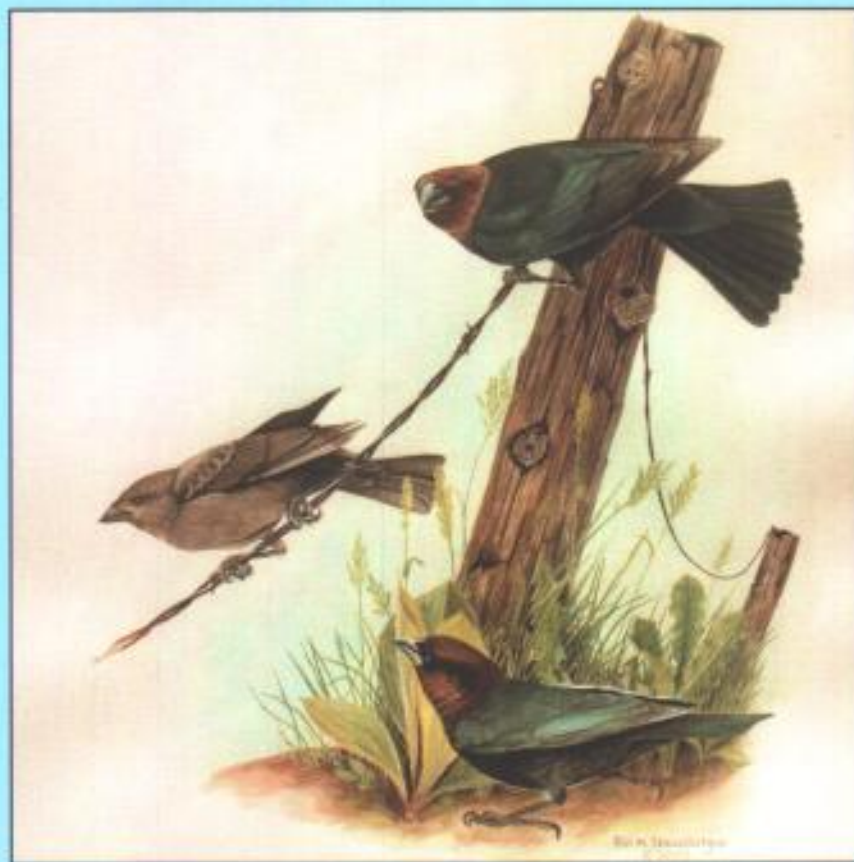


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Management of Cowbirds and Their Hosts: Balancing Science, Ethics, and Mandates

CATHERINE P. ORTEGA, JAMESON F. CHACE, AND BRIAN D. PEER, EDITORS

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**Management of Cowbirds and Their Hosts:
Balancing Science, Ethics, and Mandates**

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Cover: Female Brown-headed Cowbird (*Molothrus ater*) attended by two suitors. Watercolor painting by Bill Strausberger. Courtesy of Mark Hauber.

MANAGEMENT OF COWBIRDS AND THEIR HOSTS: BALANCING SCIENCE, ETHICS, AND MANDATES

BY

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and Brian D. Peer

From the Editor

While we were putting this monograph together, those of us in the United States experienced a very contentious presidential election. My country seems more polarized than I have ever seen it, even during the days of the Vietnam war. Today, we Americans live in either a red or a blue state. If we are pro-war, we are patriots; if we question the war, we are traitors. Everything must be black or white, good or bad; there seems to be little tolerance for reasoned positions in the middle of any issue.

The topic of this monograph suggests that such polarized thinking has extended to those of us involved in avian conservation. The Brown-headed Cowbird (*Molothrus ater*) and its close relatives are distinct among New World birds for reproducing solely through brood parasitism, laying their eggs in other species' nests. This contrasts with the Old World brood-parasitic cuckoos (*Cuculus* spp.), whose system of parasitism involves an individual focus on a single host, highly mimetic eggs to match that host, and complex genetic relationships, such that a single cuckoo population can parasitize multiple host species. Cowbirds are generalist parasites, willing and able to dump their single type of egg into any nest available, including totally inappropriate locations in some cases. Most of the potential foster parents have evolved ways of avoiding this parasitism, because of its reproductive costs. This seemingly crude form of brood parasitism is of great interest to avian ecologists and evolutionists, and the comparison of Old World and New World parasitism systems seems to me a largely unexplored field of study. Thus, to many ornithologists, the cowbird is an intriguing beast, one of nature's treasures that survives despite the attempts of its hosts to develop ways to make life difficult for it.

In some situations, though, cowbird parasitism has become so common and successful that it has threatened the very existence of a host species. Our society's polarizing tendency can be seen in a common response to such cases: demonizing cowbirds as evil, immoral, lazy, wretched, and even socially dysfunctional. Of course, in most cases, where cowbird parasitism might be the final blow to a species' existence, the cowbird—just doing what comes naturally—is parasitizing a host species that has suffered from human activities that have greatly reduced the host species' range and abundance. In many cases, cowbird removal from those limited populations has resulted in local population increases, perhaps saving the host species from extinction. Thus, when the Partners in Flight program showed that cowbird parasitism might be a factor in more widespread declines of populations of migratory birds, there were some who felt that it was time to wage war on the cowbird across its range. As in a bad John Wayne movie, the posse was forming to head out of Dodge and fix this cowbird problem once and for all!

Obviously, a native species doing what it evolved to do should never be judged on moral grounds, even if the reality is that it must be removed in some situations. In this monograph, we see some of the best cases of conservation success from cowbird control, along with a few cases where such control does not seem to work. New information on how cowbirds function in finding both host nests and food suggests management options, whereby cowbird removal might be stopped or greatly curbed. As scientists and conservationists in this new century, should we not explore all possible avenues of bird management, with the goal of finding ways to preserve threatened species without killing thousands of cowbirds annually for as long as any of us will live? There must be some reasonable middle ground that preserves both endangered birds and cowbirds, and our job as scientists is to find it and promote it. This monograph provides a great step in the proper direction. Fixing the current polarization of U.S. society seems a far more daunting task.

John Faaborg



INTRODUCTION

RESEARCH DIRECTIONS AND COWBIRD (*MOLOTHRUS* SPP.) MANAGEMENT

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ABSTRACT.—The collection of papers in this *Ornithological Monograph* resulted from a symposium entitled “Ecology and Evolution of Host–Parasite Interactions and Cowbird Management,” which the authors organized for the American Ornithologists’ Union Annual Meeting in Urbana, Illinois, in 2003. The purpose of the symposium was to share knowledge and ideas among researchers and managers. The unifying theme focused on research that contributes to management of cowbirds and their hosts. The papers were selected because they deal with critical management issues: laws, efficacy of cowbird control, endangered hosts, landscape and landscape-use issues, and evolutionary implications. Cowbirds discussed include Brown-headed (*Molothrus ater*), Bronzed (*M. aeneus*), and Shiny cowbirds (*M. bonariensis*); hosts discussed include Yellow-shouldered Blackbird (*Agelaius xanthomus*), Least Bell’s Vireo (*Vireo bellii pusillus*), Southwestern Willow Flycatcher (*Empidonax traillii extimus*), Black-capped Vireo (*Vireo atricapilla*), and Kirtland’s Warbler (*Dendroica kirtlandii*). Each chapter also highlights the need for future research.

RESUMEN.—El conjunto de trabajos de este *Ornithological Monograph* es el resultado de un simposio titulado “Ecología y Evolución de las interacciones Hospedero-parásito de cría y Manejo de los *Molothrus* spp. parásitos.” que fue organizado por los autores durante el Congreso Anual de la “American Ornithologists’ Union” en Urbana, Illinois durante el año 2003. El propósito de este simposio fue que los investigadores y los responsables de las prácticas de manejo pudieran compartir sus conocimientos e ideas. El tema unificador se centró en aquellas investigaciones que contribuyeran al manejo de los tordos parásitos y sus hospederos. Los trabajos fueron seleccionados en base a que trataran cuestiones críticas de manejo: leyes, eficacia en el control de los tordos parásitos, hospederos en peligro, cuestiones a nivel paisaje y uso del ambiente, e implicancias evolutivas. Los trabajos incluyeron a los parásitos *Molothrus ater*, *M. aeneus*, y *M. bonariensis*, así como a los hospederos *Agelaius xanthomus*, *Vireo belli pusillus*, *Empidonax traillii extimus*, *Vireo atricapilla*, y *Dendroica kirtlandii*. Además, cada capítulo resalta la necesidad de futuras investigaciones.

