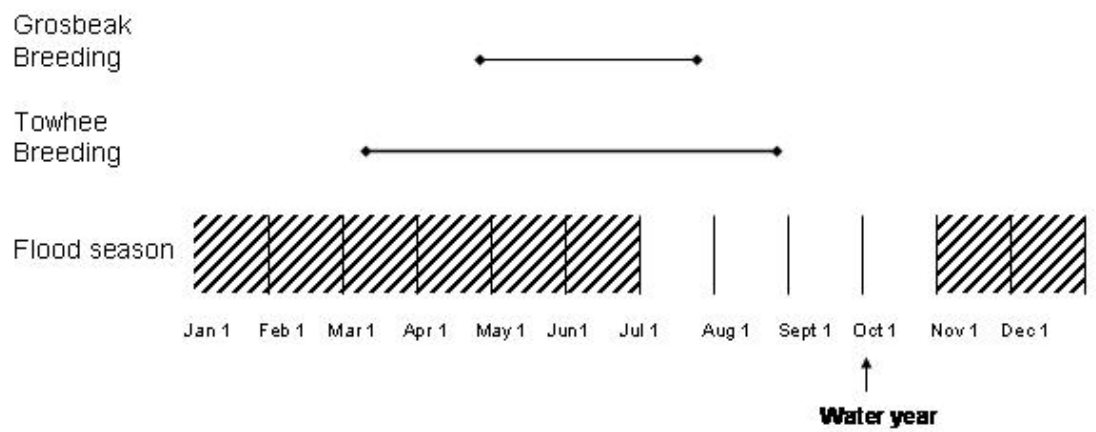
Figure 3. Schematic timeline of Black-headed Grosbeak and Spotted Towhee breeding seasons in relation to flood season in the Sacramento River Valley.
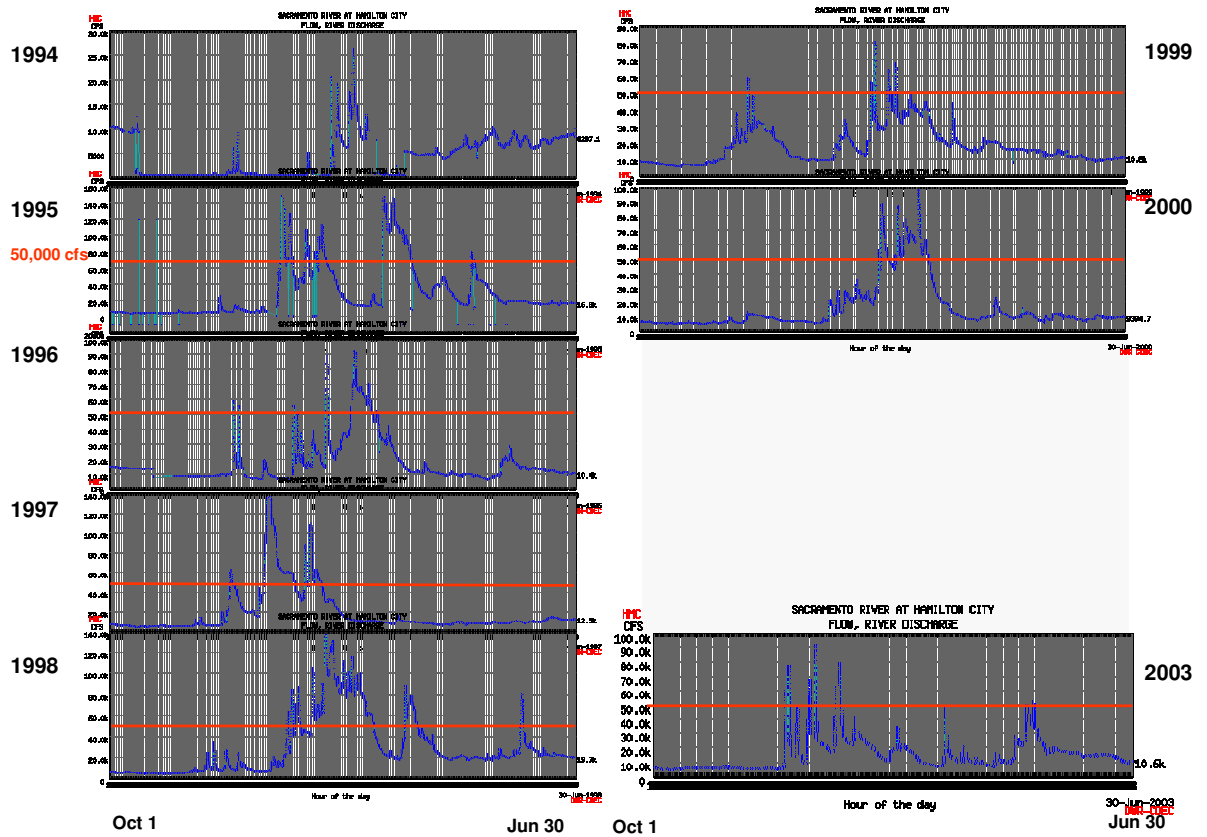
Sacramento River Hydrographs

Figure 4. Sacramento River hydrographs between October 1 and June 30, 1994-2003, based on hourly river discharge data. Horizontal line at 50,000 cubic feet per second (cfs) indicates flow rate at which study sites become inundated during high water events. Source: California Department of Water Resources (online custom graph plotter not working for years 2001 and 2002).
