RESEARCH ARTICLE

Does Restored Riparian Habitat Create Ecological Traps for Riparian Birds Through Increased Brown-Headed Cowbird Nest Parasitism?

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ABSTRACT

A growing concern among restoration ecologists is inadvertently creating ecological traps, yet identifying ecological traps is difficult, particularly over a large region and for an entire suite of species. Here we use an example to show that restoration ecologists can evaluate the risk of creating ecological traps. We reviewed the literature and synthesized data to evaluate the risk that restored riparian forests create ecological traps for riparian birds by attracting dense populations of the brood parasite, Brown-headed Cowbird (*Molothrus ater*; hereafter cowbird) in the Central Valley of California, U.S. We found that most riparian bird populations are not highly vulnerable to cowbird parasitism, that there were no differences in cowbird density or parasitism rates between restored and remnant riparian forests, and that the riparian bird community responded positively to restoration. We concluded that riparian restoration in California's Central Valley has a low risk of creating ecological traps through cowbird parasitism. We recommend that restoration ecologists consider the potential for creating an ecological trap early and throughout the restoration design and implementation process, and include plans to monitor species responses to restoration, both in restored areas and in source populations nearby, as well as any specific conditions associated with a potential trap.

Keywords: brood parasite, cowbird trapping, nest predation, population sink, seasonal fecundity

One of the goals for many restoration programs is to provide high quality habitat for wildlife, but restored sites can become ecological traps if they attract wildlife that ultimately experience reduced fitness (Battin 2004). Ecological traps are the result of habitat selection cues becoming decoupled from true habitat quality, and were initially associated with rapid anthropogenic habitat degradation (Gates and Gysel 1978). However, a growing number of researchers have begun to identify ecological traps associated with habitat restoration and conservation management practices, including butterflies in restored wetlands in the United States (Severns 2011), birds nesting in grasslands managed by grazing in Europe (Pakanen et al. 2011), and fish using fish ladders in rivers in South America (Pelicice and Agostinho 2008).

Identifying ecological traps is difficult, since it requires intensive research to show not just that the population is a sink (i.e. that reproduction rates are not high enough to offset mortality rates), but also that individuals prefer the trap to other higher quality habitat (Battin 2004). The difficulty is further compounded when considering restoration over large spatial scales that may affect an entire suite of species. Thus, restoration ecologists require an alternative approach, such as assessing the risk of creating an ecological trap. The restored riparian forests of the Central Valley of California, U.S. present an opportunity to examine the risk of ecological traps for a suite of riparian bird species over a large region. Over 95% of riparian forests have been lost in the region, which was once a vast mosaic of floodplain forest and wetlands, supported by the regular meandering and flooding of the Sacramento and San Joaquin rivers and their tributaries (Katibah 1984, RHJV 2004). In recent decades, state, federal, and private organizations have worked together to protect and restore riparian ecosystems by planting riparian vegetation, restoring or mimicking natural hydrology, and reconnecting floodplains and habitat fragments (RHJV 2004). While the goal of such projects is to provide functional riparian habitat, they could indirectly harm riparian bird populations if restored riparian habitat

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attracts dense populations of Brown-headed Cowbirds (*Molothrus ater*).

The Brown-headed Cowbird (hereafter cowbird) ranges from southeast Alaska throughout Canada and the United States, and south to central Mexico (Lowther 1993). Like the other members of the *Molothrus* genus, which range throughout the western hemisphere, it is infamous for its reproductive strategy of brood parasitism: laying eggs in the nests of at least 248 species and burdening host parents with raising their young (Lowther 2013). This strategy has been widely successful for cowbirds, which have greatly expanded their range over the past 200 years (Rothstein and Peer 2005). Because cowbirds regularly remove host eggs, and cowbird nestlings typically hatch earlier and outcompete their smaller nest-mates, cowbirds can reduce the quantity and quality of host offspring (Mayfield 1977, Ortega 1998, Lorenzana and Sealy 1999). Consequently, cowbirds have been implicated in the range-wide declines of many passerine birds (Mayfield 1977, Lowther 1993).

We evaluated the risk that riparian restoration in California's Central Valley creates ecological traps for riparian bird populations through the effects of cowbird nest parasitism. We review the literature and synthesize new data to address each of the following questions: 1) Which riparian bird species are most vulnerable to cowbird parasitism? 2) Are cowbird densities or parasitism rates higher in restored than remnant riparian areas? 3) Are Central Valley riparian areas likely to be sinks because of cowbird parasitism? and 4) Do riparian bird populations respond positively to habitat restoration despite potential cowbird impacts? We also review recommended restoration and management practices that can minimize the effects of cowbirds. Using this example, we discuss how restoration practitioners can evaluate the risk of creating ecological traps even in the absence of detailed demographic monitoring.