BROWN-HEADED COWBIRDS (*Molothrus ater*; hereafter “cowbirds”) are cunning survivors to some people and pesky vermin to others, a dichotomy that is neither new nor surprising. Historically, people who anthropomorphized cowbirds generally held the most negative opinions of them. Although that dichotomy still exists as a trend, many people apparently appreciate the individuality and bizarre reproductive behavior of cowbirds but view them

as a nemesis to their hosts. Today, the more important dichotomy seems to be between two occupational perspectives on cowbird control: in general, managers favor intensive control, often widescale and in perpetuity; whereas academic researchers favor conservative control, targeted specifically for endangered hosts only until recovery goals are met.

Cowbirds entered the political arena with the listing of Kirtland’s Warbler (*Dendroica kirtlandii*; U.S. Fish and Wildlife Service 1976) because controlling cowbirds through lethal means became part of the recovery plan. Since

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then, cowbird control has been included in the recovery plans of four additional hosts. The political force of cowbird control is also evident in the perceived necessity to form the North American Cowbird Advisory Council, whose goals are to (1) provide information on cowbird biology and results of management activities; (2) summarize perspectives and opinions for assessing cowbird–host interactions and conducting cowbird management activities; (3) develop and update protocols for management options, implementing specific cowbird management activities, establishing a need for management, and monitoring the efficacy of management activities; and (4) develop education and outreach activities for a variety of people.

In his keynote address at the 1993 North American Research Workshop on the Ecology and Management of Cowbirds, Steve Rothstein, co-chair of the North American Cowbird Advisory Council, noted that when he began his studies in the 1960s, he seemed to be the only person interested in cowbirds. During the 1990s, interest in cowbirds surged; a WorldCat search revealed that the number of master's theses and doctoral dissertations in the 1990s increased 5–7 \times from the numbers in the previous three decades (Fig. 1). The focus of many of those theses and dissertations has also changed, from natural history to management. The surge of information is reflected in scientific journals, as well. Therefore, managers have a wealth of information available to them. However, even with more than 30 years of cowbird control, we seem to be asking the same questions, for which we do not have clear answers: Should we control them locally, specifically to benefit endangered hosts? Should we control them on a regional level? Should we target them during winter, when they are congregated in huge flocks? Should we control them at all?

Although some of the published information (e.g. on improving the efficacy of management programs) can be useful for managers, more information is needed on the actual efficacy of cowbird management. Still largely missing from the plethora of papers and dissertations are data that would help address questions such as "at what point can an endangered host population afford experimental cessation of a cowbird control program?" or "does cowbird control really have to continue in perpetuity?"

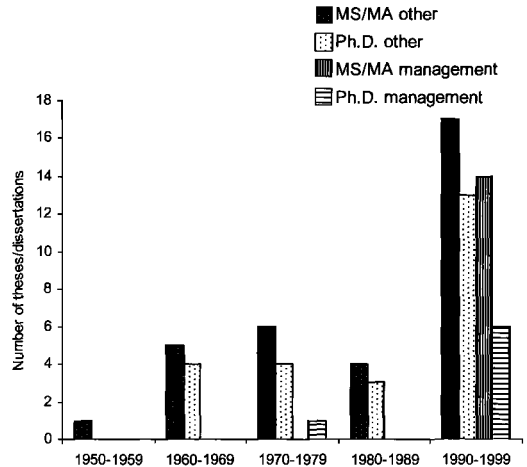


FIG. 1. Number of master's theses and doctoral dissertations about Brown-headed Cowbirds from 1950 through 1999.

The present collection of papers resulted from the symposium "Ecology and Evolution of Host–Parasite Interactions and Cowbird Management," which the authors organized for the American Ornithologists' Union Annual Meeting in Urbana, Illinois, in 2003. The purpose of the symposium was to share knowledge and ideas among researchers and managers. The unifying theme focused on research that contributes to management of cowbirds and their hosts.

The importance of dialogue between researchers and managers is inarguable, as evidenced by two well-attended national meetings on cowbird management—one in 1993 (Smith et al. 2000) and one in 1997 ("Research and Management of Brown-headed Cowbirds in Western and Eastern Landscapes," Sacramento, California; Morrison et al. 1999). The 2003 symposium continued and revitalized the dialogue of the previous meetings.

The papers here were selected specifically because they deal with issues critical to management of cowbirds and their hosts: laws, efficacy, endangered hosts, landscape and landscape-use issues, and evolutionary implications. As the title "Management of Cowbirds and Their Hosts: Balancing Science, Ethics, and Mandates" suggests, management of cowbirds and their hosts is a balancing act that requires consideration of numerous issues that are often controversial. C. P. Ortega et al. (Chapter 1) cover the history leading to those controversies,

some ethical issues of cowbird control, and the laws that protect cowbirds, as well as laws allowing them to be controlled.

A. Cruz et al. (Chapter 4) report on efforts to recover the endangered Yellow-shouldered Blackbird (*Agelaius xanthomus*) population in Puerto Rico from Shiny Cowbird (*M. bonariensis*) parasitism—perhaps one of the most successful programs of cowbird control and host management. Since 1980, a combination of cowbird trapping, cowbird egg removal, and artificial nest construction has reduced parasitism frequency to near zero, enabling a 2.5-fold increase in the Yellow-shouldered Blackbird population. In the face of that success, a dark lining appears; as Cruz and his colleagues relate, 50% of the Yellow-shouldered Blackbird nests in the newly established colonies are parasitized. Without habitat restoration and management at a larger scale, it appears that Yellow-shouldered Blackbird recovery will depend on continued efforts by the Department of Natural and Environmental Resources of Puerto Rico.

In the riparian habitat of the southwest, expensive and time-consuming cowbird removal has been the focus of endangered-species recovery plans for the Least Bell's Vireo (*Vireo bellii pusillus*) and Southwestern Willow Flycatcher (*Empidonax traillii extimus*). As B. E. Kus and M. J. Whitfield (Chapter 2) relate, those efforts have diminished cowbird parasitism while boosting populations of Least Bell's Vireos, but not of Southwestern Willow Flycatchers. The authors effectively argue that cowbird removal is a short-term crisis management tool. Once populations recover, continuing cowbird removal drains resources from potentially more productive, large-scale efforts of habitat restoration and management that might lead to long-term recovery. The time is ripe for careful and rigorous experimentation, refocusing the management effort on broad-scale, long-term strategies in southern California and perhaps with Yellow-shouldered Blackbirds in Puerto Rico and Black-capped Vireos (*V. atricapilla*) in Texas.

R. M. Kostecke et al. (Chapter 3) report on the recovery of Black-capped Vireos at Fort Hood, Texas, which is at once a great success story of cooperation between government and nongovernmental organizations to recover an endangered host population through intensive management and a reminder that cowbird management will persist even after recovery goals

have been met. Reduction of cowbirds through complete removal of cattle from Black-capped Vireo habitat on Fort Hood is not politically realistic, nor would it likely reduce cowbird foraging opportunities, given the rapid urban sprawl in the Texas hill country. Kostecke and his colleagues are left with a long-term management program that may be indefinitely focused on local cowbird control, a harsh reality that many managers can perhaps relate to.

An adaptive management program to reduce cowbird parasitism should mirror the multiple spatial and temporal scales to which cowbirds respond. All too often, management strategies are focused on the proximate without consideration of the ultimate factors involved, as seen in examples from Fort Hood (Chapter 3) and Puerto Rico (Chapter 4). That can lead a project and a host population into perpetual dependence on human intervention.

Three papers deal specifically with issues of appropriate scales of space and time, recognizing the needs of managers to solve problems in the here and now. With the management goal of reducing cowbird abundance and distribution, J. F. Chace et al. (Chapter 5) examine the factors that regulate cowbirds across spatial scales. At the continental scale, cowbird numbers decline with distance from the Midwest; however, parasitism varies across regional scales, largely increasing in areas of low forest cover and high fragmentation. Expanding the continuity of host habitat should be the primary step in any cowbird management program. At the landscape scale, cowbirds appear to be regulated largely by density and locations of feeding opportunities, sometimes independent of livestock. However, the single most productive management strategy in many areas is also the most politically contentious—removal of cattle up to 15 km (Curson et al. 2000) from focal host breeding areas.

C. B. Goguen et al. (Chapter 6) explore the interactions between American bison (*Bos bison*) and cowbirds in New Mexico and find that the long-distance commuting behavior of cowbirds is an adaptive trait for following the nomadic movements of free-ranging bison, a behavior that poses one of the great challenges for managers today. Some foraging opportunities, however, cannot be moved, either physically (e.g. suburban backyards) or politically (e.g. cattle in west Texas); therefore, priority must

be placed on the first point: establishing a large contiguous breeding area for hosts.

