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Management of the brown-headed cowbird: implications for endangered species and agricultural damage mitigation

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Abstract: The brown-headed cowbird (*Molothrus ater*; cowbird) is unique among North American blackbirds (Icteridae) because it is managed to mitigate the negative effects on endangered songbirds and economic losses in agricultural crops. Cowbird brood parasitism can further affect species that are considered threatened or endangered due to anthropogenic land uses. Historically, cowbirds have often been culled without addressing ultimate causes of songbird population declines. Similar to other North American blackbirds, cowbirds depredate agricultural crops, albeit at a lower rate reported for other blackbird species. Conflicting information exists on the extent of agricultural damage caused by cowbirds and the effectiveness of mitigation measures for application to management. In this paper, we reviewed the progress that has been made in cowbird management from approximately 2005 to 2020 in relation to endangered species. We also reviewed losses to the rice (*Oryza sativa*) crop attributed to cowbirds and the programs designed to reduce depredation. Of the 4 songbird species in which cowbirds have been managed, both the Kirtland's warbler (*Dendroica kirtlandii*) and black-capped vireo (*Vireo atricapilla*) have been removed from the endangered species list following population increases in response to habitat expansion. Cowbird trapping has ceased for Kirtland's warbler but continues for the vireo. In contrast, least Bell's vireo (*V. bellii pusillus*) and southwestern willow flycatcher (*Empidonax traillii extimus*) still require cowbird control after modest increases in suitable habitat. Our review of rice depredation by cowbirds revealed models that have been created to determine the number of cowbirds that can be taken to decrease rice loss have been useful but require refinement with new data that incorporate cowbird population changes in the rice growing region, dietary preference studies, and current information on population sex ratios and female cowbird egg laying. Once this information has been gathered, bioenergetic and economic models would increase our understanding of the damage caused by cowbirds.

Key words: black-capped vireo, brown-headed cowbird, crop depredation, *Empidonax traillii extimus*, endangered species conservation, Kirtland's warbler, least Bell's vireo, *Molothrus ater*, *Setophaga kirtlandii*, southwestern willow flycatcher, *Vireo atricapilla, Vireo bellii pusillus*

The brown-headed cowbird (*Molothrus ater*; cowbird; Figures 1 and 2) is an obligate avian brood parasite native to North America (Peer et al. 2017). Through the 1980s, most research on cowbirds focused on questions regarding basic biology and coevolutionary interactions with hosts. In the 1980s through the early 2000s, the research focus shifted to cowbird management in relation to threatened and endangered species (Rothstein and Peer 2005). Rothstein and Peer (2005) brought attention to the misinformation regarding cowbirds and endangered species management. In the last 15 years, a more progressive management approach has been used with greater success (Cooper et al. 2019, Stanton et al. 2019).

Because cowbirds associate with other blackbirds (Icteridae) and are prone to consume agricultural crops, they are also managed to mitigate crop damage, most notably in the southern rice (*Oryza sativa*) growing region of the United States. Cummings et al. (2005) estimated blackbird damage to rice in Texas, Louisiana, Missouri, Arkansas, and California,

Figure 1. Female brown-headed cowbird (*Molothrus ater*; *photo courtesy of B. Peer*).

Figure 2. A least Bell's vireo (*Vireo bellii pusillus*) nest that has been parasitized by a brown-headed cowbird (*Molothrus ater*; *photo courtesy of B. Kus*).

USA in 2001 at $21.5 million USD. However, the amount of damage caused by cowbirds compared to more common blackbirds (e.g., red-winged blackbirds; *Agelaius phoeniceus*) is poorly documented, and the models generated to reduce cowbird crop depredation require revision (Peer and Abernathy 2017). From 2009 to 2015, 3.4 million cowbirds were killed under the auspices of crop protection in Louisiana (United States Department of Agriculture [USDA] Animal and Plant Health Inspection Service [APHIS] 2015). In comparison, cowbird control to benefit the endangered Kirtland's warbler (*Setophaga kirtlandii*) removed 158,555 cowbirds in Michigan, USA between 1972 and 2014 (Cooper et al. 2019).

Cowbird control to reduce crop damage has received less research attention compared to endangered species management. As such, additional research is needed to justify the continued control measures. In this paper, we update the progress on cowbird and endangered species research and management from approximately 2005 to 2020 and point out the need for additional information and updated modeling for agricultural-related management.

Methods

We reviewed the literature primarily for research that had been conducted on cowbird control for endangered and threatened species after 2005 to November 11, 2020 in North America. In addition to reviewing published papers, we included unpublished reports and found additional references using Google Scholar and searched for terms such as brown-headed cowbird, Kirtland's warbler, black-capped vireo (*Vireo atricapilla*), least Bell's vireo (*V. bellii pusillus*), and southwestern willow flycatcher (*Empidonax traillii extimus*). Similarly, we reviewed the cowbird–rice issue by searching for relevant papers and used the search terms brown-headed cowbird, blackbirds, and rice depredation. We did not limit the time frame of this search.

Results and discussion

Cowbird control to manage endangered and threatened species

Avian brood parasites are linked to their host populations. In the case of specialist brood parasites, the population-level effects are generally not as significant because the parasites are typically less common than their hosts and become even less common if their hosts decline (Rothstein and Robinson 1998). Furthermore, these hosts have coevolved with the parasite to minimize the negative effects of parasitism (Rothstein and Robinson 1998).