Which Central Valley Riparian Bird Species are Most Vulnerable to Cowbird Parasitism?

Cowbird parasitism reduces nest success for host species, yet it may not affect seasonal fecundity, the total number of offspring produced during the breeding season. Even if some nest attempts are parasitized, enough total offspring may still be produced by species that quickly abandon parasitized nests and rebuild (Ortega 1998) or species that are relatively large (> 16–20 g) and are able to raise their own young along with cowbird young (Lorenzana and Sealy 1999, Hosoi and Rothstein 2000), although additional breeding effort may come at the cost of reduced adult survival (Payne and Payne 1997). Seasonal fecundity impacts may also be minimized in species with relatively long breeding seasons and multiple nest attempts (Pease and Grzybowski 1995) or species that begin nesting much earlier than cowbirds (Ellison 1999). Thus, the effects of cowbird parasitism on seasonal fecundity will vary among species with different life histories, body sizes, and behavioral responses.

We assessed the relative vulnerability of 12 Central Valley riparian-associated bird species to cowbird nest parasitism. We included federal and state protected species, California Bird Species of Special Concern, and focal species identified by the Riparian Habitat and Central Valley joint ventures (RHJV 2004, CVJV 2006, Shuford and Gardali 2008). We also included Lazuli Bunting (*Passerina amoena*), which was reported as strongly declining in the Sacramento Valley (Gardali et al. 2006). We excluded cavity-nesting species (e.g., Bank Swallow, *Riparia riparia*), which are rarely parasitized by cowbirds (Strausberger and Ashley 1997). We reviewed the literature for each species to summarize: 1) parasitism frequency; 2) host adult mass; 3) ability to fledge host young with cowbird young; 4) likelihood of abandoning parasitized nests; and 5) migratory status, as a proxy for length of breeding season (Table 1).

The results of our literature review indicated that cowbirds rarely parasitize three of these 12 species, which are likely to be unsuitable hosts. Yellow-billed Cuckoos (*Coccyzus americanus*) have a very short incubation period, giving cowbird eggs little chance of hatching with the host chicks (Hughes 1999). Tricolored Blackbirds (*Agelaius tricolor*) nest in dense colonies, which may help repel cowbirds (Peer et al. 2005). In Black-headed Grosbeaks (*Pheucticus melanocephalus*), both parents incubate, rarely leaving the nest exposed to cowbirds (Ortega and Hill 2010). In addition, these species are larger than cowbirds and their nestlings are likely large enough to successfully compete with cowbird nestlings (Lorenzana and Sealy 1999).

Three species are frequent cowbird hosts, but are medium to large (> 16 g) and on average, are able to fledge at least one of their own young along with a cowbird: Blue Grosbeak (*Passerina caerulea*; Whitehead et al. 2000), Yellow-breasted Chat (*Icteria virens*; Whitehead et al. 2000, Eckerle and Thompson 2001), and Song Sparrow (*Melospiza melodia*; Arcese et al. 2002). A fourth species, Spotted Towhee (*Pipilo maculatus*), is also large, but to our knowledge only one study has quantified the effects of parasitism on nest success in this species, and found that they were frequently unable to fledge their own young with a cowbird (Small 2005, Small et al. 2007). However, Spotted Towhees, in addition to Song Sparrows, are also year-round residents, with long breeding seasons, multiple nest attempts, and multiple broods. Thus, we considered these four species have a relatively low vulnerability to parasitism.

The remaining five species are also frequent cowbird hosts, but are small (< 16 g), migratory with short breeding seasons, and on average fledge fewer than one of their own young in a parasitized nest: Lazuli Bunting (Greene et al. 1996, Gardali et al. 1998), Willow Flycatcher (*Empidonax*

Table 1. Expected vulnerability of 12 Central Valley, CA, riparian species to nest parasitism by Brown-headed Cowbirds.