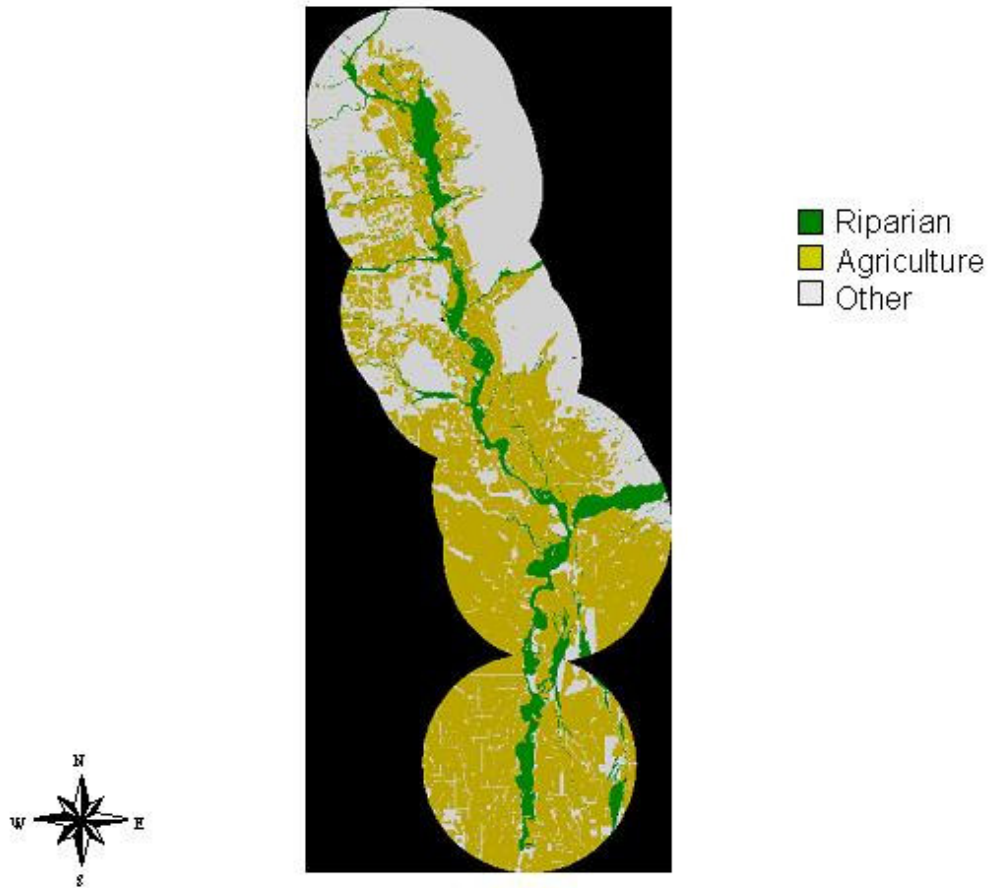
Figure 5. Landscape cover type of study region, middle Sacramento River Valley, CA, defined as "riparian" (restoration and forest combined), "agriculture," (row crop, orchard, rice) or "other." Based on CA Department of Water Resources data, 1998.
