Original Article

Managing Brown-Headed Cowbirds to Sustain Abundance of Black-Capped Vireos

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ABSTRACT Brood parasites can appreciably decrease fecundity of susceptible songbird hosts, which can often cause a decrease in host abundance. Wildlife managers use brown-headed cowbird (*Molothrus ater*) management to reduce parasitism frequency and benefit the conservation of the endangered black-capped vireo (*Vireo atricapilla*); however, intensity of management needed to increase vireo abundance is not well-understood. We used sensitivity analyses of population models for black-capped vireos to assess effects on abundance of particular changes in parasitism frequency. Our models suggest that the parasitism frequency vireos can tolerate while maintaining abundance in a particular location is ≤30%. If parasitism frequency is high, trapping cowbirds during ≥1 of every 3 years may be sufficient for reducing parasitism enough to maintain abundance at managed locations. Cowbird management programs may need to be intensive in initial years to increase abundance of vireos being managed if the initial abundance is low. Rotating locations of traps each year among managed locations may be effective for maintaining vireo abundance while decreasing overall trapping effort and making more efficient use of management funds. Increasing and restoring habitat concurrent with cowbird management would likely further increase the likelihood of establishing and maintaining vireo abundance in managed locations.

KEY WORDS brood parasitism, cowbird trapping, *Molothrus ater*, nest parasitism, sensitivity analysis, *Vireo atricapilla*.

Brown-headed cowbirds (*Molothrus ater*; hereafter, cowbird) are an obligate brood parasite that can reduce fecundity in songbirds (Robinson et al. 1995). Songbirds have various behavioral and population-level responses to cowbird parasitism. Some songbirds are able to identify and reject cowbird eggs from nests, whereas other species accept the cowbird egg and raise the offspring as their own (Rothstein 1990). Cowbirds are suspected as a primary cause of declines in abundance in some songbird species that accept cowbird eggs (Brittingham and Temple 1983, Rothstein and Robinson 1994), but declines often co-occurred with other deleterious impacts, especially loss of breeding habitat (Rothstein and Peer 2005). Anthropogenic landscape change (e.g., introduced livestock, human-built structures) has increased the breeding range of cowbirds in North America (Rothstein 1994). Some songbird species, such as least Bell's vireo (*Vireo bellii pusillus*) and southwestern willow flycatcher (*Empidonax traillii extimus*), are thought to have declined, in part, because of expansion of the cowbird breeding range (Rothstein 1994). We focused on the black-capped vireo (*V. atricapilla*; hereafter, vireo), which in contrast to the other previously mentioned species, occurs in the historical breeding range of cowbirds (Graber 1961, Rothstein and Peer 2005). Managers use cowbird management as a tool to reduce parasitism and benefit the conservation of the vireo. However, the intensity of management needed to increase vireo abundance is not well-understood.

Cowbirds were identified as a primary threat to reproduction in the vireo and led, in part, to listing the vireo as federally endangered in 1987 (USFWS 1991, Grzybowski 1995). Vireos rarely fledge offspring from parasitized nests because cowbird nestlings outcompete vireo nestlings for food (Grzybowski 1995). Additionally, cowbird adults are nest predators (Stake and Cimprich 2003, Conkling et al. 2012). Parasitism frequency in vireos is variable throughout its breeding range, but has been documented in central Texas, USA, as high as 85% on Fort Hood (Kostecke et al. 2005), 100% in Coryell County (Farrell et al. 2011), and 75% on Kerr Wildlife Management Area (Grzybowski 1995) prior to initiation of cowbird trapping.

Various techniques have been used to manage cowbirds to reduce impacts on host reproduction. Trapping and shooting of cowbirds have been used to reduce impacts of cowbird

Received: 24 June 2012; Accepted: 26 November 2012

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parasitism on the vireo in Texas (Kostecke et al. 2005, Summers et al. 2006*b*) and Oklahoma (Grzybowski 1995). Other cowbird management techniques include removal of livestock from breeding habitat (Goguen and Mathews 1999), removing or addling cowbird eggs laid in host nests (Morrison and Averill-Murray 2002), placing fake cowbird eggs in host nests (Ortega et al. 1994), and inhibiting cowbird fertility through chemical compounds administered via food supplements (Avery et al. 2008). Although rarely discussed directly as a cowbird management technique, restoration can be used to increase area of breeding habitat of cowbird hosts and increase likelihood of host breeding success in an area (Rothstein and Peer 2005).