Species	Parasitism frequency	Host adult mass (g)	Ability to fledge host young in a parasitized nest	Likelihood of abandoning/burying parasitized nest	Migratory status	Expected vulnerability	Conservation status				
							Federal	CA	BSSC	CVJV	RHJV
Brown-headed Cowbird[1]	—	Large (30–40)	—	—	Migrant	—					
Tricolored Blackbird[2]	Rare	Very large (40–70)	—	—	Resident	—			X		X
Yellow-billed Cuckoo[3]	Rare	Very large (55–65)	—	—	Migrant	—		SE		X	
Black-headed Grosbeak[4]	Rare	Very large (40–50)	—	—	Migrant	—				X	X
Spotted Towhee[5]	Common	Large (34–41)	Few (<1)[a]	Low (<10%)	Resident	Low				X	
Blue Grosbeak[6]	Common	Large (26–31)	Yes (>1)	Low(<10%)	Migrant	Low					X
Yellow-breasted Chat[7]	Common	Large (23–30)	Yes (>1)	Moderate (30%)	Migrant	Low			X	X	X
Song Sparrow[8]	Common	Medium (17–20)	Yes (>1)	Low (<10%)	Resident	Low				X	X
Lazuli Bunting[9]	Common	Small (13–18)	Few (<1)	Moderate (25%)	Migrant	High					
Willow Flycatcher[10]	Common	Small (11–14)	Few (<1)	High (50–60%)	Migrant	High	FE[b]	SE			X
Yellow Warbler[11]	Common	Small (9–11)	Few (<1)	High (60–70%)	Migrant	High			X	X	X
Common Yellowthroat[12]	Common	Small (9–10)	Few (<1)	Moderate (20–30%)	Migrant	High				X	X
Least Bell's Vireo[13]	Common	Small (7–10)	Few (<1)	Moderate (29%)	Migrant	High	FE	SE			X

Notes: Where available, data from California are presented. Scientific names of all species are presented in the text. Conservation status refers to federal and California endangered species (FE, SE), California Bird Species of Special Concern (BSSC; Shuford and Gardali 2008), Central Valley Joint Venture focal species (CVJV 2006), and Riparian Habitat Joint Venture Focal Species (RHJV 2004). Data sources include: [1]Lowther 1993; [2]Beedy and Hamilton 1999; [3]Hughes 1999; [4]Ortega and Hill 2010; [5]Greenlaw 1996, Small 2005, Small et al. 2007; [6]Whitehead et al. 2000, Lowther and Ingold 2011; [7]Whitehead et al. 2000, Eckerle and Thompson 2001; [8]Arcese et al. 2002; [9]Greene et al. 1996, Gardali et al. 1998; [10]Sedgwick and Iko 1999, Sedgwick 2000, Uyehara et al. 2000; [11]Lowther et al. 1999; [12]Guzy and Ritchison 1999; [13]Kus et al. 2010. Additional data on likelihood of abandoning nests obtained for several species from Hosoi and Rothstein 2000. [a]Data are available from only one study in the Sacramento Valley (Small 2005, Small et al. 2007). [b]Only the Southwestern subspecies of Willow Flycatcher has federal endangered status.