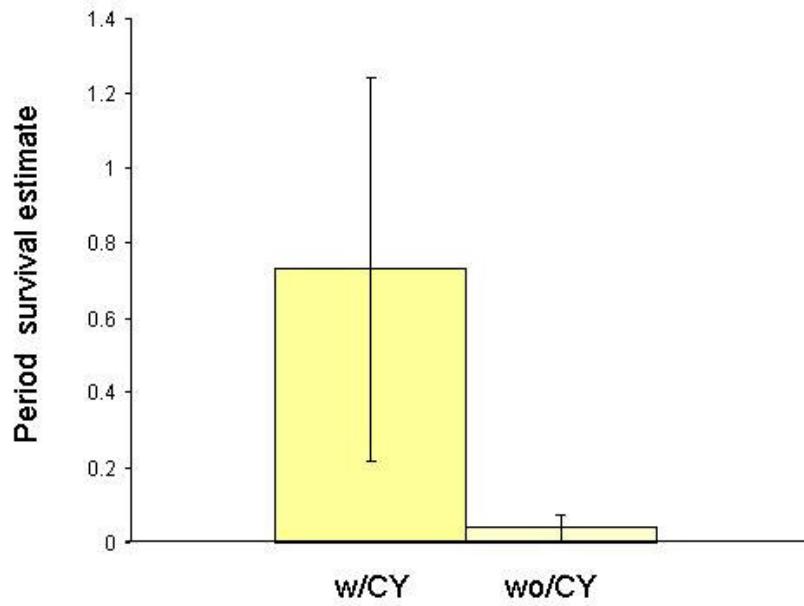
Figure 6. Spotted Towhee nest survival estimates along the Sacramento River, CA, 1994-2003, for nests with cowbird young, compared to nests without cowbird young. Error bars represent 95% confidence intervals.
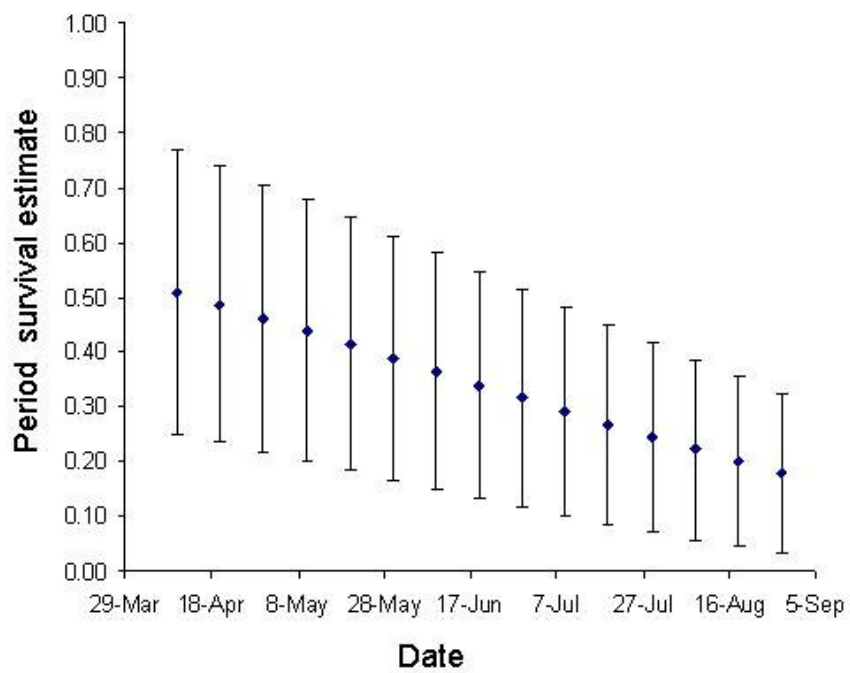
Figure 7. Model-based estimates of Spotted Towhee period nest survival along the Sacramento River, CA, 1994-2003, as related to calendar date.