Trapping, shooting, relocating livestock, and increasing area of breeding habitat may be useful for vireo conservation. Cowbird trapping programs have successfully reduced parasitism frequency. For example, parasitism was reduced from 90% to 10% in 3 years by trapping cowbirds on Fort Hood, Texas (Kostecke et al. 2005). Likewise, shooting a small number of female cowbirds per unit area effectively reduced parasitism frequency and increased fledging success of the vireo on Fort Hood (Summers et al. 2006*b*). Cowbird trapping programs can decrease parasitism frequency in targeted areas but have had mixed success with increasing abundance of host species because parasitism does not always limit host abundance (Rothstein and Cook 2000, Rothstein and Peer 2005). There is some evidence, however, that cowbird trapping increased vireo abundance when trapping co-occurred with other cowbird management actions and an increase in area of vireo habitat (Kostecke et al. 2005, Rothstein and Peer 2005), all of which likely contributed to increases in abundance. Additionally, parasitism frequency has been shown to decrease with distance from grazing (Goguen and Mathews 2000), which suggested that relocating livestock is a potential management technique for vireos.

It is currently unknown whether cowbird management techniques applied in 1 year continue to reduce parasitism frequency in subsequent years. Parasitism frequency remained below the recommended level of about 60% (Smith 1999) after 5 years of trapping cessation on part of Fort Hood (Kostecke et al. 2010). Their results were confounded, however, because cowbird trapping and shooting occurred on other parts of Fort Hood and on nearby private land (Kostecke et al. 2010). There is conflicting evidence that shooting female cowbirds in target management areas has a carry-over effect in subsequent years (Stutchbury 1997, Summers et al. 2006*b*). These results suggest that annual cowbird management may be unnecessary depending on various circumstances and management goals.

We investigated how cowbird management can be used to sustain vireo abundance in managed locations. The vireo's breeding range covers a broad geographic area from Tamaulipas, Mexico to central Oklahoma, USA (Graber 1961, Grzybowski 1995). State and federal cowbird management programs are limited to a small number of public properties and randomly implemented, volunteer-based programs on private properties. There is currently no overall strategy to reduce cowbird abundance on private lands, which comprise most of the vireo's habitat in Texas (McFarland et al. 2012), despite the U.S. Fish and Wildlife Service using cowbird trapping as mitigation for impacts to vireo habitat (e.g., USFWS 2005, Loomis Partners Inc. 2009). As a first step in developing an overall strategy for cowbird management, our objectives were to 1) determine what parasitism frequency vireos can tolerate while maintaining abundance and how changes in parasitism frequency affect abundance; 2) determine how often cowbird management actions need to be implemented (e.g., every yr, every 2 yr) to maintain abundance; and 3) provide a recommended approach to managing cowbirds to sustain vireo abundance in managed locations.

METHODS

To better understand how varying parasitism frequencies influence vireo population dynamics and how cowbird management can be used efficiently, we compared the effects of different parasitism frequencies on vireo abundance in an area under management. We focused on vireos under management because we assumed the goal of cowbird management was to maintain or increase vireo abundance in a particular location such as a specific property or group of nearby properties. We used Program RAMAS Metapop 5.0 (Applied Biomathematics, Setauket, NY) to investigate the parasitism frequency that vireos under management can withstand without declining (i.e., while maintaining lambda [λ] > 1.0, a metric of population growth rate) over a 100-year time period. We also investigated sensitivity of λ to changes in parasitism frequency to determine the magnitude of changes in λ corresponding to particular changes in parasitism frequency (Wisdom and Mills 1997).

We based our modeling approach on Beardmore et al. (1996) and Woodworth (1999), who used a stage-based matrix model to investigate population dynamics of songbirds. We used their approach to address our specific objectives. Our model assumed one population for simplicity because we focused on management of the vireo in a particular location and there is little evidence for subpopulation structure (Zink et al. 2010). The model had 2 life stages, hatch-year and after-hatch-year, to enable different parameters for survival (probability of annual survival) and fecundity (no. of F fledglings/F/yr) for each life stage. We set probability of annual survival at 0.43 for hatch-year females (after fledging) and 0.57 for after-hatch-year females based on mark–recapture model estimates using color-banding and re-sight data from Kostecke and Cimprich (2008). The initial proportion of the 2 life stages used for all simulations was 0.8 for hatch-year to 1.0 for after-hatch-year, based on our average estimate of number of female offspring fledged per female per year across parasitism frequencies (Table 1). The model included females only for simplicity, making fecundity the number of female offspring per female and survival parameters applicable to females only. Although excluding males does not bias our conclusions, we do not imply males are unnecessary for reproduction and

Table 1. Fecundity and number of female offspring/female/year, for black-capped vireos, corresponding to frequency of brood parasitism by brown-headed cowbirds when nest predation is 50%. Estimates were based on using recently collected field data from Kerr Wildlife Management Area (Pope 2011), Devil's River State Natural Area (Smith et al. 2012), Balcones National Wildlife Refuge (M. L. Morrison, Texas A&M University, unpublished data), and a ranch in southern Edwards county (M. L. Morrison, unpublished data) to adjust estimates from Beardmore et al. (1996).