In contrast, generalist parasites such as the female cowbird that do not specialize on a given host species (Alderson et al. 1999, Strausberger and Ashley 2005) can potentially have a negative effect on smaller host populations (Rothstein and Robinson 1998). Cowbirds do not pose a conservation threat in most of their range, and the vast majority of host populations are not at risk from parasitism (Ortega et al. 2005). Hosts that are currently at risk can be linked directly to human activity because any asymmetric relationships between cowbirds and their hosts that would have alone led to host extinctions must have occurred long ago (Rothstein and Peer 2005) because cowbirds have been in North America for about 1 million years (Rothstein et al. 2002).

Currently, there are 4 host populations that are or recently have been the focus of cowbird control: Kirtland's warbler in Michigan; black-capped vireo in Texas and Oklahoma, USA, and in Mexico; the southwestern willow flycatcher in several states; and the least Bell's vireo in California, USA. Cowbird culling has been the most frequent response to management of these endangered species (Rothstein and Peer 2005). Culling initially benefits individual hosts that may have otherwise raised cowbirds instead of their own young, but the long-term benefits to the population without habitat restoration have been mixed (Rothstein and Peer 2005).

Reducing cowbird populations using lethal methods is a common management strategy for human–wildlife conflicts because in the minds of constituents, dead birds cannot parasitize nests or depredate crops (Peer et al. 2003; B. D. Peer, Western Illinois University, personal observation). These actions are much easier than addressing the larger, more complex issue that is central to the decline of every one of these endangered species, which is loss of habitat, and habitat restoration takes time and does not produce immediate results. Rothstein and Peer (2005) described the shortcomings of some management actions involving cowbirds and endangered species. They recommended that once habitat has been restored and populations of endangered host species have increased substantially, cowbird trapping should be experimentally reduced to determine whether enlarged host populations could sustain renewed parasitism. Below we summarize the current status of these management programs for each host population.

Kirtland's warbler

Kirtland's warbler was the subject of the first cowbird management program and is likely the most well-known endangered songbird in the United States. For this reason, we devoted extra attention to its long history of management. Unlike other North American birds endangered by cowbird parasitism, the Kirtland's warbler has historically had a very low population size and a limited breeding range (Bocetti et al. 2020). The warbler's unusually limited range is related to habitat specialization with nesting largely limited to a small portion of the large range of Jack pine (*Pinus banksiana*) forests 5–23 years after a fire (Bocetti et al. 2020). The species was not described until 1851, and its nesting grounds in northern lower Michigan were not found until 1903 (Wood 1904). Some of the first records of nesting showed that cowbird parasitism was occurring as early as the 1920s (Leopold 1924).

Mayfield (1960) published a complete census of the warbler that was designed to be done every 10 years starting in 1951. The first census recorded 432 singing males and the second in 1961 found 501. The third census revealed only 201 singing males in 1971 (Mayfield 1972). Data from 1963 to 1971 indicated that cowbird parasitism had increased to about 67% of warbler nests compared to 48% from 1903 to 1949 (Walkinshaw 1983).

Cowbird trapping and removal by federal, state, and private agencies began in 1972 and rapidly intensified over the species' entire range within a few years (Kelly and DeCapita 1982). This was the first large-scale government-sponsored cowbird control program to aid any endangered species, although there had been limited local cowbird trapping in the 1960s undertaken by private individuals concerned with the warbler's status (Walkinshaw 1983). To further boost nesting success, blue jays (*Cyanocitta cristata*), which are nest predators, were removed and relocated at least during the early years of cowbird control (Shake and Mattsson 1975). The warbler was placed on the first endangered species list in 1967, and the recovery plan listed a population of 1,000 breeding pairs as the recovery goal (Byelich et al. 1976).

Intensive cowbird control continued after 1972, resulting in 98,427 cowbirds euthanized by 1995 (DeCapita 2000) and thousands more after that (Cooper et al. 2019). Data on warbler productivity showed that the number of young produced per nest increased substantially after cowbird control reduced parasitism to nearly zero (Kelly and DeCapita 1982). However, the population hovered at around 200 singing males for the first 18 years of cowbird control (DeCapita 2000).

The warblers began to increase rapidly in the late 1980s by occupying a large tract of new suitable habitat that started to become available because of an intended controlled fire in 1980, known as the Mack Lake Burn, which went out of control and burned 10,500 ha, >40 houses, and killed 1 person (Simard et al. 1983). This event effectively ended the controlled burn program. However, the increase in the warbler population to >700 singing males by 1995 was due largely to birds breeding in new habitat created by the Mack Lake Burn (DeCapita 2000). By 2000, the 5–23 post-fire window for suitable warbler habitat was ending, but land managers learned to plant Jack pines after logging operations in a way that mimicked the spatial pattern of young trees that occurs naturally after a fire (Michigan Department of Natural Resources [MDNR] et al. 2015). The rapid increase in the warbler starting in 1989 on the Mack Lake Burn shows that the species was habitat-limited despite people's perceptions in the 1970s that suitable habitat existed but was not occupied (Mayfield 1972).