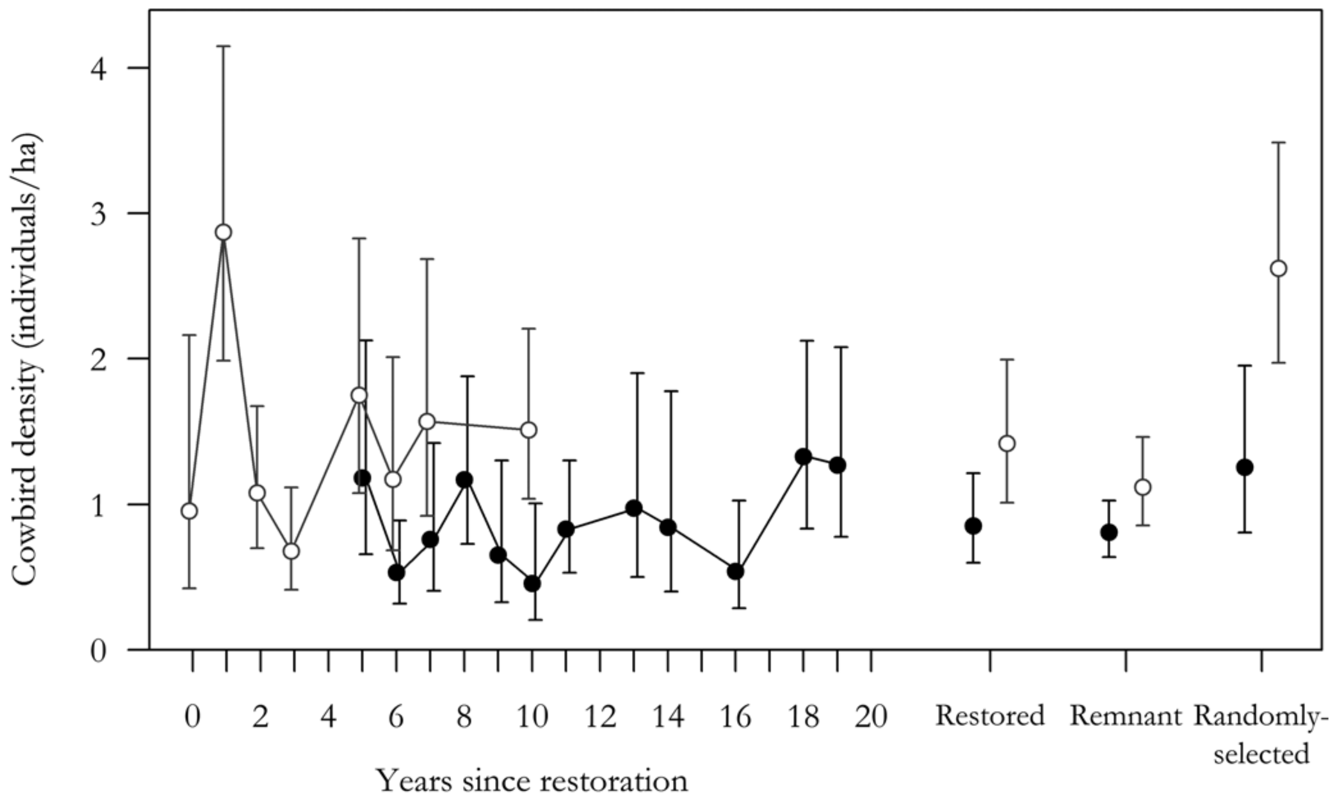

Figure 1. Mean Brown-headed Cowbird densities (individuals/ha) at remnant and restored riparian sites in the Sacramento River National Wildlife Refuge in the Sacramento Valley and the San Luis National Wildlife Refuge Complex in the San Joaquin Valley (2002–2012), and mean densities at randomly selected riparian points in both valleys (2012). Also shown are densities at restored sites with respect to year since restoration. Filled black points represent sites in the Sacramento Valley, and open points represent sites in the San Joaquin Valley.

traillii; Sedgwick and Iko 1999, Sedgwick 2000, Uyehara et al. 2000), Yellow Warbler (*Dendroica petechia*; Lowther et al. 1999), Common Yellowthroat (*Geothlypis trichas*; Guzy and Ritchison 1999), and Least Bell's Vireo (*Vireo bellii pusillus*; Kus et al. 2010). Cowbird parasitism results in high levels of nest failure in these species, reflected in their moderate to high likelihood of abandoning parasitized nests (summarized in Table 1). Thus, we considered these five species to be among the most vulnerable to cowbird parasitism.

Our vulnerability assessment indicates that not all Central Valley riparian bird populations are equally vulnerable to cowbird parasitism and will vary in the level of parasitism they can tolerate. While highly vulnerable populations may only tolerate parasitism rates under 30% (Laymon 1987), many populations may be able to tolerate parasitism rates of up to 60% (Smith 1999). Thus, the risk of an ecological trap will depend on the species in question, as well as the local rates of nest parasitism.

Are Cowbird Densities or Parasitism Rates Higher in Restored than Remnant Riparian Areas?

Between 2002 and 2012, we surveyed birds throughout the Central Valley, including ten sites in the Sacramento River National Wildlife Refuge (NWR) in the Sacramento Valley and 11 sites in the San Luis NWR Complex in the San Joaquin Valley. These sites included a total of 103 survey points in remnant riparian areas and 73 survey points in restored riparian areas, which were always at least 200 m apart. Remnant riparian areas were those that existed prior to restoration efforts on the Sacramento and San Joaquin rivers and in which no active restoration has occurred. In contrast, restored areas were the result of active planting and other management activities, and were in agriculture prior to their restoration. They varied in planting density and time since restoration (see Gardali and Holmes 2011), representing a broad range of riparian habitat available to birds.

In 2012, we also surveyed 60 randomly selected points in riparian vegetation (regardless of restoration status) within 2 km of the main stem of each river, including approximately 160 river-km of the Sacramento River from Red Bluff to Colusa and 320 river-km of the San Joaquin River from Friant Dam to the confluence with the Stanislaus River. The 2 km buffer captured most of the floodplain of each river and the majority of extant riparian vegetation. The minimum distance between points was 224 m, but the average distance between points was > 1 km.