Parasitism frequency	Fecundity
0	1.365
10	1.225
20	1.08
30	0.93
40	0.775
50	0.615
60	0.445
70	0.26
80	0.055
90	0.0

parental care for the vireo. We used fecundity values expected with 50% nest predation because we were uninterested in the effects of predation frequency on population dynamics, and this value is consistent with field observations (Stake and Cimprich 2003, Pope 2011, Smith et al. 2012). We varied parasitism frequency from 0% to 90% by 10% increments to capture variability in fecundity. We calculated vireo fecundity values by adjusting estimates from Beardmore et al. (1996) based on our nest monitoring data from Kerr Wildlife Management Area (Pope 2011), Devil's River State Natural Area (Smith et al. 2012), Balcones National Wildlife Refuge (M. L. Morrison, Texas A&M University, unpublished data), and a ranch in southern Edwards county (M. L. Morrison, unpublished data; Fig. 1). Based on these data collected from several locations across the vireo's breeding range in Texas, our estimates of fecundity were 1–2 young/female lower than estimates from Beardmore et al. (1996). We set standard deviation of fecundity equal to 100% of the fecundity estimates based on descriptive statistics of our data. Initial population size was set to 200, carrying capacity 400, and density dependence was set to ceiling to incorporate regulatory effects of population density and carrying capacity on fecundity and survival. Setting density dependence to ceiling in RAMAS is similar to, but simpler than, the Beverton–Holt function; growth or decline of the population at each time step depends on the vital rates in the stage matrix and the function does not assume the population will recover from low densities. If abundance exceeds the ceiling at a time step, then abundance is reduced to the ceiling for the next time step. We used this initial population size based on our preliminary results from varying initial population size, which indicated that sensitivity of initial population size to extinction risk decreased above population size of 200.

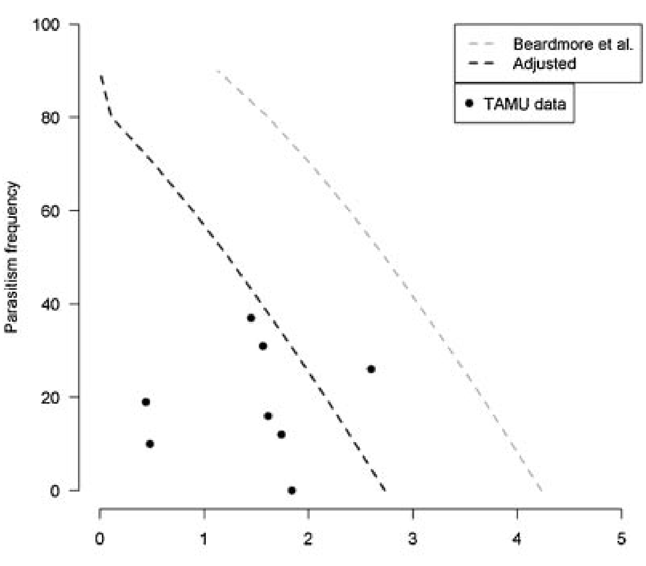

Figure 1. Annual fecundity values (no. of F offspring/F/yr) for black-capped vireos used by Beardmore et al. (1996) with 50% predation, fecundity we observed in the field based on our nest monitoring data from Kerr Wildlife Management Area (Pope 2011), Devil's River State Natural Area (Smith et al. 2012), Balcones National Wildlife Refuge (M. L. Morrison, Texas A&M University, unpublished data), and a ranch in southern Edwards county (M. L. Morrison, unpublished data, and adjusted values used in our models.