The warbler population has continued to grow and now numbers about 2,400 singing males (Cooper et al. 2019). Besides northern Lower Michigan, small numbers of warblers breed in the Upper Peninsula of Michigan, Wisconsin, USA, and intermittently in southern Ontario, Canada (Bocetti et al. 2020). Breeding in the main core population is now largely limited to managed artificially created habitat, and creation of new habitat is likely to be sustainable because it is compatible with the local logging industry. Managers had long assumed that cowbird control was likely needed in perpetuity (Byelich et al. 1976, Bocetti et al. 2020) and that the warbler was a "conservation reliant species."

Cooper et al. (2019) highlighted the value of applying adaptive management in the recovery of the warbler. This study was a major event in the storied history of efforts to study and save this species, and it demonstrated that cowbird trapping is not necessary at the present to sustain this species. Trapping was gradually reduced over 4 years starting in 2015 with no trapping in 2018 (Cooper et al. 2019). Between 2015 and 2018, only 4 (0.8%) of 514 Kirtland's warbler nests were parasitized. Currently, there is no trapping within the core range of the Kirtland's warbler nor in Michigan's Upper Peninsula (which seems to have always had few cowbirds), but there is control protecting the small populations in Wisconsin (MDNR et al. 2015). Cooper et al. (2019) also used Breeding Bird Survey data to analyze cowbird population trends for the warbler's core breeding area, the entire Great Lakes Region and the cowbird's entire range. Decreasing trends were found for all 3 spatial scales with the core breeding area showing the greatest rate of decrease at 3.7% per year.

Cooper et al. (2019) provided an excellent model for the adaptive management advocated by Rothstein and Peer (2005), and it has resulted in major changes. However, it is surprising that adaptive management was not implemented much earlier given that population monitoring confirmed a stable warbler population until the late 1980s and then a sharp increase afterward (MDNR et al. 2015). Cowbird trapping, which has cost as much as $110,000 USD a year in government funding in recent years (Cooper et al. 2019), continued for 43 years from 1972 until 2015 without assessing whether it could be modified or ended. Initiating cowbird trapping in 1972 was the right move because the population seemed to be plummeting based on the census 10 years earlier, and parasitism data implicated cowbirds as the likely cause for the decline (Mayfield 1972). But continuing the same management approach with no assessment for >4 decades was a mistake in our view. Part of the problem relates to regulatory considerations and the difficulty of securing funding for endangered species. For example, management funds are less available once a species has been delisted from the endangered species list (MDNR et al. 2015).

Given human nature, it is not unexpected that management efforts in general assume considerable inertia and little assessment and modification if they appear to be working, even if they can be improved. For example, as early as 1993 at a national cowbird workshop, a U.S. Fish and Wildlife Service [USFWS] biologist, when asked whether the agency was considering easing up on trapping in light of a warbler population that had increased nearly 4-fold since 1972, responded that they would like to try easing cowbird control but they were concerned that if funding for cowbird trapping was decreased, the funds could not be restored if an increase in trapping was necessary in the future (S. I. Rothstein, University of California, Santa Barbara, personal observation). An alternative funding source other than the Endangered

Species Act has now been set up for the continued management of the Kirtland's warbler, and this provides flexibility for the money to be used either for cowbird trapping or for other management activities (USFWS 2019).

Sustaining cowbird control at an intensity greater than is needed may enable the warbler to occupy all available habitat in its core breeding range as excess young may disperse and found new populations. However, Mayfield (1983) suggested that Kirtland's warbler has always produced many potential founders because its small core breeding range keeps many yearlings from finding their natal site when they return to breed. In addition, funding that was directed at cowbird control over many years could have been used for direct efforts to found new populations such as cross fostering (Brewer and Morris 1984) and playback of warbler song, which appears to have helped establish new populations in Wisconsin (Anich and Ward 2017).

While it is easy to criticize management inflexibility in retrospect, available data on warbler numbers before 2015 when adaptive management began (Cooper et al. 2019) suggest that cowbird control could have been eased earlier. The warbler population increased by more than a factor of 5 from 200 to 1,085 singing males by 2001, and by more than a factor of 10 to 2,090 by 2012 (USFWS 2019). If cowbirds were having the same impact on warbler recruitment in 2012 after the 10-fold population increase that they had when the population was near 200 in 1972, the cowbird population would also have had to have had a roughly tenfold increase. Such an increase in a native species over only several decades is highly unlikely except for an endangered one undergoing recovering. Moreover, Cooper et al. (2019) demonstrated that cowbird numbers had decreased over the entire period since cowbird control began. So, it seems evident that inertia kept management activities constant until 2015.

Despite the dramatic decline in warblers between 1961 and 1971, it is reasonable to hypothesize that the population was no longer declining in 1971. Clearly, habitat was limited because the warblers did not begin to increase for >15 years after cowbird parasitism was nearly eliminated until a large tract of new breeding habitat was created accidentally by the Mack Lake Burn. Concluding that the warbler was decreasing and headed toward extinction in 1971 due to cowbird parasitism means that cowbird control just happened to begin when the warbler population had declined to the carrying capacity it would have for the next ~15 years. It is perhaps more parsimonious to conclude that the warbler population was already stable in 1971 and limited by habitat at about 200 pairs.