We used point count methods (Ralph et al. 1993, 1995) to survey all points twice during the breeding season (late April through early July), with skilled observers recording the estimated distance to all birds detected during a five-minute period. We used standard distance-sampling methods to fit detection functions to our data and estimate the density of cowbirds in restored and remnant riparian areas on the wildlife refuges, as well as at the randomly selected points in each valley (Buckland et al. 2001). Analyses were conducted using R (R Core Team, Vienna, Austria) with the package Distance (Miller 2012). We treated points as independent replicates, but recognize that points within remnant and restored sites may violate assumptions of independence. Thus, the variance of our cowbird density estimates may be underestimated (Buckland et al. 2001), but should be similarly underestimated at both remnant and restored sites. Further, comparisons between density estimates at restored and remnant sites will be conservative, since the true 95% confidence interval will actually be larger. Our randomly selected points are independent and allow for more general inference to the entire region.

At the randomly selected riparian points, cowbird densities averaged 1.26 birds/ha along the Sacramento River (95% CI: 0.81–1.95), and 2.62 birds/ha along the San Joaquin River (95% CI: 1.97–3.49; Figure 1). We hypothesize that the higher cowbird densities along the San Joaquin River reflect the relatively small amount of riparian vegetation along this river, such that survey points are more likely to fall closer to agricultural or dairy operations than points along the Sacramento River. At the remnant riparian sites located in the Sacramento River NWR and the San Luis NWR Complex, cowbird densities averaged 0.81 (95% CI: 0.64–1.03) and 1.12 (95% CI: 0.86–1.46) birds/ha, respectively, suggesting that cowbird densities are lower in areas of more extensive riparian vegetation. In comparison, at the restored riparian sites in the Sacramento River NWR and the San Luis NWR Complex, cowbird densities averaged 0.85 (95% CI: 0.60–1.22) and 1.42 (95% CI: 1.01–1.99) birds/ha, respectively, similar to densities at the remnant riparian sites. There was also no clear pattern in cowbird density as a function of time since restoration (Figure 1). At restoration sites on the Sacramento River, the 95% confidence intervals in almost all years post-restoration overlapped with mean estimates for both the remnant and randomly-selected points. At restoration sites on the San Joaquin River, cowbird densities were sometimes slightly higher than at remnant sites, but generally similar or slightly lower than the estimate from the randomly selected sites. We found no evidence that restored sites attracted unusually high densities of cowbirds.

Table 2. Cowbird parasitism rates in remnant and restored habitat for suitable hosts with the largest sample sizes. (a) Sacramento River National Wildlife Refuge (1993–2003). (b) San Joaquin River National Wildlife Refuge (2007–2009). Shown are the percent of parasitized nests (%), the total number of nests monitored with known parasitism status (n), and the results of a Fisher exact test for a difference in the parasitism rates in remnant and restored riparian areas (*p*). Scientific names of all species are presented in the text. **p* < 0.05.

(a)

Species	Remnant		Restored		
	%	n	%	n	*p*
Spotted Towhee	47.2	161	25.6	125	<0.001*
Black-headed Grosbeak	16.2	204	14.2	141	0.651
Blue Grosbeak	16.7	6	50.0	18	0.341
Lazuli Bunting	59.2	49	70.0	70	0.244
Common Yellowthroat	61.5	13	40.0	10	0.414
Lesser Goldfinch	0.0	14	7.1	14	1.000
American Goldfinch	28.6	7	31.7	41	1.000
Total	32.8	454	30.5	419	0.513

(b)

Species	Remnant		Restored		
	%	n	%	n	*p*
Spotted Towhee	33.3	12	25.4	71	0.724
Song Sparrow	23.1	26	27.2	136	0.810
Red-winged Blackbird	25.0	12	0.0	40	0.010*
Lesser Goldfinch	0.0	4	20.0	20	1.000
American Goldfinch	16.7	6	26.5	68	1.000
Total	23.3	60	23.0	335	1.000

Because nest parasitism rates may be correlated with cowbird densities (Hoover and Brittingham 1993, Uyehara et al. 2000), we also expected to find little difference in rates of nest parasitism between restored and remnant riparian sites. In the Sacramento River NWR (1993–2003) and the San Joaquin River NWR (2007–2009), we searched for and monitored nests of open-cup, understory-nesting species that are parasitized by cowbirds. Using standard protocols (Martin and Geupel 1993, Martin et al. 1997), we checked nests on average every three days, recording nest contents and parasitism status. We calculated parasitism rates in remnant and restored habitat within each refuge for suitable host species with the largest sample sizes, including six of the species discussed in the previous section as well as Red-winged Blackbird (*Agelaius phoeniceus*), Lesser Goldfinch (*Carduelis psaltria*), and American Goldfinch (*Carduelis tristis*). The only significant differences between parasitism rates in remnant and restored habitat were for Spotted Towhee in the Sacramento