We also investigated how parasitism frequency and λ may change if cowbirds were trapped every year, or every second, third, fourth, or fifth year. For the purposes of modeling, we assumed parasitism frequency with annual cowbird trapping was 10% the first year and increased by 10% for each non-trapped year up to 50%. These parasitism frequencies were based on an apparent lag-effect, in which parasitism frequency does not immediately return to un-trapped levels following a year of trapping (Kostecke et al. 2010). Thus, we assumed parasitism frequency when cowbirds were trapped every other year averaged to 15%, every third year averaged to 20%, every fourth year to 25%, and every fifth year to 30%.

RESULTS

Lambda was negatively associated with parasitism frequency and was lower than 1.0 for parasitism frequency above 30% (Fig. 2). The trend was nonlinear, with λ decreasing more strongly with greater parasitism frequency, particularly above 50% parasitism. Lambda decreased from 1.10 at 0% parasitism to 0.92 at 40% parasitism, whereas λ decreased from 0.87 at 50% parasitism to 0.57 at 90% parasitism.

Lambda was positively associated with cowbird trapping frequency (Fig. 3). Lambda increased by about 0.02 when trapping frequency was increased from every fifth year to every year. We found that the largest difference in λ occurred between not trapping (0.87) and trapping every fifth year (0.98; Fig. 3). Lambda was >1.0 when trapping occurred every third year or more frequently.

DISCUSSION

Our models suggest the parasitism frequency that vireos can tolerate while maintaining abundance in a location is ≤30% because under this condition λ was >1.0. Our estimate was similar to previous estimates of parasitism frequency for λ equal to 1.0, which was 26% for Puerto Rican vireo (*Vireo latimeri*; Woodworth 1999) and 17–44% for lazuli bunting (*Passerina amoena*) depending on survival estimates (Greene 1999). Using a different modeling approach and

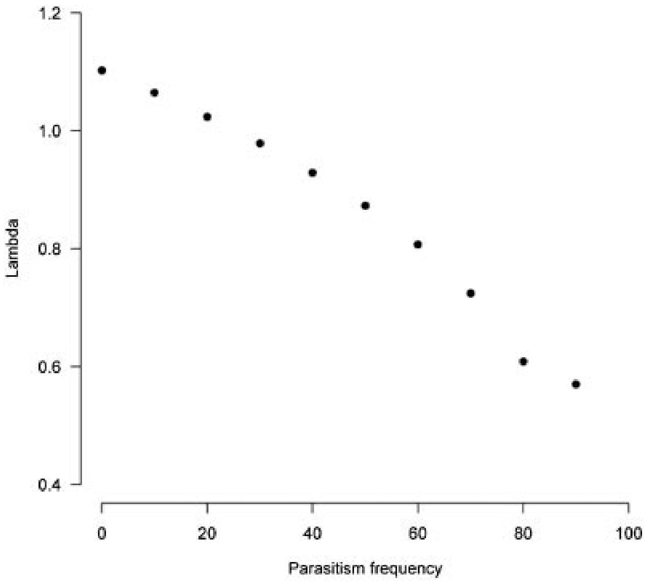

Figure 2. Model results for λ (population growth rate) of black-capped vireos given varying parasitism frequency by brown-headed cowbirds varying from 0% to 90%, with nest predation constant at 50%. Calculations were made using RAMAS Metapop (Applied Biomathematics, Setauket, NY).

data from Fort Hood available at the time, Tazik and Cornelius (1993) concluded that parasitism frequency above 50% would be the major factor limiting black-capped vireo reproductive success. We were fortunate to have access to data from a broader geographic range, better estimates of adult and juvenile survival, and updated population modeling techniques, which resulted in differences in our approach to similar question addressed by Tazik and Cornelius (1993). All of these estimates are model-based, which means they have numerous assumptions and are only as good as the data used for parameters in the models. It is worth noting that all of these estimates were <60% parasitism (50% for vireo species) suggested as general rule by Smith (1999) for initiating cowbird management. Smith (1999) stated that the recommended threshold for management might seem high, but explained that evidence showing population-level responses when parasitism was <50% was lacking.