While the 70% level of cowbird parasitism Walkinshaw (1983) reported for the 1960s would cause a decline, this 70% figure was not a range-wide assessment and was limited temporally and to certain study areas. The population level of the warbler in 1972 provides a test of the hypothesis that the population was already stable in 1971 and not declining. Cowbird control did not begin until 1972, so there should have been a decline between 1971 to 1972 if cowbird parasitism were affecting the warbler at the population level. But the warbler population did not decrease between 1971 and 1972. Of course, there is no way to know for sure whether cowbird control saved a declining warbler population from extinction or whether the population would have remained stable even without cowbird control (Rothstein and Peer 2005). While we propose that statements about cowbird control saving the species from extinction be stated as a hypothesis and not a certainty, we repeat that cowbird control was absolutely the appropriate action in the early 1970s. We also recognize the enormous success of the Kirtland's warbler management program, but we argue that it might have been achieved at a lesser cost had adaptive management been applied earlier.

Least Bell's vireo and southwestern willow flycatcher

The least Bell's vireo is a migratory songbird dependent on riparian habitat for breeding (USFWS 1998). Once common in coastal and interior lowlands throughout California and northern Baja California, the species had been extirpated from most of its historic range by the mid-1980s and was restricted to a handful of drainages in southern California (Kus and Whitfield 2005). Declines were attributed largely to habitat loss associated with agriculture and urban development, and secondarily to cowbird parasitism (Kus and Whitfield 2005). As such, recovery for the vireo has

Figure 3. A modified Australian crow (*Corvus* spp.) trap that is frequently used to trap brown-headed cowbirds (*Molothrus ater*; *photo courtesy of M. Whitfield*).

focused on protecting and restoring riparian habitat to increase availability of suitable breeding sites as well as reducing brood parasitism to improve vireo fecundity and facilitate population growth (USFWS 1998). Similarly, the southwestern willow flycatcher is dependent upon riparian habitat, and its population decline has been exacerbated by cowbird parasitism (Kus and Whitfield 2005). However, unlike for vireos, cowbird control has not resulted in rebounding flycatcher populations, and the bird is still struggling.

Cowbird management in southern California included the capture and removal of cowbirds from vireo breeding areas and "manipulation" of vireo nests to remove cowbird eggs (Kus 1999). Cowbird trapping is the more common form of control, with nest monitoring and manipulation providing back-up protection in instances where nests are located and visited for other purposes such as demographic monitoring. Cowbirds are removed using modified Australian crow (*Corvus* spp.) traps in riparian areas and nearby sites that provide attractive foraging conditions for cowbirds, such as dairies and equestrian centers (USFWS 1998; Figure 3). They are typically operated daily between late March and mid-July, which spans most of the vireo's breeding season. Male cowbirds are usually released and females humanely euthanized or held until July and then released.

Vireo nest monitoring provides an alternative or additional opportunity to reduce the impact of parasitism by removal of cowbird eggs from nests. This is a procedure that requires nuance, guided by the number of parasite and host eggs, the stage of laying or incubation, and the timing and frequency of future nest visits by field investigators, all of which are considered in determining the safest course of action to avoid nest abandonment (Kus 1999). Often, cowbird eggs are replaced with plaster eggs to avoid a reduction of the combined clutch size that can trigger abandonment (Rothstein 1982).

Cowbird control has been effective in reducing the incidence of parasitism in vireo populations and consequently increasing seasonal productivity (Kus and Whitfield 2005). For example, at 3 well-studied drainages in San Diego County, California with long-term data, the average proportion of vireo nests parasitized annually dropped by 49–91% following implementation of cowbird trapping, and the average number of young fledged per pair doubled or tripled (Kus and Whitfield 2005). Importantly, productivity at all 3 sites increased to the level required for population stability if not growth (approximately 2 fledglings per pair).

Manipulation of vireo nest contents is also effective in boosting productivity by allowing nests to remain active following parasitism and avoiding a fate of fledging only cowbird young, which is the usual outcome for parasitized vireo nests. At a San Diego County site in a year without cowbird trapping, 46% of nests (n = 41) were parasitized; of these, over half remained active following removal of cowbird eggs. While some of these nests were later depredated, those that were successful were responsible for the production of 26% of all young fledged in the study area (n = 27; Lynn and Kus 2014). Assuming that in the absence of manipulation all parasitized nests would have failed to fledge vireo young, nest manipulation offers a way to reverse some of the negative effects of parasitism on vireo productivity.

While increasing vireo productivity is the proximate goal of cowbird management, ultimately management success is measured by the currency of species recovery: population growth. Vireo response to cowbird control has been significant by a number of metrics. Local populations, depending on carrying capacity, have typically increased on a scale of order of magnitude following initiation of cowbird control (Kus and Whitfield 2005). As local populations increased, dispersal facilitated re-

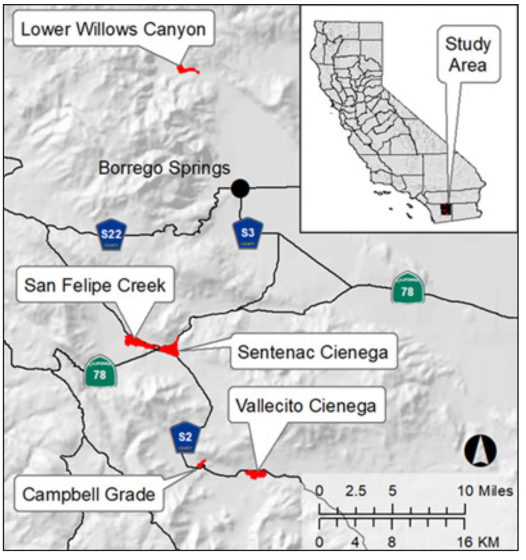

Figure 4. Location of 5 point-count areas for least Bell's vireo (*Vireo bellii pusillus*) population surveys from 2017 to 2020 in Anza-Borrego Desert State Park, California, USA.

colonization of the historic range, including the highly urbanized Los Angeles Basin and a few locations in the Central Valley of California (USFWS 2006). Three decades after listing, least Bell's vireo numbers have grown 15-fold (USFWS 2006; U.S. Geological Survey [USGS], unpublished data), and the species is well-positioned in terms of abundance and distribution for continued expansion.