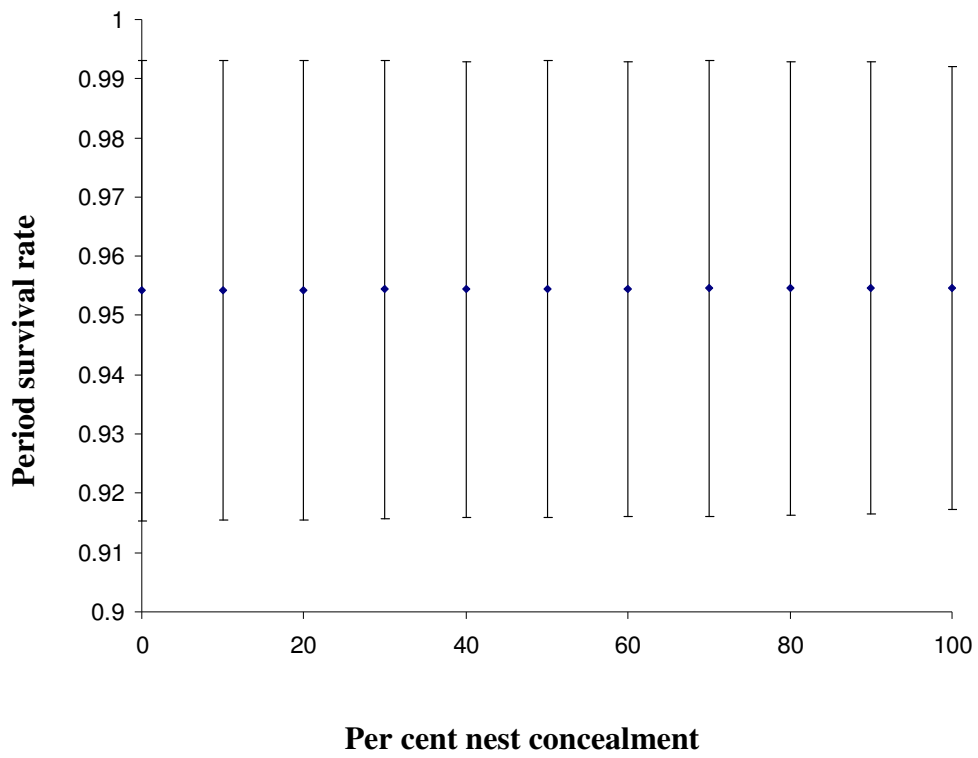
Figure 8. Model-based estimates of Spotted Towhee period nest survival along the Sacramento River, 1994-2003, as related to per cent nest concealment, based on 6 averaged ocular estimates.
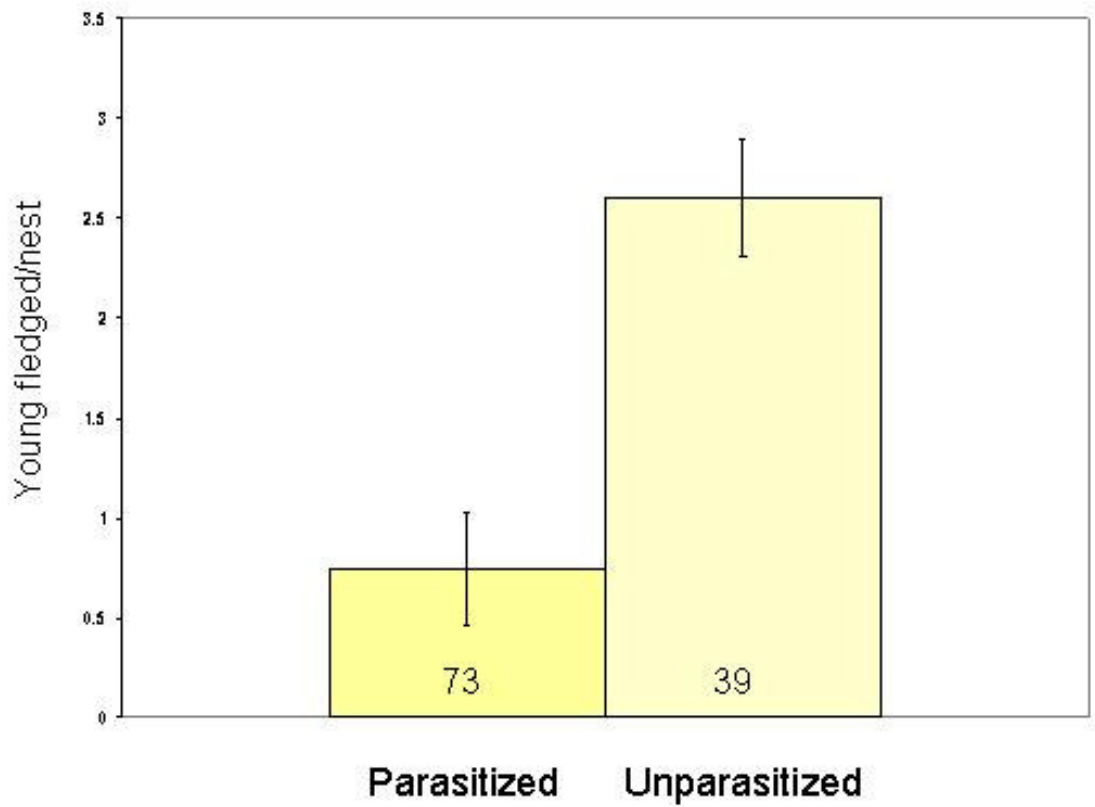
Figure 9. Comparison of number of Spotted Towhee young fledged from parasitized vs. unparasitized, of non-depredated nests along Sacramento River, CA, 1994-2003.
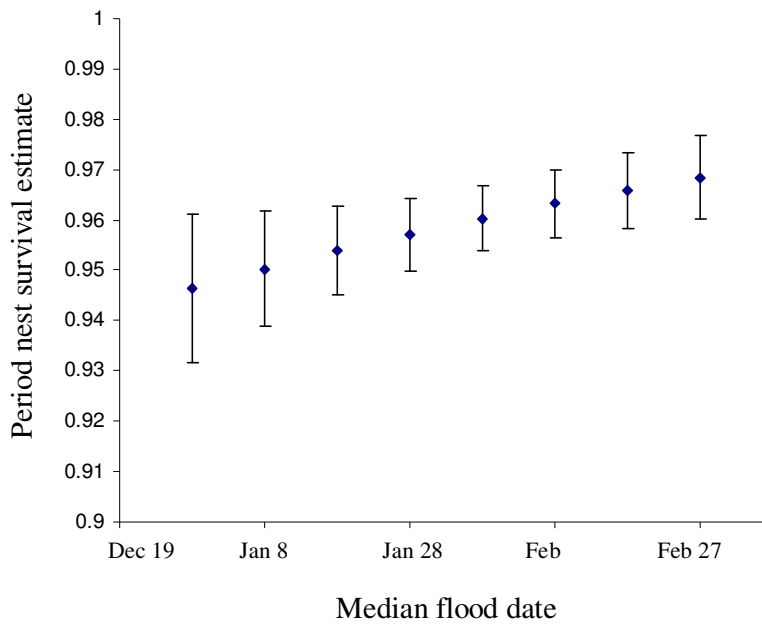
Figure 10. Model-based period nest survival estimates for Black-headed Grosbeak in Sacramento Valley, 1994-2003, in relation to median flood date.

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VITA

Stacy L. Small was born in the Ohio River Valley, at the confluence of the Beaver and Ohio Rivers on the Pittsburgh Low Plateau Section of the Appalachian Plateaus Province of Pennsylvania. Her love of rivers and swampy places developed in this region, and she pursued undergraduate studies in Ornithology, Restoration Ecology, and Political Economy and Social Change, earning a Bachelor's of Arts and Sciences at The Evergreen State College, Olympia, WA in 1994.

She went on to work for PRBO Conservation Science as a field intern, following color-banded Song Sparrows and Wrentits in the coastal scrub of west Marin County, California. It was there that she read the works of Margaret Morse Nice and was inspired to pursue a career as an avian ecologist. She stayed with PRBO as a staff biologist, shifting her focus to riparian systems. Her dissertation research developed as part of the PRBO Sacramento River Project, a long term restoration monitoring project, which she supervised for six years.

Stacy also plays the violin and has performed in numerous small orchestral ensembles around the U.S., including classical, opera, film, musical, experimental rock and folk ensembles.