Time may be on the side of some hosts. Theoretically, host populations should evolve adaptive responses to cowbirds, become less successful hosts, and eventually be targeted less by cowbirds. B. D. Peer et al. (Chapter 7) point out that cowbirds were probably more common within the past 10,000 years when mammalian megafauna were present, which suggests that most hosts nesting in open areas had contact with cowbirds or are derived from populations that had contact with cowbirds. Numerous hosts that are not currently parasitized may have evolved and maintained defenses from past bouts of parasitism. That is important for two reasons. First, it suggests that not every "newly exposed" host population is in need of cowbird control programs because many of them have retained defenses from past bouts of parasitism or are derived from such populations. Second, hosts that are currently the focus of cowbird control programs, such as Black-capped Vireo, Bell's Vireo, and Southwestern Willow Flycatcher, respond adaptively to parasitism. Peer et al. suggest that increased populations of those hosts warrant experimental relaxation of cowbird control to determine whether those hosts can sustain parasitism and whether those defenses will spread through the populations.

S. I. Rothstein and B. D. Peer (Chapter 8) review the history of cowbird management and point out that the majority of beliefs about cowbirds that have heightened their profile as a threat to North American passerines are not true or are exaggerated. Among those beliefs are that the cowbird is increasing in range and abundance, that it has increased its range over the past 250–300 years, that new host populations are defenseless and prone to extinction, that cowbird parasitism reduces the population size of host species, and that cowbird control increases the reproductive output of host populations. Rothstein and Peer discuss the excesses of cowbird management and how it may actually inhibit recovery of endangered species, and provide an overview of the Southwestern Willow Flycatcher recovery plan, a model for the conservation of endangered songbirds.

It is clear that reducing cowbird parasitism on endangered host species requires (1) clear goals for recovery; (2) a clear understanding of the ultimate factors that regulate distribution and

abundance of cowbirds and subsequent parasitism frequencies; (3) involvement and cooperation of the larger community, focusing management at the broadest spatial and temporal scales necessary; and (4) a management program that is clearly defined with experimental measures of control efficacy and that will produce repeatable results and transferable conclusions.

Each chapter in this volume highlights, often explicitly, the need for future research. Information most needed for assessing the efficacy of cowbird management includes the following.

(1) A more complete understanding of host population persistence across varying levels of parasitism pressure would provide managers more confidence in relaxing cowbird control to determine (a) appropriate cowbird reduction goals, (b) whether larger host populations in which defenses are already present can sustain parasitism, and (c) whether those defenses spread through the populations (see Chapter 2).

(2) We are a long way from understanding the evolutionary implications of cowbird control. Nevertheless, many researchers agree that cowbird control theoretically could have profound effects on the frequency of adaptive antiparasite defense in host populations and may also affect efficacy of cowbird control itself by favoring trap-shy cowbirds. Any future studies investigating evolution of rejecter behaviors and the level of parasitism pressure necessary to retain those adaptations (see Chapter 7) would add greatly to knowledge that can be applied to management.

(3) Further information on the relationship of cowbird clutch size and commuting distance (see Chapter 6) would allow us to more accurately predict the indirect effects of grazing and the efficacy of cowbird control.

(4) By necessity, recovery plans mandate habitat restoration and cowbird control concurrently. Therefore, it is difficult to determine which has a greater effect on recovering populations. We presume that both do. Studies, using surrogate populations (e.g. Warbling Vireos [*V. gilvus*]), that separate those confounding variables would aid in recovery goals and in determining when we can relax cowbird control.

(5) In addition to understanding host responses to habitat restoration, understanding responses of cowbirds to habitat restoration and reduction of supplemental foraging locations would help us better predict patterns of

parasitism; for example, would parasitism on Black-capped Vireos remain low if cattle were removed from Fort Hood and the greater community reduced supplemental feeding opportunities? (See Chapter 3.)

(6) To address cowbird control at the appropriate spatial scale, we need a better understanding of local factors that determine cowbird abundance and landscape-level factors that influence the distribution and abundance of cowbirds that are (a) not in forested landscapes and (b) not feeding with cattle (see Chapters 5 and 4, respectively).

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CHAPTER 1

ISSUES AND CONTROVERSIES OF COWBIRD (*MOLOTHRUS* SPP.) MANAGEMENT

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ABSTRACT.—Brood-parasitic Brown-headed Cowbirds (*Molothrus ater*) have been implicated in the Federally-endangered status of five hosts as well as in declines of numerous other Nearctic–Neotropical passerines that breed in North America. Cowbird control is an integral management strategy in the recovery plans of all five hosts. Although there are a few exceptions, a line appears to be drawn between managers, whose main objective is to increase host population numbers, mainly through cowbird control, and academic researchers, who want empirical evidence that cowbirds cause declines and that cowbird control actually works. The objectives here are to (1) provide a brief summary of the status of cowbird hosts, (2) provide background on when and why cowbird management became controversial, (3) discuss the federal laws protecting cowbirds and inconsistencies in interpretation of laws, (4) discuss some concerns about widescale cowbird control, and (5) discuss some management issues regarding Bronzed Cowbirds (*M. aeneus*) and Shiny Cowbirds (*M. bonariensis*).

RESUMEN.—El tordo parásito de cría *Molothrus ater* ha sido implicado en la situación de “Federalmente en peligro” de cinco especies de hospedadores, así como de otros numerosos Paserines Neártico-Neotropicales que se reproducen en Norteamérica. El control de los tordos parásitos es una estrategia de manejo integral dentro del plan de recuperación de dichas cinco especies de hospedadores. Si bien existen algunas pocas excepciones, sería necesario trazar una vía de comunicación entre las personas a cargo del manejo en sí, cuyo objetivo principal es incrementar el tamaño poblacional de los hospedadores mediante el control de los tordos parásitos, y los investigadores académicos que buscan evidencias empíricas que demuestren que dicho control realmente funciona. Los objetivos aquí desarrollados son: (1) proveer de un breve compendio sobre la situación de los hospedadores de los tordos parásitos, (2) proveer de la información básica acerca de cuándo y por qué el manejo de los tordos puede transformarse en una medida controvertida, (3) discutir las leyes federales que protegen a los tordos y las inconsistencias en la interpretación de las mismas, (4) discutir algunos asuntos relativos al manejo a gran escala de los tordos parásitos, y (5) discutir brevemente algunas cuestiones de manejo referidas a otras dos especies de tordos parásitos: *M. aeneus* y *M. bonariensis*.

BROOD-PARASITIC BROWN-HEADED COWBIRDS (*Molothrus ater*) have been implicated in the declines of several Nearctic–Neotropical passerines that breed in North America. Farther south, Bronzed Cowbirds (*M. aeneus*) and Shiny Cowbirds (*M. bonariensis*) have also been implicated in the declines of several species. Whether or not cowbirds have caused passerine

declines has been debated for several decades without clear resolution (Morrison et al. 1999, Smith et al. 2000). Although there are a few exceptions, a line appears to be drawn between managers, whose main objectives is to increase host population numbers, mainly through cowbird control, and academic researchers, who want empirical evidence that cowbirds cause declines and that cowbird control actually works.

At times, the arguments are passionate, as was evident at two major national meetings on

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the ecology and management of cowbirds (see Morrison et al. 1999 and Smith et al. 2000) and at the cowbird symposium (Ecology and Evolution of Host-Parasite Interactions and Cowbird Management) at the American Ornithologists' Union Annual Meeting in Urbana, Illinois, in 2003. The arguments are not necessarily "bad" or a waste of energy, so long as they keep the dialogue going. The tension may serve as a checks-and-balances system, with both sides questioning, evaluating, and justifying their points of view.

Our objectives in the present chapter are to (1) provide a brief summary of the status of cowbird hosts, (2) provide background on when and why cowbird management became controversial, (3) discuss the federal laws protecting cowbirds and inconsistencies in interpretation of those laws, and (4) discuss some concerns about widescale cowbird control.

STATUS OF COWBIRD HOSTS

A majority of declining North American passerines are "biological hosts" of the Brown-headed Cowbird. Biological hosts are those that (1) are parasitized on a regular basis, (2) do not reject cowbird eggs, and (3) are known to successfully raise cowbirds (Ortega 1998). A simple analysis of BBS data shows that passerine population declines are probably coincidental with cowbird populations. Of 229 native passerine species in the BBS database (excluding Brown-headed Cowbirds and Bronzed Cowbirds), 145 (63.3%) are biological hosts. Of 67 species that have declined between 1966 and 2002, 73.1% are hosts; of 15 species that have declined only between 1980 and 2002, 53.3% are hosts; of 48 species that increased between 1966 and 2002, with no declines between 1980 and 2002, 52.1% are hosts; of 10 species that increased only between 1980 and 2002, 80% are hosts; and of 89 species without apparent trends, 61.8% are hosts ($P > 0.1$, $\chi^2 = 7.394$, $df = 4$).