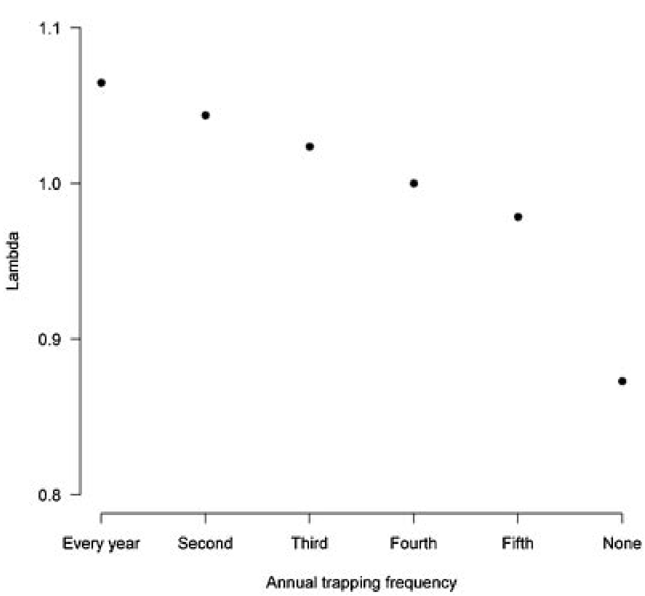

Figure 3. Model results for λ (population growth rate) of black-capped vireos for different scenarios of annual trapping for brown-headed cowbirds. Calculations were made using RAMAS Metapop (Applied Biomathematics, Setauket, NY).

Based on our models, trapping cowbirds during ≥1 of every 3 years may be sufficient for reducing parasitism enough to maintain $\lambda > 1.0$. We are unaware of previous investigations of the annual frequency recommended for cowbird management. Cowbird management programs may need to be intensive in initial years to increase abundance of vireos being managed if the initial abundance is small. Most previous cowbird management programs were implemented annually (Kostecke et al. 2005, Rothstein and Peer 2005). Rotating locations of traps in an area with multiple properties under vireo management is a potential way to maintain abundance on each property while also decreasing the overall trapping effort.

Based on our results and the literature, we proposed a flowchart that shows a process of deciding whether a property is a good candidate for vireo conservation and subsequent suggestions for management guidelines (Fig. 4). To manage for recovery of vireos on broad spatial scales, managers should first decide which properties are good candidates for successful conservation of vireos based on the specified criteria below to make the best use of conservation efforts and funds. Evaluation of a property begins with identifying whether vireo habitat currently exists (McFarland et al. 2012) or whether restoration can create and maintain habitat, and how much area can provide habitat. Knipps (2011) found that properties managed for vireos were more likely to maintain breeding individuals if those properties had vireos before management began. Properties proximate to known locations of vireos and those supporting larger abundances should be prioritized to build on existing conservation efforts where vireos are known to occur. Although vireos may be able to locate newly available breeding habitat, it seems more likely that vireos select breeding habitat, in part, based on site fidelity (Kostecke and Cimprich 2008) and the presence of conspecifics (Ward and Schlossberg 2004).

If a property meets the criteria above and is selected, then managers must decide how to manage the property for vireos. Guidelines for managing vireo habitat are available from Texas Parks and Wildlife Department (TPWD 2003), which focus on maintaining vegetation in a mid-successional stage in central Texas. Recommendations in the western region of the breeding range, where less rainfall occurs, are to not manipulate the vegetation because it rarely grows to a condition unusable by vireos. We recognize the possibility that vegetation manipulation may be useful in some riparian areas to return the vegetation to an earlier successional stage that is usable by the vireo; however, the majority of the habitat in western region of Texas is relatively stable (Smith 2011). Next, management of cowbird parasitism