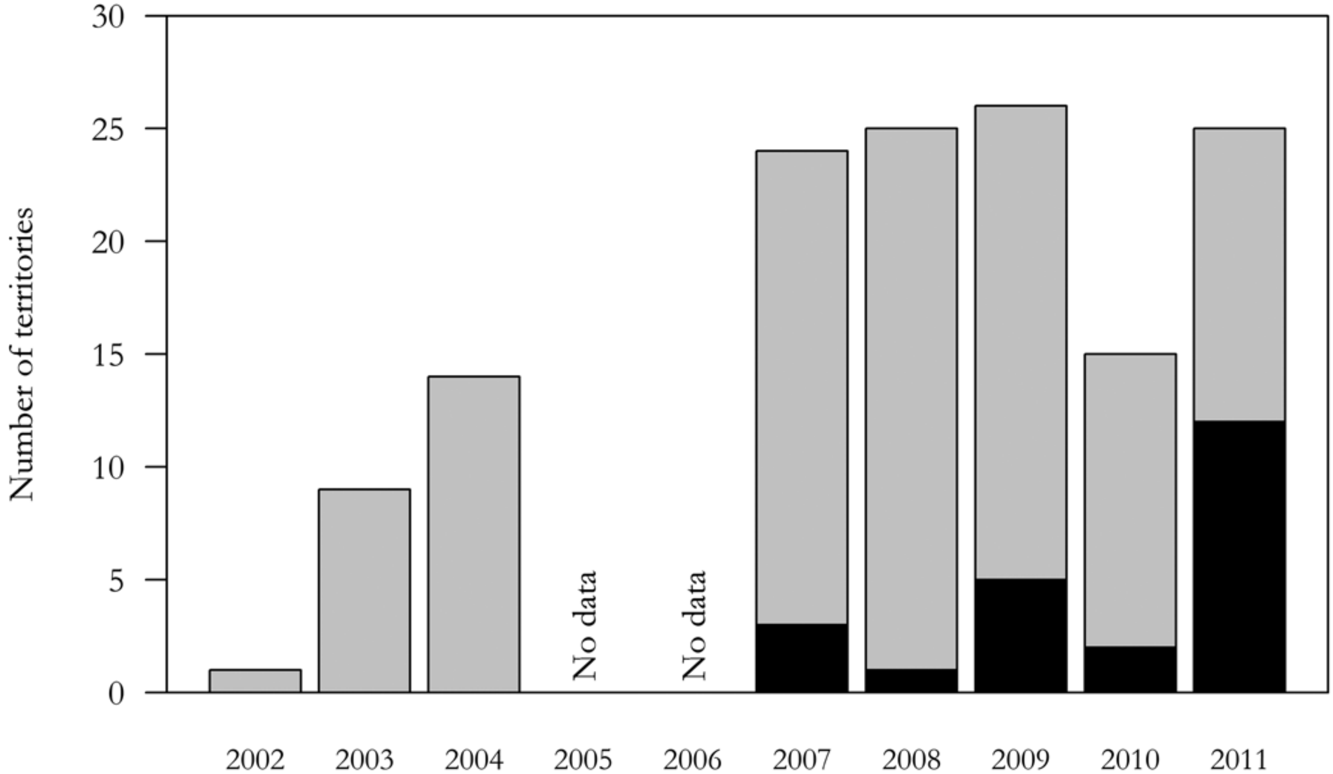

Figure 2. Increase in the total number of Yellow Warbler territories in the San Joaquin River National Wildlife Refuge (2002–2004, 2007–2011) including both remnant (gray) and restored (black) riparian sites. Note: No data were available in 2005–2006, and survey effort in restored sites was reduced in 2010.

River NWR (Fisher's exact test, $p < 0.001$) and Red-winged Blackbird in the San Joaquin River NWR ($p = 0.010$), both of which had higher parasitism rates in the remnant riparian habitat (Table 2). Combining all species, we found no significant difference between remnant and restored sites in the Sacramento River NWR ($p = 0.513$) or the San Joaquin River NWR ($p = 1.000$). The similarity in cowbird density and parasitism rates in restored and remnant sites suggests that cowbirds do not pose a greater threat in restored riparian areas.