Five passerines listed as federally endangered or threatened under the Endangered Species Act (ESA) are cowbird hosts: Southwestern Willow Flycatcher (*Empidonax traillii extimus*; U.S. Fish and Wildlife Service [USFWS] 2001), Least Bell's Vireo (*Vireo bellii pusillus*; Franzreb 1988, USFWS 1998), Black-capped Vireo (*V. atricapilla*; USFWS 1991), Kirtland's Warbler (*Dendroica kirtlandii*; USFWS 1976a),

and Golden-cheeked Warbler (*D. chrysoparia*; USFWS 1992). Black-capped Vireos, Kirtland's Warblers, and Golden-cheeked Warblers are not in the BBS database and are, therefore, excluded from the above analysis. In the BBS database, Least Bell's Vireos and Southwestern Willow Flycatchers are pooled with other populations of Bell's Vireos and Willow Flycatchers, respectively. Associated with their status under the ESA, each species has a small range and restricted habitat needs. Nevertheless, cowbirds have been implicated in the declines of all those federally endangered hosts (Mayfield 1973, 1977; Shake and Mattsson 1975; Goldwasser et al. 1980; Grzybowski et al. 1986, 1994; Franzreb 1987; Sedgwick and Knopf 1988; Harris 1991).

The goal of the ESA is to increase populations so that species no longer need protection under the ESA. Therefore, the ultimate goal of the ESA is to de-list species. In addition to the ecological benefits of recovery, for each species that is de-listed, funds become available for other species in greater need of protection. Each recovery plan identifies de-listing or down-listing goals. Theoretically, when those goals have been achieved, the USFWS considers down-listing the species or removing it from the list. Although the recovery plans for each of the five listed passerines differ with regard to specific recovery goals, all recovery plans identify cowbird control as one of the management tools that should be considered.

THE CONTROVERSY OVER COWBIRDS AND COWBIRD CONTROL

Cowbirds, particularly Brown-headed Cowbirds, have a long history of being disrespected and even loathed by humans, as is evident in early and contemporary secondary literature. They are accused of being wretched, immoral, pests, arch villains, lazy, social outcasts, and killers—among many other epithets (see Ortega 1998). Application of such moralistic terms to nonhuman organisms reflects, at least to some degree, an illogical expectation that other organisms should live by human standards of behavior.

Such emotional responses can be dangerous in the context of wildlife management. Disdain for certain animals, such as coyotes (*Canis latrans*) and wolves (*C. lupis*), has led to widescale slaughter and mismanagement,

ultimately leading to unbalanced predator:prey ratios in many habitats. When the general public is allowed or encouraged to cull disdained animals, enthusiasm can get out of hand; people often do not understand the animals' ecological role or the inappropriateness of expecting them to live by human cultural standards.

Adding fuel to the fire, Mayfield (1977) suggested that cowbirds were "agents of extermination" for endangered Kirtland's Warblers. A few years later, Brittingham and Temple (1983) assumed that cowbird numbers were increasing. Flaws in that assumption have been covered elsewhere (Ortega 1998); in fact, BBS data indicate that Brown-headed Cowbird numbers have significantly declined over the past several decades, including during the time when the Brittingham and Temple (1983) article was published and in the region in which their study was conducted. Nevertheless, Brittingham and Temple (1983) continue to be cited by authors who claim that cowbird numbers are increasing; for example, the article is cited in the Black-capped Vireo Recovery Plan in reference to cowbird population growth.

Controversy over cowbird control intensified in the early 1990s, after the Least Bell's Vireo, Black-capped Vireo, and Golden-cheeked Warbler were listed as endangered, and further escalated after the Southwestern Willow Flycatcher was listed. The arguments between academic researchers and managers became so passionate that they deteriorated into shouting matches at the national cowbird meetings. Those arguments, well documented in the literature (Schram 1994, Smith 1994, Grzybowski and Pease 1999, Ortega 2000, Rothstein 2004), are still unresolved.

Is the researchers' criticism of cowbird control based on hysteria or facts? Perhaps both; but flawed assumptions and emotions regarding cowbirds should have no place in management programs. Additionally, it has long been suspected by some researchers that cowbird control is partially driven by monetary interests (Rothstein 2004), which also should play no role in cowbird control.

LAWS PROTECTING COWBIRDS

The Migratory Bird Treaty with Canada (Convention between the United States and Great Britain [for Canada]) for the Protection of Migratory Birds was adopted to protect birds that

migrate between the United States and Canada to ensure preservation of species that are either harmless or beneficial to humans. The treaty sets beginning and ending dates for migratory-bird hunting seasons, prohibits hunting insectivorous birds, but allows killing of birds with a permit when the birds are injurious to agriculture. Signed in Washington, D.C., on 16 August 1916, the treaty was ratified by the U.S. Senate on 1 September 1916 and by Great Britain on 20 October 1916. Implementing legislation for the United States was accomplished by enactment of the Migratory Bird Treaty Act (MBTA) in 1918 (16 USC 703-711; 40 Stat. 755). The MBTA prohibits the taking of migratory birds, stating (§703):

Unless and except as permitted...it shall be unlawful at any time, by any means or in any manner, to pursue, hunt, take, capture, kill, attempt to take, capture, or kill, possess, offer for sale, sell, offer to barter, barter, offer to purchase, purchase, deliver for shipment, ship, export, import, cause to be shipped, exported, or imported, deliver for transportation, transport or cause to be transported, carry or cause to be carried, or receive for shipment, transportation, carriage, or export, any migratory bird, any part, nest, or eggs of any such bird, or any product, whether or not manufactured, which consists, or is composed in whole or part, of any such bird or any part, nest, or egg thereof, included in the terms of the conventions between the United States....

Other treaties were enacted with the United Mexican States for protection of migratory birds and game mammals on 7 February 1936; with the Government of Japan for protection of migratory birds and birds in danger of extinction, and protection of their environment, on 4 March 1972; and with the Union of Soviet Socialist Republics for the conservation of migratory birds and their environments on 19 November 1976.

The species protected by MBTA are listed in 50 CFR § 10.13 and include all cowbirds, as members of the Family Icteridae and as listed in the 1972 amendment to the Mexican convention. The USFWS has responsibility for administering MBTA and managing all migratory avian species protected by MBTA.

The MBTA prohibits intentional taking of migratory birds unless a specific permit has been issued. Permitting requirements are found in 50 CFR part 13 (General Permit Procedures) and 50 CFR part 21 (Migratory Bird Permit). Permits

issued for taking of Brown-headed Cowbirds include "scientific collecting" (§ 21.23), "special purpose" (§ 21.27), and "depredation" (§ 21.41). No permit is required to take birds under the specific depredation orders (§§21.42–21.47).

DEPREDATION ORDER

Depredation Order (DO) § 21.43 states:

A Federal permit shall not be required to control yellow-headed, red-winged, rusty, and Brewer's blackbirds, cowbirds, all grackles, crows, and magpies, when found committing or about to commit depredations upon ornamental or shade trees, agricultural crops, livestock, or wildlife, or when concentrated in such numbers and manner as to constitute a health hazard or other nuisance....

Although Brown-headed Cowbirds are included in the DO, inconsistent interpretations exist among USFWS regions. For example, many actions currently used to control cowbirds under the DO in Region 2 (covering Arizona, New Mexico, Oklahoma, and Texas) may not be covered by the DO in other USFWS regions. The DO requires that individual birds being targeted must be "depredating or about to depredate...wildlife."

Therefore, we believe that the DO should not cover adding cowbird eggs, removing cowbird nestlings, killing male or juvenile cowbirds (all of which are incapable of nest parasitism), killing cowbirds outside the breeding season, or trapping nontarget species. However, direct selective removal of adult female Brown-headed Cowbirds during the breeding season may be allowed under the DO because parasitism or removal of host eggs is considered to be "committing depredation on wildlife" as defined in § 21.43. Additionally, because the DO does not specifically refer to Brown-headed Cowbirds, only to "cowbirds," Bronzed and Shiny Cowbirds could also be covered in the DO if they were documented as depredating on wildlife. It is inappropriate to use the DO to justify Brown-headed Cowbird trapping as mitigation for habitat loss and destruction.