One example of success is a trapping program in Anza-Borrego Desert State Park in San Diego County that began in 1986 and coincided with increases in the least Bell's vireo population from 35 territories in 1986 to 220 in 2016 (McDonald et al. 2011, Clark and Hyland 2018). Trapping program costs, trapping risks to non-target native breeding birds, low numbers of cowbirds trapped in recent years in the park, and the large vireo population led to the experimental cessation of cowbird trapping in 2017. The park decided to assess baseline conditions with regard to cowbirds, nesting birds, and cowbird control without the potential confounding effects of cowbird trapping (Whitfield and Stanek 2017).

This assessment involved point count surveys in 6 riparian sites within 5 geographic areas from 2017 to 2020 (Figure 4). Relatively few cowbirds were detected despite the removal of cowbird traps. For example, between 2017 and 2020, average cowbird detections (male and female) across all sites increased from 1.5 to 3.06, and the number of female cowbirds detected increased from 0.33 to 0.89 per site (Whitfield and Stanek 2020). Similar to the cowbird trend, the average number of birds detected at survey points also increased, from 12.6 to 13.7. During this time, the vireo remained one of the most detected species in surveys.

An examination of past cowbird trapping data (2010–2016) showed that cowbird captures dramatically decreased from 2014 to 2016 (Whitfield and Stanek 2017). Most of the cowbirds trapped in past years were likely non-breeding birds (i.e., wintering or migrating), and the number of cowbirds trapped likely did not accurately reflect breeding population numbers. After 4 years of no trapping, female cowbird numbers are still low (average of 0.11 females per point count station). These results show the value in assessing cowbird control programs, although it is not appropriate to generalize from 1 study area to another (below). They also show the importance of local factors when planning cowbird control measures and demonstrate the need for future multiyear surveys to ensure that local cowbirds do not increase or that vireos decrease to a point where the latter are endangered.

Cowbirds have also been managed on the Santa Clara River (SCR) in Ventura County, California since the early 1990s (Figure 5). Trapping was initiated in 1993, presumably to benefit small populations of the least Bell's vireo and southwestern willow flycatcher, and was conducted with increasing intensity until about 2015 (Griffith Wildlife Biology 2006, 2013). Since 1993, vireo numbers increased in Ventura County, but flycatcher numbers have not increased. Until 2005 it appeared that the use of traps to manage cowbird densities benefitted vireos, although habitat availability may have also been limiting them. After the winter of 2005, the usefulness of continued intensive trapping became questionable because of increased availability of high-quality riparian breeding habitat (L. S. Hall, Western Foundation of Vertebrate Zoology [WFVZ], A. Alvarado, California State University Channel Islands [CSUCI], and D. Kamada, WFVZ, unpublished report; L. S. Hall, WFVZ, and A. J. Searcy, Creosote Biological LLC, unpublished report). Floods in 2005 scoured the native riparian vegetation of the SCR (Stillwater

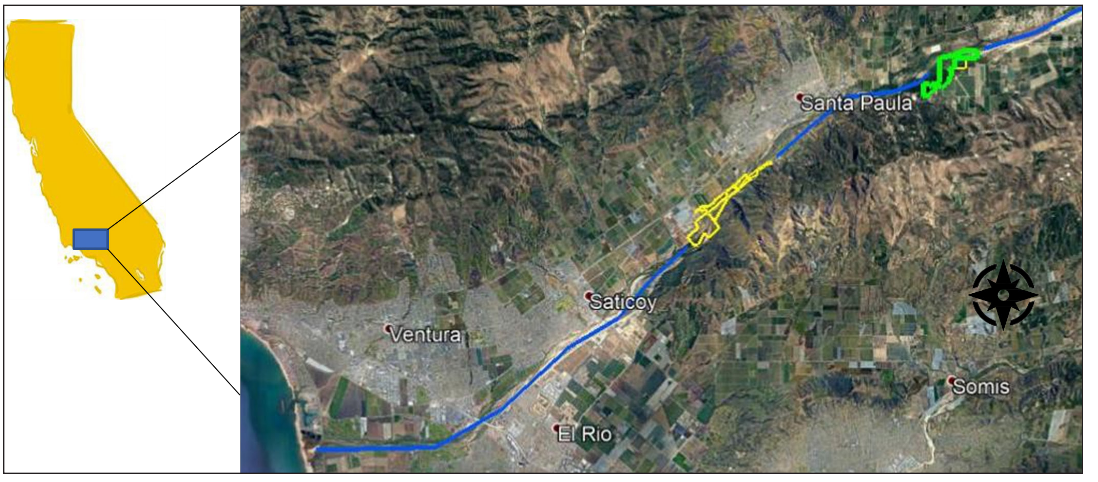

Figure 5. Location of the Hedrick Ranch Nature Area (in green) and a Nature Conservancy property (in yellow) studied between 2010 and 2020 on the Santa Clara River (in blue, running from the northeast to the Pacific Ocean) in Ventura County, California, USA.