Are Central Valley Riparian Areas Likely to be Sinks Because of Cowbird Parasitism?

Although cowbirds are not a greater threat in restored than remnant sites, cowbirds could be heavily impacting birds in both types of riparian habitat. For example, Lazuli Bunting populations in the Sacramento Valley have high cowbird parasitism rates (> 60%) and low reproductive success (0.33 fledglings/nest) in both remnant and restored riparian (Table 2; Gardali et al. 1998). Declining population trends in the Sacramento Valley further suggest these populations are sinks (Gardali et al. 2006). Similarly, Small et al. (2007) found that Spotted Towhee populations in the Sacramento Valley were also likely to be sinks. However, if riparian bird populations in the Central Valley are sinks, there are several reasons why cowbird parasitism may not be the primary cause for many species. First, except for Lazuli Bunting, cowbird parasitism rates were far below the estimated 60% maximum tolerable rate (Table 2; Smith 1999), and cowbird populations in California are not increasing (Sauer et al. 2012), suggesting they are not a serious current or imminent threat to most Central Valley riparian bird populations. Second, nest predation rates are likely to play a significant role in creating sink populations. Several studies have identified nest predation as having a greater influence on reproductive success than nest parasitism (e.g., Ellison 1999, Sedgwick and Iko 1999, Grzybowski and Pease 2000), such that some populations would be sinks even without any cowbird parasitism (Trine 1998, Fletcher et al. 2006). Indeed, for Spotted Towhee populations in the Sacramento Valley, Small et al. (2005, 2007) found that despite a 38% parasitism rate and few host fledglings produced per parasitized nest, the primary limiting factor was nest predation.

Riparian bird populations may be limited by nest predation, as for Spotted Towhee, or cowbird parasitism, as appears to be the case for Lazuli Bunting, but high rates of nest predation and parasitism are both common symptoms of a larger threat: habitat loss and fragmentation. Since cowbirds are most abundant near anthropogenic food sources (Goguen and Mathews 1999) and parasitism rates are highest in fragmented habitat (Robinson et al. 1995), the conversion of riparian habitat to anthropogenic land uses simultaneously reduces available habitat and increases cowbird pressure. Habitat fragmentation has also led to the loss of large predators and growth of meso-predator populations (Ortega 1998), which contribute to high nest-predation rates in habitat fragments (Robinson and Wilcove 1994). Consequently, habitat loss and fragmentation, not cowbirds or nest predators, are the primary causes of many bird population declines and the ultimate factors limiting population growth (Whitfield and Sogge 1999, Kus and Whitfield 2005, Rothstein and Peer 2005). Habitat restoration is therefore more likely to alleviate the risk of nest predation and parasitism than create a population sink or ecological trap.

Do Riparian Bird Populations Respond Positively to Habitat Restoration?

If restoration indirectly harmed riparian bird populations by attracting dense populations of cowbirds, we might expect these populations to respond negatively to restoration. However, riparian restoration projects in the Sacramento Valley have resulted in dramatic increases in the local population sizes of most bird species (Gardali et al. 2006, Golet et al. 2008). Local population increases alone do not rule out the possibility of a sink or trap, since they could reflect the immigration of birds from nearby source habitats (Battin 2004). However, population increases at the nearby remnant riparian sites were also observed, suggesting instead that restoration may have benefitted bird communities throughout the region (Gardali et al. 2006). Further, there were no differences in nest survival between remnant and restored sites (Small et al. 2007), indicating that remnant and restored sites function equally well as breeding habitat. A notable exception is Lazuli Bunting, which declined in both remnant and restored riparian sites in the Sacramento Valley (Gardali et al. 2006). We hypothesize that these declines may reflect a combination of nest predation, parasitism, and more specific habitat needs that are not yet being met, such as a shrub layer with sufficient forest openings (Greene et al. 1996, Scott et al. 2003).

In the San Joaquin Valley, we documented the re-establishment and subsequent increase of Yellow Warblers following restoration at the San Joaquin River NWR (Figure 2). We considered Yellow Warblers to be highly vulnerable to cowbird parasitism (Table 1), and while they were once a common breeder in the Central Valley (Grinnell and Miller 1944), they had been largely extirpated from the region (RHJV 2004). The discovery of a breeding pair on the refuge in 2002 sparked efforts to monitor the population, and during the breeding seasons of 2002–2004, we searched for Yellow Warbler nests and mapped Yellow Warbler territories. In June 2007–2011 we specifically searched for singing Yellow Warbler males defending territories, albeit with reduced effort in 2010 in restored areas. The number of Yellow Warbler territories has steadily increased since 2002, in both restored and remnant areas (Figure 2). The strong positive response of riparian birds to habitat restoration supports the conclusion that habitat loss is a major limiting factor for most riparian bird populations in the Central Valley.