DEPREDATION PERMIT

The USFWS is authorized to issue depredation (DPRD) permits for removal of migratory

bird species, but the applicant must demonstrate that the problem species is threatening or causing immediate damage to real property. That is sometimes difficult to do for Brown-headed Cowbirds because few data show that the effect of parasitism is threatening host species or that trapping is effective (Ortega and Ortega 2001, Morrison and Averill-Murray 2002.). The DPRD permits states, "Permittees may not use blinds, pits, or other means of concealment, decoys, duck calls, or other devices to lure or entice birds within gun range." Currently, DPRD permits are issued to cover the use of lures, such as individuals left in traps. Furthermore, the accidental trapping of "nontarget" species would be a technical violation of MBTA and could not be authorized by permit. For a DPRD permit, USFWS requires (1) evidence of biologically significant parasitism linked to depressed host-productivity rates, (2) an estimate of the number and species of nontargets that could be affected, and (3) methods to minimize mortality and other effects in nontarget populations. Generally, USFWS will issue cowbird DPRD permits only for the direct protection of endangered or threatened species, or species of special concern.

SCIENTIFIC COLLECTION PERMIT

Scientific collection (SCCL) permits are issued for the scientific study of birds and their populations. They are issued to individuals collecting birds on behalf of scientific institutions and agencies for education and scientific purposes. They are issued for removal of cowbirds only if a legitimate scientific question is being asked. In such cases, enough detail should accompany the permit request to allow evaluation of the sufficiency of methods. Requirements for an SCCL include (1) statement and documentation of the problem and objectives in a scientifically credible format, including valid scientific methods; (2) scientific personnel and institutions conducting the work; and (3) protection of all species potentially affected by the study.

SPECIAL PURPOSE–MISCELLANEOUS PERMIT

Special purpose–miscellaneous (SPMS) permits can also be issued when the applicant demonstrates a legitimate purpose not otherwise provided for by any standard permit. Such permits will not be issued for Brown-headed

Cowbird control and removal if the only purpose is removal of cowbirds to decrease parasitism rates on other species.

REGIONAL DIFFERENCES IN THE U.S. FISH AND
WILDLIFE SERVICE'S INTERPRETATION OF LAWS
PROTECTING COWBIRDS

The USFWS is organized into seven field regions, and all permits under MBTA are issued at the regional level. The language authorizing taking of birds under the MBTA does not provide explicit guidance on the appropriate legal instrument that USFWS should issue to individuals or organizations that wish to legally trap and remove cowbirds. Consequently, USFWS field regions have differed in their interpretation of regulations, with regions issuing permits under different authorities and with different standard conditions. Some USFWS regions have issued DPRD, SPMS, or SCCL permits for cowbird trapping, whereas other regions have allowed the action under the DO. The USFWS recognizes the need for inter-regional consistency on this topic and attempted to draft policy to standardize requirements for issuance of a permit for such purposes and to determine the appropriate standard conditions for permits involving cowbird trapping and removal. These efforts were put on hold by Region 2 with issuance of a letter from the Regional Director to Texas Parks and Wildlife Department (RZ/MB/SP-MB CL 1-25), stating that many actions used to control cowbirds are covered under the DO. However, the same actions are not covered under the DO in other regions. In the interim, some regional staff agreed on issuing such permits under DPRD, though regional policies and interpretations continue to differ.

CONCERNS ABOUT WIDESCALE CONTROL OF
COWBIRDS

Cowbirds are easy to trap—particularly with decoy traps; they are gregarious and attracted to other cowbirds, as well as to food and water. Trapping cowbirds requires far less effort than enhancing or restoring habitat, particularly when land ownership is in fragmented private holdings. Although cowbird control is, at best, only a stop-gap approach, some managers in charge of recovering endangered species view

cowbird control as an in-perpetuity solution (G. Echrich pers. comm.), and widescale winter control of cowbirds was suggested by Laymon (1987), Schram (1994), and Grzybowski and Pease (1999). Grzybowski and Pease (1999) suggested a policy in which “exploiting large aggregations of cowbirds appears a relatively feasible and cost-effective mechanism of enhancing regional songbird reproductive performance.” Although such methods may appear inviting to managers responsible for controlling cowbirds, most academic researchers have rejected them for myriad reasons, including cowbirds not being a problem throughout their range, concerns about ethical issues, and concerns about disrupting the ecology and evolution of host–parasite relationships (Smith 1994, Ortega 2000, Rothstein 2004).

Brown-headed Cowbirds are neither a major problem throughout their range nor a serious threat to all their major hosts. Even in areas where Brown-headed Cowbirds are implicated in host declines, other causes have also been identified. In each case, habitat loss and changes in land use have been the primary reasons for the declines (Franzreb 1990; USFWS 1991, 1992; Probst and Weinrich 1993; Hatten and Paradzick 2003). Additionally, many hosts can raise their own offspring along with cowbirds (references in Ortega 1998). It is primarily hosts with incubation periods 4–5 days longer than the cowbird's that experience the most negative effects of parasitism (Ortega 1998). The number of host offspring successfully raised is often lower in parasitized nests; however, the assumption that parasitized nests are destined to failure is unequivocally incorrect.

In the southern United States and California, some cowbirds appear to be residents; most other individuals migrate between breeding and wintering grounds (Lowther 1993). However, the migration pattern of cowbirds is complex and not well understood. It is clear from Coon and Arnold's (1977) banding study that cowbirds from one wintering location spread throughout the country to breed, and cowbirds from one breeding location spread throughout the southern states to winter. Only a very small proportion of cowbirds captured in winter would breed in the same location. Therefore, “regional control” is a misnomer, in that such efforts target the entire range, not just a region (Ortega 2000). The practice is not

only ineffective, but also raises concerns about evolutionary implications.

To our knowledge, the evolutionary implications of widespread control are not addressed at the management level. Though speculative at this point, such implications should be considered for both hosts and cowbirds. Some host populations appear to have some incipient defense mechanisms. For example, many Warbling Vireos (*V. gilvus*) in the eastern United States and Canada reject cowbird eggs (Sealy 1996, Sealy et al. 2000). Relaxing selective pressure from cowbirds could affect hosts that have well-established anti-parasite defense mechanisms if cowbird eradication becomes long-term and widespread. Although widescale control does not target for phenotype or behavior (other than flocking behavior), trapping targets individuals that are unwary of traps. Eventually, a persistent trapping effort may result in trap-wary individuals that will be difficult to catch. Targeted and persistent trapping may also result in sex ratios that are not natural to the area, and the effects of changing sex ratios are unknown.

Researchers have also been concerned about the ethical implications of control programs. The primary concern is that if animal-rights activists become alarmed over massive destruction of cowbirds, they may be able to effect a change in policy and potentially jeopardize well-justified control programs. Animal-rights advocates historically have had a powerful voice and have been able to change activities and methods of scientists (Mayer et al. 1994, Webb and Jackson 1996). Ethical issues have already been raised by individuals in the general public. For example, a woman from outside of Comfort, Texas, whose name is withheld to protect her privacy, came forward during the breeding season of 2002. Referring to her neighbor, who participates in the program promoted by Texas Parks and Wildlife (see below), she wrote (to C.P.O.):

I am appalled by the concept of this cowbird trap and "support" of this program through groups such as the Texas Cattlemen's Assoc and Tx. Parks and Wildlife. This neighbor periodically slaughters the birds inside by beating them with a tennis racquet—so my first reaction is to direct PETA [People for the Ethical Treatment of Animals] and the Humane Society after him. However, I'd prefer to pursue administrative and regulatory channels first.

This individual, who works for an environmental group, has not yet approached the Humane Society or PETA, but she continues to be concerned about the future prospects for cowbirds in Texas.

CONCERN ABOUT COWBIRD CONTROL AT FORT HOOD, TEXAS

In the 1990s, at Fort Hood, Texas, which has critical habitat for Golden-cheeked Warblers and Black-capped Vireos, local ranchers and landowners became aware of some research on those endangered species. The ranchers, who leased grazing rights on Fort Hood, were unhappy with the resulting management recommendations when they were asked to remove several hundred head of cattle (Deike 2000). In an effort to diffuse the growing distrust and contention between the managers at Fort Hood and local ranchers, lessees, and landowners, a collaborative effort to trap cowbirds was undertaken by Texas Parks and Wildlife, the Texas Cattlemen's Association, The Nature Conservancy, and landowners. Texas Parks and Wildlife coordinates the collaborative effort and provides financial incentives for landowners who want to participate in the program (Texas Parks and Wildlife 2005).

Texas Parks and Wildlife assures the public that trapping and killing of Brown-headed Cowbirds by citizens is covered under the DO. The agency's website states: "Brown-headed Cowbirds are included among this small group of eight non-protected bird species that may be...killed at any time and their nests or eggs may be destroyed" (Texas Parks and Wildlife 2005). However, as noted above, we believe it is inappropriate to interpret the DO as covering actions against males, juveniles, and eggs, though it may cover selective removal of females during the breeding season. If any nontarget protected species are captured and held, even for as little as an hour during the breeding season, the capture could result in loss of the nestlings. Death of nontarget protected species, nearly unavoidable in cowbird trapping operations, is a technical violation of MBTA, and no permit is available under MBTA to cover such takes. Also, cowbird control programs implemented by citizens could have an unknown effect on nontarget species, and their activities could harm the species targeted for protection (Terpening 1999).