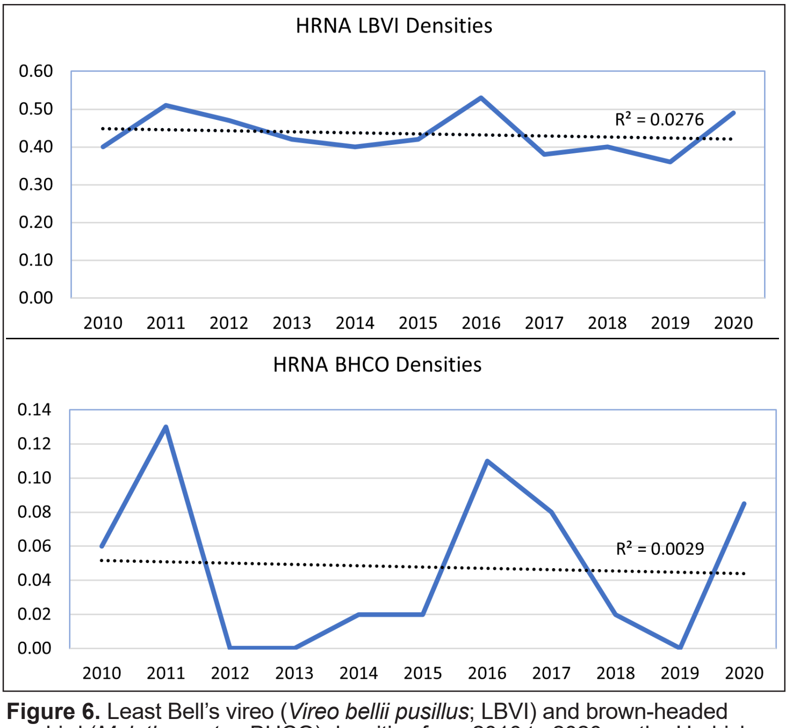

Figure 6. Least Bell's vireo (*Vireo bellii pusillus*; LBVI) and brown-headed cowbird (*Molothrus ater*; BHCO) densities from 2010 to 2020 on the Hedrick Ranch Nature Area on the Santa Clara River, Ventura County, California, USA.

Sciences and URS Corporation, unpublished report). In some sections of the river, the floods redistributed plant seeds from the main channel to the outer terraces, in particular where active removal of non-native giant reed (*Arundo donax*) had occurred prior to flooding. On 1 property, the Hedrick Ranch Nature Area (HRNA; Figure 5), deposition of native plant seeds resulted in rapid growth of native willows (red willow [*Salix laevigata*], sandbar willow [*S. exigua*], and arroyo willow [*S. lasiolepis*]), mulefat (*Baccharis salicifolia*), black cottonwood (*Populus trichocarpa*), and small perennial shrubs and annuals. These plants changed the habitat from an open, degraded river edge to a native riparian woodland between 2005 and 2010. The effect on vireos was dramatic: breeding territories increased from a few pairs to >2 dozen (L. S. Hall and M.

J. Kuehn, WFVZ, unpublished report), thus strongly indicating that a shortage of habitat was a factor in the low vireo numbers before 2005. In 2010, the WFVZ conducted systematic counts of bird species on the HRNA to determine long-term densities and richness. The results from 2010 to 2020 for vireos and cowbirds showed that although vireo numbers were relatively high and stable, cowbirds exhibited clear declines, especially from 2011 to 2015 and again from 2017 to 2019 (Figure 6). In addition, no parasitism was recorded in this area from 2015 to 2017 (L. S. Hall, WFVZ, A. Alvarado, CSUCI, and D. Kamada, WFVZ, unpublished report; L. S. Hall, WFVZ, and A. J. Searcy, Creosote Biological LLC, unpublished report).

The WFVZ also monitored vireo nests on other SCR properties from 2016 to 2020 (L. S. Hall, WFVZ, unpublished report; L. S. Hall, WFVZ, and R. Corado, CSUCI, unpublished data). On these properties, on which no cowbird trapping was conducted from 2016 to 2020, nest parasitism ranged from 0–14.3% annually, but >90% of parasitized nests were located in sparsely vegetated terraces above the main channel of the river rather than in denser native riparian vegetation. Thus, these studies provided further support that dense native vegetation can create a barrier to cowbird parasitism.

Cowbird numbers seem to have declined on the SCR despite relatively few cowbird traps being operated there since 2015 for at least 3 reasons: active restoration of native riparian woodlands has occurred on 6 large properties over the past 15 years; there has been a decrease in the number of horse ranches in the river valley over the past 20 years; and cowbird numbers appear to have declined generally in southern California. The larger-scaled demographic changes in cowbird densities, coupled with site-specific riparian vegetation restoration, have resulted in least Bell's vireo numbers increasing to at least 500 pairs on the SCR by 2018 (Stanton et al. 2019).