Recommended Restoration and Management Practices for Minimizing Cowbird Impacts

Restoring and maintaining forest habitat are commonly recommended as the best long-term solutions to reducing cowbird impacts (Robinson et al. 1993, Chace et al. 2005). However, there are several specific recommendations that restoration practitioners can adopt to minimize the risk of creating an ecological trap. These include improving the continuity of large tracts of habitat, widening narrow corridors, and minimizing edge habitat (Robinson et al. 1993, Ortega 1998, Chace et al. 2005, Rothstein and Peer 2005), which may have the added benefit of reducing nest predation rates (Paton 1994, Robinson et al. 1995). Within forested habitats, Staab and Morrison (1999) advise managing for a dense shrub layer, where host nests may be more difficult for cowbirds to find. Another approach is to minimize the availability of nearby cowbird food sources, such as those provided by agricultural areas, livestock, golf courses, bird feeders, and camp grounds (Goguen and Mathews 1999, Uyehara et al. 2000, Chace et al. 2005). If cowbird food sources are abundant, cowbirds may be able to saturate even the highest quality forest habitat (Robinson et al. 1993). Eliminating grazing and mowing near riparian areas is recommended, particularly during the breeding season, as well as relocating or consolidating dairies and feedlots (Laymon 1987, Ortega 1998, Goguen and Mathews 1999).

A frequently adopted management approach is trapping and killing adult cowbirds. However, it is strongly recommended that cowbird control be used only as a short-term measure for small, at-risk populations that are heavily impacted by nest parasitism, and should never be used as mitigation for permanent habitat loss (Robinson et al. 1993, Ortega 1998, Rothstein and Peer 2005). Trapping may only be effective over the short-term because cowbirds disperse widely and will quickly recruit into areas where cowbirds have been removed (Decapita 2000, Griffith and Griffith 2000, Rothstein and Peer 2005). Thus, trapping must continue annually, and may not be cost-effective in the long term. Further, widespread trapping may select for cowbirds that avoid traps, further decreasing effectiveness

(Rothstein and Peer 2005). Trapping may also prevent host species from developing defenses against nest parasitism (Kus and Whitfield 2005, Peer et al. 2005). Finally, cowbird traps have inadvertently captured and killed non-target species, including endangered ones (Terpening 1999, Rothstein and Peer 2005).

Short-term cowbird trapping may be helpful in stabilizing highly vulnerable populations, such as the Least Bell's Vireo, for which cowbird trapping resulted in increased reproductive success and population growth (Kus and Whitfield 2005). However, trapping programs should be regularly evaluated for effectiveness, and clear goals should be set for when trapping can stop (Ortega 1998, Kus and Whitfield 2005, Rothstein and Peer 2005). Management decisions must continually weigh the costs and benefits of continuing to trap against putting those funds toward the other management recommendations above (Rothstein and Peer 2005).

Conclusions

Although identifying ecological traps is difficult without detailed demographic data, we recommend considering the risk of creating an ecological trap early and throughout the restoration design and implementation process. This includes adopting recommended restoration practices for minimizing risk, identifying ecological traits that may put certain species at increased risk (e.g., vulnerability to brood parasitism), monitoring changes in risk factors following restoration (e.g., cowbird density), and monitoring the response of vulnerable populations at restoration sites and nearby reference sites.

Applying this process to the restored riparian habitat in California's Central Valley, we concluded that the risk of restoration having created ecological traps through cowbird parasitism was low. Aside from small, already endangered populations, there is little evidence that cowbirds are a serious threat to most bird populations (Rothstein and Peer 2005). Further, there was no difference in cowbird density or parasitism rates between restored and remnant sites, and there was a strong positive response in riparian bird populations to restoration. Thus, the threat of cowbird parasitism should not hinder riparian restoration efforts in California's Central Valley, and we recommend continued work to restore riparian habitat, while keeping in mind the recommended practices for minimizing cowbird impacts. In other regions, particularly those with larger tracts of remnant riparian forest that may have substantially lower cowbird densities and parasitism rates than observed here, we recommend applying this process to examine the local risk of creating ecological traps in restored riparian habitat.

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