It is unfortunate that the local ranching community that would eventually be affected was not included in finding solutions based on the endangered species research. Research and management recommendations should involve any community that could be affected. Nevertheless, to entice ranchers and other landowners into cowbird trapping, an activity that is every bit as contentious and potentially controversial as grazing, is not the best answer.

OTHER COWBIRDS

BRONZED COWBIRDS

Bronzed Cowbirds are generalist brood parasites that occur from northern Colombia into southern Texas, southern New Mexico, and southwestern and western Arizona (Lowther 1995). In winter, they are locally abundant around grain elevators in southern Texas (Lowther 1995), are generally rare and local in Arizona (mostly in feedlots), and are very rare to irregular in southern New Mexico (the first winter record in New Mexico was in 1995; B. Howe pers. comm.). Bronzed Cowbirds expanded their range following the first records in Arizona in 1909, with a noticeable spread northward in Texas after 1951 (Lowther 1995). That expansion was probably accelerated by an increase in agricultural production (Lowther 1995).

Limited trend information is available from the BBS. In 2002, 545 Bronzed Cowbirds were recorded on 70 routes (Sauer et al. 2003), an increase from 1977, when 213 were counted on 22 routes (Lowther 1995). No significant trends were detected for the survey period (1966–2002) except in Arizona (-7.5 , $P = 0.04$, $n = 15$) and the Western BBS region, which includes Arizona (Sauer et al. 2003).

The two subspecies that occur in the United States have different trends. *Molothrus aeneus aeneus* is common and possibly increasing in south Texas. It has not yet been recorded with certainty in New Mexico (S. O. Williams III pers. comm. to B. Howe). The BBS trend for Texas is nonsignificantly positive (1.3% year⁻¹, $P = 0.42$, $n = 49$, 1966–2002), though recently the trend has been significantly negative (-3.2% year⁻¹, $P = 0.07$, $n = 48$, 1980–2002; Sauer et al. 2003). Bronzed Cowbirds have been suspected as a factor in the decline of Hooded Orioles

(*Icterus cucullatus*) along the lower Rio Grande (Pleasants and Albano 2001).

Molothrus aeneus loyei in Arizona and southern New Mexico is less common and more riparian-oriented than *M. a. aeneus*, especially in middle-elevation mountain canyons in Arizona. It is decreasing in Arizona (Sauer et al. 2003), but it has increased in New Mexico where it was first recorded in the southwest corner in 1947 and had spread across the southern third of the state as a summer resident by the mid-1990s (S. O. Williams III pers. comm. to B. Howe).

Eighty-two species are parasitized by Bronzed Cowbirds, with 32 species recorded as rearing Bronzed Cowbird young (Lowther 1995). Bronzed Cowbirds appear to prefer *Icterus* orioles, including Hooded, Audubon's (*I. graduacauda*), Streak-backed (*I. pustulatus*), and Altamira (*I. gularis*) orioles, as hosts (Friedmann 1963). The endangered Golden-cheeked Warbler has been documented as a host species (Friedmann and Kiff 1985); however, more recently, there are no records of parasitism of Golden-cheeked Warblers (G. Echrich pers. comm.). No threatened or endangered species are regular hosts of Bronzed Cowbirds, and they are not actively being managed. However, they are often killed in Brown-headed Cowbird control programs.

SHINY COWBIRDS

Shiny Cowbirds, originally from South America, Trinidad, and Tobago, are generalist brood parasites that successfully colonized the West Indies during the 1900s (Cruz et al. 1985, 1989, 2000; Lowther and Post 1999). Shiny Cowbirds arrived in the United States through Florida (Lowther and Post 1999, Cruz et al. 2000) and are provided full protection under the MBTA as members of the family Icteridae.

The spread of Shiny Cowbirds through the West Indies has been well documented (Cruz et al. 1985, 2000; Lowther and Post 1999). In the United States, Shiny Cowbirds have increased from 1 bird reported in 1985 to 109 in 1990 (Lowther and Post 1999). Shiny Cowbirds were first sighted on the Florida Keys in 1985, and by the 1990s, they were reported in other Florida localities and as far north as the Carolinas and Maine and as far west as Texas and Oklahoma (Cruz et al. 1998).

Throughout the Shiny Cowbird's range, 232 species are recorded as its hosts, with 74 species

recorded as rearing cowbird young (Lowther and Post 1999). Like Brown-headed Cowbirds, Shiny Cowbirds have been implicated in the declines of some of their hosts. On Puerto Rico, Shiny Cowbirds parasitize the endangered Yellow-shouldered Blackbird (*Agelaius xanthomus*; USFWS 1976b) and numerous other species, including other icterids, vireos, and warblers (Cruz et al. 1989, Woodworth 1997, Nakamura and Cruz 2000). On Martinique, Shiny Cowbirds have been implicated in the population decline of Martinique Orioles (*I. bonana*). Greater Antillean Orioles (*I. dominicensis*) are heavily parasitized on Puerto Rico and Hispaniola, and they have also been recorded as a Shiny Cowbird host in Cuba (J. W. Wiley pers. comm).

There is no documentation of parasitism by Shiny Cowbirds in Florida, though four species—Black-whiskered Vireo (*V. altiloquus*), Prairie Warbler (*D. discolor*), Northern Cardinal (*Cardinalis cardinalis*), and Red-winged Blackbird (*A. phoeniceus*)—are known to have been hosts to unidentified cowbirds within the south Florida range of the Shiny Cowbird (Cruz et al. 1998, Lowther and Post 1999).

Relatively little is known about the current status of the Shiny Cowbird and its hosts in South America. According to the Red Data Book (Collar et al. 1992), out of 138 South American species that are potential Shiny Cowbird hosts, Shiny Cowbirds have been implicated in the endangered status of Saffron-cowled Blackbirds (*Xanthopsar flavus*) and Forbe's Blackbirds (*Curaeus forbesi*). Loss of wetlands and conversion of pastures to plantations are more important in the endangered status of Saffron-cowled Blackbirds than Shiny Cowbird parasitism (Fraga et al. 1998). It must be noted that nests were known for only 26 of the 138 species (Collar et al. 1992); therefore, lack of knowledge regarding basic breeding biology of most of those species precludes knowledge about the possible effect of Shiny Cowbird parasitism.

CONCLUSION

Cowbird control is an easy alternative to the difficult problem of implementing strategies that address habitat loss and land-use changes, but cowbird control does not contribute to the objective of self-sustaining host populations. It is a year-to-year stop-gap measure that

ideally should not be viewed as a long-term solution because it is counterproductive to sound conservation strategies in the goals of the ESA. Cowbird control should never be based on unscientific, anthropomorphic disrespect for their cunning and successful reproductive strategy. Cowbird control programs that are questionably legal, especially those that involve the general public, such as the program in the Fort Hood area, have little social value and place private citizens in jeopardy of violations of federal law.

Instead, the real issues that are preventing self-sustaining populations of threatened and endangered birds must be addressed; in every case of endangered cowbird hosts, the primary issue is habitat loss. Furthermore, responsible management, based on sound scientific evidence that can tease apart effects of cowbird control and habitat or land-use changes, is the only way to meet the goals of the ESA. Responsible management must also include education and making the best of all opportunities to enhance, restore, and protect critical habitat. Such opportunities include purchase of conservation easements and incentives for landowners to donate them, which is a win-win alternative—the target birds (as well as other wildlife) gain habitat, and landowners often benefit financially, particularly in states that allow purchase of tax credits by a second party. Funds saved from expensive cowbird control programs can be used for such alternative management strategies, which would contribute to the success of self-sustaining populations of target birds and other wildlife.