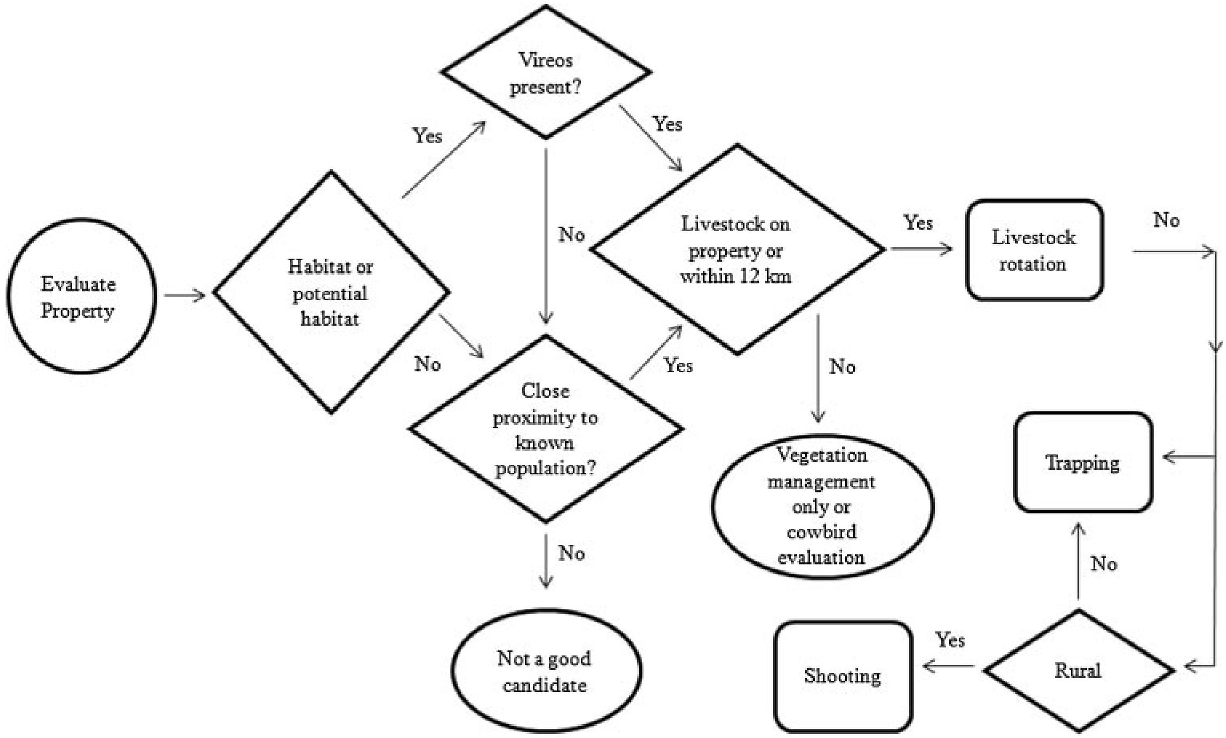

Figure 4. Flow chart showing suggested criteria used to evaluate whether a property should be considered for black-capped vireo management and, if so, how to manage for brown-headed cowbirds. Oval boxes indicate the beginning and end of the flowchart process, diamond boxes indicate yes or no decisions, and rectangles indicate a suggested action.

should be considered. Cowbird presence and abundance are associated with particular conditions, particularly the presence of livestock $\leq$12 km from the property (Goguen and Mathews 2000), but also with exotic wildlife ranching or other areas where food and water is readily available. Ideally, a conservation program would first assess parasitism frequency to determine whether management is needed before implementing a cowbird management program. Our results suggest cowbird management may be needed if parasitism frequency is $\geq$30%. Cowbird trapping programs have successfully reduced parasitism on vireos in central Texas (Kostecke et al. 2005). Shooting programs are potentially less expense than trapping programs (Summers et al. 2006*a*), but may be infeasible in non-rural areas because of safety concerns (Siegle and Ahlers 2004). The economic impact of removing livestock across areas large enough to reduce parasitism frequency would be substantial.

Currently, there is no overall strategy for removing cowbirds or managing vireo habitat in Texas except on a few state and federal properties; programs to remove cowbirds on private lands, where the majority of vireo habitat occurs, have little coverage and are uncoordinated. Most cowbird removal programs in Texas do not monitor parasitism frequency in areas where trapping occurs. Therefore, it is unknown whether management efforts are benefitting targeted vireo management areas. Monitoring programs to estimate parasitism frequency will be useful for identifying whether cowbird management is needed, how often it is needed, and its effectiveness. Nest monitoring is time-consuming, but implementing cowbird management that is ineffective or unnecessary is wasteful of limited conservation funds.

MANAGEMENT IMPLICATIONS

We suggest that an overall strategy should be developed to reduce parasitism frequency, enhance and create vireo habitat, and monitor impacts on vireo abundance on public and private lands to ensure that limited funding is used effectively. For example, cowbird removal focused in areas with large amounts of potential vireo habitat rather than small areas with potential habitat for a few territories only (McFarland et al. 2012) would likely be more cost-effective in increasing vireo abundance. Additionally, subsequent monitoring of vireo abundance in managed areas would inform managers if modification in management strategy is needed. Based on our results, annual cowbird trapping may be unnecessary after initial intense trapping efforts to increase vireo abundance in a managed area; traps deployed every 2–3 years may maintain vireo abundance and reduce overall effort of vireo management compared with annual trapping.

ACKNOWLEDGMENTS

The Institute of Renewable Natural Resources, Texas A&M University supported our work. We thank M. Colon, D. Morgan, and T. Pope for this use of data they collected; many field technicians for assistance collecting data; and landowners and managers for allowing access to properties. Careful readings and thoughtful comments by anonymous reviewers improved this manuscript.

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Associate Editor: Koper.