Stanton et al. (2019) modeled vireo population viability over the next 50 years on the SCR by evaluating the relative impacts of habitat restoration and cowbird control on vireo populations. They concluded that the more habitat that is restored on the river, the higher the carrying capacity for vireos, even with some cowbird parasitism limiting vireo fledgling production. Their model indicated that complete elimination of cowbirds is unwarranted because management objectives for the population can still be reached with some level of parasitism (Stanton et al. 2019). The model findings and field observations on the SCR are promising for those responsible for managing cowbirds to enhance populations of protected bird species: they strongly suggest that heavy, systematic trapping of cowbirds may not be necessary for enhancing populations of endangered native birds where native vegetation and habitat quality have been restored.

Black-capped vireo

The black-capped vireo breeds in scrubby open woodlands in Texas, Oklahoma, and Mexico (USFWS 2018*a*). Most of the lands it occupies in Texas and Oklahoma are privately owned with the exception of Fort Hood, Texas, for which much of the data on this species has been collected (USFWS 2018*a*). Similar to the Kirtland's warbler, the black-capped vireo was recently delisted (2016) due to its substantive population growth. When it was listed in 1987, there were 350 singing males detected, and cowbird parasitism rates at Fort Hood, Texas were >90%, which resulted in the initiation of cowbird control in the late 1980s (Hayden et al. 2000).

Surveys from 2009 to 2014 recorded 5,244 singing males across the breeding range in Texas, Oklahoma, and Mexico, and the final ruling delisting the species reported a population in excess of 14,000 singing males (USFWS 2018*b*). Currently, 40% of the breeding population exists at Fort Hood and the Kerr Wildlife Management Area in Texas as well as Fort Sill and Wichita Mountains Wildlife Refuge in Oklahoma (USFWS 2018*a*).

The vireo is within the historic range of the cowbird, and thus it is one of the species in which human activity, rather than cowbird parasitism, led to the population decline (Rothstein and Peer 2005). The vireo benefited from the creation of new habitat (Rothstein and Peer 2005), and trapping was experimentally stopped in portions of Fort Hood, following the increase in the population. However, parasitism frequencies subsequently increased, and it was concluded that trapping should continue (Kostecke et al. 2010), although nest predation was the most significant cause of nest failure (USFWS 2018*a*).

The difference in responses between Kirtland's warbler and the black-capped vireo is likely due to landscape (Cooper et al. 2019). In Michigan, the habitat is heavily forested, which is not the preferred habitat of cowbirds (Cooper et al. 2019), whereas in Texas, the area surrounding the vireos is agricultural and has large numbers of cattle *(Bos taurus)*, both of which are preferred by cowbirds (Cook et al. 1998). The USFWS (2018*a*) indicated that the greatest risks for the vireo are loss of habitat, the presence of livestock, and habitat succession, in addition to cowbird parasitism. Eliminating cattle grazing from the Fort Hood area would likely decrease the need for cowbird trapping (Cook et al. 1998), but this does not appear to be feasible politically anytime soon (see Rothstein and Peer 2005). Moreover, Texas Parks and Wildlife continues to allow homeowners to kill cowbirds if they deem them pests after minimal training (https://tpwd.texas.gov/huntwild/wild/nuisance/cowbirds/training.phtml), and cowbirds may be legally killed in some parts of the United States under the Depredation Order for Blackbirds, Cowbirds, Grackles, Crows and Magpies (50 CFR 21.43).

Cowbird control to mitigate agricultural loss

While the effects of cowbird parasitism on hosts' fitness and the impact on endangered species are well-documented, we cannot say the same about the damage to agricultural crops caused by cowbirds. Under a directive from the U.S. Congress, USDA APHIS Wildlife Services (WS) began managing blackbirds in the 1980s to help alleviate blackbird damage (USDA APHIS 2015). The decision to target blackbirds, and in particular red-winged blackbirds and cowbirds, was based on roadside surveys conducted in 1979 in the rice-growing region of southwestern Louisiana (Wilson 1985) and an analysis of cowbird diet (Meanley 1971). In the spring, when most damage occurs, red-winged blackbirds were the most frequently observed species in 77–80% of the surveys. Cowbirds were the second most common species encountered, but they were a distant second, being the most commonly encountered species in only 20–21% of surveys. Recent data from the Breeding Bird Survey showed a -0.66% survey-wide annual decline of cowbirds from 1966 to 2015 (Sauer et al. 2017), and Partners in Flight reported a 23% decline from 1970 to 2014 (Rosenberg et al. 2016). Declines in Louisiana have been even greater based on Christmas Bird Count (National Audubon Society 2010) and Breeding Bird Survey data (-1.08% annual decline from 1967 to 2015; Sauer et al. 2017; reviewed in Peer and Abernathy 2017).

Louisiana WS constructed a model to determine the number of cowbirds to be eliminated from the local population to reduce damage to tolerable levels (USDA APHIS 2015). The model suggested a fall population of 51.7 million cowbirds using a 1:1 secondary sex ratio and that female cowbirds lay 40 eggs annually. Based in part on these calculations, WS estimated that 1 million cowbirds could be killed annually (USDA APHIS 2015) and >3 million were killed from 2009 to 2015 (USDA APHIS 2015).