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CHAPTER 2

PARASITISM, PRODUCTIVITY, AND POPULATION GROWTH: RESPONSE OF LEAST BELL'S VIREOS (*VIREO BELLII PUSILLUS*) AND SOUTHWESTERN WILLOW FLYCATCHERS (*EMPIDONAX TRAILLII* *EXTIMUS*) TO COWBIRD (*MOLOTHRUS* SPP.) CONTROL

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ABSTRACT.—Cowbird (*Molothrus* spp.) control is a major focus of recovery-oriented management of two endangered riparian bird species, the Least Bell's Vireo (*Vireo bellii pusillus*) and Southwestern Willow Flycatcher (*Empidonax traillii extimus*). During the past 20 years, annual trapping of cowbirds at Least Bell's Vireo and Southwestern Willow Flycatcher breeding sites has eliminated or reduced parasitism in comparison with pretrapping rates and, thereby, significantly increased seasonal productivity of nesting pairs. Enhanced productivity, in turn, has resulted in an 8-fold increase in numbers of Least Bell's Vireos; Southwestern Willow Flycatcher abundance, however, has changed little, and at some sites has declined despite cowbird control. Although generally successful by these short-term measures of host population response, cowbird control poses potential negative consequences for long-term recovery of endangered species. As currently employed, cowbird control lacks predetermined biological criteria to trigger an end to the control, making these species' dependence on human intervention open-ended. Prolonged reliance on cowbird control to manage endangered species can shift attention from identifying and managing other factors that limit populations—in particular, habitat availability. On the basis of our analysis of these long-term programs, we suggest that cowbird control be reserved for short-term crisis management and be replaced, when appropriate, by practices emphasizing restoration and maintenance of natural processes on which species depend.

RESUMEN.—El manejo orientado hacia la recuperación de dos especies de aves ribereñas *Vireo belli pusillus* y *Empidonax traillii extimus* se ha focalizado principalmente en el control de los *Molothrus* spp parásitos. Durante los pasados 20 años, la captura anual de los *Molothrus* en las áreas de nidificación de *Vireo belli pusillus* y *Empidonax traillii extimus* ha eliminado o reducido el parasitismo en comparación con las tasas previas a la captura y, en consecuencia, ha incrementado significativamente la productividad estacional de las parejas reproductivas. Ese mejora en productividad, a su vez, ha resultado en que el número de *Vireo belli pusillus* se incrementara 8 veces. La abundancia de *Empidonax traillii extimus* en cambio, ha variado poco, e incluso en algunos sitios, se ha reducido a pesar del control de los *Molothrus*. Aunque aparentemente el control de *Molothrus* fue exitoso por los resultados obtenidos a corto plazo, el control de los *Molothrus* posee consecuencias potencialmente negativas para la recuperación a largo plazo de las especies en peligro. De la forma en que es actualmente aplicado, el control de los *Molothrus* carece de criterios biológicos predeterminados que permitan dejar de aplicarlo. Esto implica que las especies que se quiera proteger dependan eternamente de la intervención humana. El hecho de que que el manejo de las especies en peligro se base en la dependencia prolongada en el control de los *Molothrus* podría distraer la atención sobre la identificación y el manejo de otros factores que limitan dichas poblaciones— en particular, la disponibilidad de hábitat. Basándonos en nuestro análisis de estos programas a largo plazo, sugerimos que el

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control de *Molothrus* quede reservado para las crisis de manejo de corto plazo. Cuando fuera apropiado, es de esperar que dicho manejo sea reemplazado por prácticas enfatizadas hacia la restauración y el mantenimiento de los procesos naturales de los cuales esas especies en realidad dependen.

LEAST BELL'S VIREO (*Vireo bellii pusillus*; hereafter "vireo") and Southwestern Willow Flycatcher (*Empidonax traillii extimus*; hereafter "flycatcher") are two federally endangered passerines that have been managed with cowbird (*Molothrus* spp.) control for the better part of the past two decades. Along with Kirtland's Warbler (*Dendroica kirtlandii*; DeCapita 2000), the vireo was one of the earliest endangered species for which cowbird control formed a prominent component of recovery-oriented management, providing a model for management of other parasitized species, such as the Black-capped Vireo (*V. atricapilla*; Hayden et al. 2000) and the flycatcher (U.S. Fish and Wildlife Service [USFWS] 2002). That, in turn, has stimulated interest in the use of cowbird control to enhance populations of riparian birds in general, many of which are major cowbird hosts (e.g. Griffith and Griffith 2000). Because managers are increasingly considering the use of cowbird control as a tool for protecting sensitive birds, it is essential that the results of established control programs and their efficacy be made available to inform their decision making. Here, we evaluate the effectiveness of cowbird control for increasing populations of vireos and flycatchers, expanding and updating earlier assessments (Whitfield et al. 1999, Griffith and Griffith 2000, Whitfield 2000), and comment on the role of cowbird management in recovery of endangered species.

STUDY SPECIES

Vireos and flycatchers share many similarities in life histories and population trends over the past half-century (Brown 1993; USFWS 1998, 2002; Sedgwick 2000). Both species are riparian obligates, limited during the breeding season to dense shrubby vegetation along the margins of rivers and lakes. Predation accounts for approximately 20–50% of nest failures annually, and pairs of both species typically attempt 1–3 nests in a season (Kus 1999, Griffith and Griffith 2000, Whitfield 2000). Breeding-site fidelity is high in

both species, and vireos and flycatchers have a similar life expectancy of 1–3 years.

Despite these similarities, vireos and flycatchers differ in their vulnerability to cowbird parasitism. Vireos begin nesting approximately two weeks before the arrival of locally breeding cowbirds; thus, the earliest nesting pairs can avoid parasitism (Kus 1999). In contrast, the flycatchers' breeding season in California completely overlaps the period of cowbird laying (mid-April to late July), and flycatchers are one of the few hosts still nesting by late summer. Male vireos participate in all aspects of nesting, including nest construction and incubation, and often sing from the nest; whereas male flycatchers' contribution is largely limited to feeding nestlings, and they are generally quiet around nest sites, which may reduce parasitism (Uyehara and Narins 1995). Vireos cannot fledge their own young from nests in which cowbirds hatch (Kus 1999), but flycatchers sometimes do so (Whitfield and Sogge 1999).

Vireos and flycatchers were considered common and widespread by late-19th-century and early-20th-century naturalists (Mearns 1890, Behle 1943, Grinnell and Miller 1944, Oberholser 1974, J. Hubbard unpubl. data). By the 1950s, both species were declining concurrently with widespread habitat loss and degradation, as agriculture, grazing, flood control, aggregate extraction, and urbanization reduced southwestern U.S. riparian forests to 5% of their former extent (Goldwasser et al. 1980, Unitt 1987). Cowbird parasitism probably played a secondary role in these declines, as vireo and flycatcher populations became small, fragmented, and unable to withstand heavy parasitism (Whitfield and Sogge 1999). Vireos were particularly susceptible to parasitism, with 100% of nests parasitized in some populations (Goldwasser et al. 1980). Parasitism was also high among flycatcher nests (Hanna 1928, Unitt 1987). When the vireo was listed as endangered under the Federal Endangered Species Act in 1986, its population included only 300 males and was restricted to a few southern California

drainages (USFWS 1998). Flycatchers were listed in 1995, at which time they still occupied most of their historic range but in much reduced numbers (Marshall 2000), with a rangewide population of ~350 territories in seven states (USFWS 2002).

Recovery plans for the vireo and flycatcher both emphasize the need to arrest and reverse the loss of riparian habitat throughout the southwest through preservation and restoration of remaining sites. However, they differ in their treatment of the need for cowbird management and its role in eventual species de-listing. The plan for the vireo, in its second draft but still not approved by USFWS, calls for reduction or elimination of threats "so that Least Bell's Vireo populations/metapopulations...are capable of persisting without significant intervention, or perpetual endowments are secured for cowbird trapping and exotic plant control in riparian habitat occupied by Least Bell's Vireos" (USFWS 1998, p. v). The recovery plan for the flycatcher, approved in 2002, takes a more conservative approach to cowbird control, recommending it only after baseline data document a parasitism frequency of more than 20–30% of nests for two or more successive years in the population under consideration (USFWS 2002).

METHODS

We evaluated vireo and flycatcher responses to cowbird control using a combination of published and new information. We supplemented data reported for vireos at Marine Corps Base Camp Pendleton, California (Camp Pendleton) in 1981–1996 (Griffith and Griffith 2000) and flycatchers at the South Fork Kern River, California (Kern) in 1989–1997 (Whitfield et al. 1999, Whitfield 2000) with data collected at these sites in recent years, and we updated analyses comparing pre- and postcontrol parasitism frequencies and host responses. We assessed the generality of results from the two sites by expanding the analyses to include additional vireo and flycatcher populations (see below), and extended earlier investigations by performing new analyses quantifying the effect of parasitism on annual productivity of both vireos and flycatchers.

Study sites.—Our assessment draws on data from long-term studies at four California sites. In addition to Camp Pendleton and the Kern River, described in detail in Griffith and Griffith (2000b) and Whitfield et al. (1999), respectively, we analyzed data from a 16-km reach of the San Luis Rey River (Kus 1999) and a 5-km reach of the San Diego River upstream of Padre Dam in San Diego County. Breeding flycatchers occur

at Kern River and at Camp Pendleton, whereas vireos nest at Camp Pendleton, the San Luis Rey, and San Diego rivers.