Developing models of human–wildlife interactions is challenging given the complex and constantly changing nature of the problems (e.g., changes in crop selection, landscape factors, among other elements). While Louisiana WS has developed a useful model for managing the blackbird depredation issue, we suggest that the model needs to be updated with additional information. First, cowbirds have a decidedly male-biased secondary sex ratio. In a review of 21 studies, there was a consistent male bias in cowbird populations, and it was as high as 6:1 in some locations (Ortega 1998). This may be due to the fast pace-of-life strategy apparently adopted by female cowbirds in which they maximize reproductive effort and sacrifice immune function and survivorship (Peer et al. 2017; see also Louder et al. 2020). Second, the estimate that female cowbirds lay 40 eggs/season by Scott and Ankney (1980) may not be applicable for the entire species. For example, genetic analyses of individual female laying behavior revealed the maximum number of eggs laid was 13 with a mean of 3–5 eggs/season (Alderson et al. 1999, Strausberger and Ashley 2005). Third, if financial resources are available, food choice studies should be conducted on cowbirds to resolve conflicting results on diet preference. The dietary analysis used for justifying control measures (Meanley 1971) reported that the annual cowbird diet in Arkansas was 46% rice. Subsequent studies, however, have found that the amount of grain

Table 1. Data needed to develop bioenergetic and economic models to describe the cowbird (*Molothrus ater*) depredation of the rice (*Oryza sativa*) crop in Louisiana, USA.

Bioenergetic model	Economic model
1. Diet preference to determine the amount of rice consumed by male and female cowbirds	1. Amount of rice consumed per bird
2. Daily energetic requirements of male and female cowbirds during the time period at which rice is vulnerable	2. Population data on cowbirds in the rice-growing region including sex ratios of flock
3. Caloric value of rice during the damage period	3. Market price of rice
4. Length of damage period	

consumed by cowbirds is not as high as previously reported (Lowther 1993). Fourth, population surveys have not been conducted recently (USDA APHIS 2015), and updated population data would be beneficial in light of the recent declines in cowbird and blackbird populations (Rosenberg et al. 2019).

We echo the sentiment of Runge et al. (2009), who suggested that harvest of migratory birds should be adjusted annually to consider population changes. This updated information could then be used to develop bioenergetic and economic models similar to those for red-winged blackbirds depredating sunflower (*Helianthus annuus*) crops (Peer et al. 2003; Table 1). In addition to targeted lethal management, supplemental techniques could be implemented including chemical repellents such as anthraquinone seed treatment and unmanned aerial systems (Avery and Werner 2017, Werner and Avery 2017, Wandrie et al. 2019).

Blackbird damage to crops can be devastating for the producer (Peer et al. 2003), and lethal management of overabundant native species is often warranted (Garrott et al. 1993). Similar to endangered species management, there should be a clear goal as to the level of tolerable crop loss and when lethal cowbird control can be reduced or even eliminated (Peer and Abernathy 2017). Cowbirds are not at risk of extinction despite their declining numbers, and it may benefit some host populations. However, cowbirds are a native species, and the U.S. public is increasingly questioning the role of lethal or direct options in the management of wildlife. Messmer et al. (1999), in a study to determine U.S. public perceptions of the management of meso-predators to enhance avian recruitment, reported that their respondents were more likely to support direct management of predators to enhance recruitment for endangered species and where the predator species were less charismatic. Respondents did not support predator control of native raptors to enhance avian recruitment. They did not include specific questions regarding brood parasites such as the cowbird. In the case of cowbirds, we have documented the benefits of lethal control coupled with habitat management to benefit a select number of songbirds that are suitable hosts and that have not evolved defenses against parasitism. The role of cowbirds as a keystone species, which could actually increase avian community diversity, remains uncertain (Friedmann 1929, Rothstein and Peer 2005). If cowbird parasitism reduces the abundance of dominant species within a community, it could theoretically lead to greater avian community diversity.

Messmer et al. (1999) concluded that the U.S. public would be more supportive of predator control to enhance avian recruitment and the direct management of wildlife to resolve human–wildlife conflicts if the control methods were strategic and supported by science. Manfredo et al. (2018) also reported that more of the U.S. public now believes that humans and wildlife are meant to coexist or live in harmony, and that for professional management of wildlife to remain relevant, managers will need to consider all public perspectives prior to implementing management actions. The management for endangered species and agricultural losses has likely suffered from inertia, but management that utilizes a more comprehensive focus should be implemented along with a clear set of guidelines on desired outcomes (Messmer et al. 1999, Rothstein and Peer 2005, Peer and Abernathy 2017, Manfredo et al. 2018).

Management implications

The successful cowbird management programs we described were adaptive and also involved habitat restoration in addition to controlling cowbirds. When the host populations were restored, cowbird control was reduced and, in some cases, eliminated. In the case of cowbirds and their wide-scale management to reduce crop damage, if it were feasible to utilize financial resources expended for wide-scale cowbird control for habitat restoration, this resource reallocation could benefit the target species as well as other species reliant on these native communities. However, before these actions can be implemented, managers will require better information on the economic impacts of cowbird crop depredation and the effects of reduction in cowbird control on continental populations.

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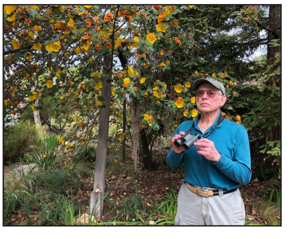

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