The four sites represent the range of conditions under which breeding vireos and flycatchers occur in California. The Kern River and Camp Pendleton are relatively large and undeveloped sites, in contrast to the San Luis Rey River, which is bordered by roads, residential and commercial developments, agricultural fields, pastures, and golf courses, all of which have increased in extent over the study period. The San Diego River site is intermediate to these sites with regard to land use, with half the narrow riparian corridor bordered by native upland vegetation and the other half lying within an urban setting.

Population size and nest monitoring.—Vireo and flycatcher numbers were determined through area searches of all riparian habitat within specified study areas. When accompanied by nest monitoring, surveys were performed at least weekly to determine the status (paired, single-floater, migrant-transient) of each bird detected and to document the nesting activities of all breeding birds (Kus 1999, Whitfield et al. 1999, Griffith and Griffith 2000). Nests were located, and their contents checked periodically, more often early in the cycle, when cowbirds are likely to deposit eggs in nests. Any cowbird eggs found in vireo or flycatcher nests were removed or addled, taking care to leave a clutch of at least two eggs whenever possible to deter abandonment (Kus 1999). Pairs were monitored throughout the breeding season to allow determination of annual nesting effort and success, parasitism frequencies, and pair productivity.

Surveys of vireos and flycatchers at Camp Pendleton have been performed each year since 1981, though surveys in 1992–1994 were less intense and are not analyzed here (Table 1). Nest monitoring was conducted for vireos in 1981–1991 and 1995–2002 and for flycatchers in 1999–2003. Vireos at the San Luis Rey River were monitored in 1984, 1986 (B. Jones unpubl. data), and annually since 1988 (except for 1997, 1998, and 2002). Monitoring data for the San Diego River vireo population were collected in 1984 (B. Jones unpubl. data), 1986 (G. Collier and B. Jones unpubl. data), and 1987–1996. At the Kern River, flycatcher surveys and nest monitoring have been conducted every year since 1989.

Cowbird control.—Cowbirds were removed from vireo and flycatcher breeding sites through annual trapping, as described in Whitfield et al. (1999) and Griffith and Griffith (2000). Cowbird trapping at vireo nesting sites was conducted between mid-March and late July, whereas trapping at flycatcher sites began in May.

Cowbird trapping was initiated at Camp Pendleton in 1983 and at the San Diego River in 1987; trapping continued at both sites throughout the study period (Table 1). Trapping was conducted annually at the

TABLE 1. Annual rates of parasitism and productivity of Least Bell's Vireos and Southwestern Willow Flycatchers at four California sites, 1981–2003.

Site	Year	Cowbird control?	Number of pairs monitored	Number of nests with eggs	Percentage of nests parasitized	Number of fledglings per pair	Source
Least Bell's Vireos							
San Diego	1984	No	18 ^a	25	80	0.2	b
	1986	No	21	40	33	1.6	c
	1987	Yes	21	29	0	2.9	d
	1988	Yes	28	44	2	3.6	d
	1989	Yes	25	38	11	3.3	d
	1990	Yes	24	37	22	2.7	d
	1991	Yes	27	42	29	1.7	d
	1992	Yes	24	46	26	2.2	d
	1993	Yes	28	61	7	4.5	d
	1994	Yes	32	62	8	2.7	d
	1995	Yes	37	56	9	2.3	d
1996	Yes	30	43	0	2.9	d	
San Luis Rey	1984	No	8 ^e	11	64	0.3	b
	1986	No	18	37	62	0.9	b
	1988	Yes	38	75	28	1.9	d
	1989	Yes	25	29	38	1.4	d
	1990	Yes	27	45	42	2.2	d
	1991	Yes	35	61	28	2.3	d
	1992	Yes	51	102	41	2.0	d
	1993	Yes	60	84	37	1.3	d
	1994	Yes	68	104	32	1.7	d
	1995	Yes	71	79	22	1.5	d
	1996	Yes	66	72	21	2.4	d
	1999	No	74	89	46	1.5	d
	2000	No	97	115	31	1.7	d
	2001	No	70	119	24	2.5	d
2003	No	58	125	56	1.4	d	
Pendleton	1981	No	14	15	47	0.6	f
	1982	No	48 ^g	93	47	2.1	f
	1983	Yes	54	86	10	2.9	f
	1984	Yes	63	78	18	1.6	f
	1985	Yes	66	26	4	3.2	f
	1986	Yes	68	32	6	2.7	f
	1987	Yes	97	70	17	2.6	f
	1988	Yes	175	244	1	2.7	b
	1989	Yes	129	166	1	3.5	h
	1990	Yes	156	151	1	3.0	h
	1991	Yes	133	124	0	3.0	h
	1995	Yes	60	89	1	2.4	i
	1996	Yes	60	74	0	2.1	h
	1997	Yes	60	81	0	2.8	h
1998	Yes	59	89	0	2.2	h	
1999	Yes	53	82	0	2.1	h	
2000	Yes	58	80	0	2.9	h	
Southwestern Willow Flycatchers							
Kern	1989	No	30	34	50	0.8	j
	1990	No	30	38	61	0.7	j
	1991	No	31	45	78	0.8	j
	1992	Yes	24	36	69	1.4	j
	1993	Yes	26	33	38	1.4	j

TABLE 1. Continued.

Site	Year	Cowbird control?	Number of pairs monitored	Number of nests with eggs	Percentage of nests parasitized	Number of fledglings per pair	Source
Kern	1994	Yes	24	32	16	1.8	j
	1995	Yes	23	34	19	1.7	j
	1996	Yes	28	29	11	2.1	j
	1997	Yes	38	51	20	1.0	j
	1998	Yes	25	31	3	1.6	d
	1999	Yes	23	29	21	1.1	d
	2000	Yes	12	19	0	1.2	d
	2001	Yes	11	13	23	1.4	d
	2002	Yes	13	16	25	1.2	d
	2003	Yes	15	26	20	2.8	d
Pendleton	2000	Yes	10	8	0	2.3	d
	2001	Yes	18	29	0	1.9	d
	2002	Yes	16	29	0	1.5	d
	2003	Yes	16	25	0	2.9	d

^a Includes data from five territories 3 km upriver of study site.

^b B. Jones unpubl. data.

^c G. Collier and B. Jones unpubl. data.

^d Present study.

^e Includes data from eight territories 2 km downriver of study site.

^f L. Salata unpubl. data.

^g Includes six pairs 3 km upriver of study site.

^h Griffith and Griffith 2000, J. C. Griffith and J. T. Griffith unpubl. data.

ⁱ B. Kus unpubl. data.

^j Whitfield et al. 1999, M. Whitfield and E. Cohen unpubl. data.

San Luis Rey River from 1988 to 1998, but historically it has been insufficient to eliminate parasitism at the site (Kus 1999). No trapping has been performed there since 1998. Cowbird control was initiated at the Kern River site in 1992 with shooting of cowbirds and expanded in 1994 to include seven traps.

Analyses.—We analyzed the effect of parasitism on vireo and flycatcher productivity using linear regression to evaluate the number of young fledged per pair as a function of annual parasitism frequency, combining data from all years. We calculated parasitism frequency, or the proportion of nests parasitized, using only nests observed with eggs; we excluded nests that failed before egg-laying had been confirmed and nests not located but known by detection of family groups. Although it is unlikely that nests in the latter group were parasitized, we excluded them to avoid a potential underestimate of parasitism created by the possible nondetection of unsuccessful nests, some of which could have been parasitized. Seasonal productivity was defined as total number of young produced per pair, including young fledged from nests not located. Possible nondetection of unsuccessful nests does not affect the calculation, because seasonal productivity is a function of successful nesting and is independent of the number of nest attempts. We obtained data for calculations from original sources of information reported in Griffith and Griffith (2000) for 1981–1996 to ensure consistency with our definitions.

Data were analyzed separately for each site. A general linear model was used to test for homogeneity of slopes and to determine the statistical legitimacy of pooling across sites.

We assessed the effectiveness of trapping for reducing parasitism frequency by comparing pre- and post-trapping averages at each site using independent-sample one-tailed *t*-tests, predicting that post-trapping parasitism frequencies would be lower. In the same manner, we compared pre- and postcontrol levels of seasonal productivity, expecting to see an increase in that parameter after control was initiated. Finally, we present data from annual surveys to evaluate population growth of vireos and flycatchers in response to cowbird control.

All statistical analyses were performed with SYSTAT 10, with significance set at $P \leq 0.05$. Means are reported \pm SD.

RESULTS

Effect of parasitism on productivity.—Seasonal productivity of vireos was inversely related to parasitism frequency at all three sites. At the San Diego River, where parasitism ranged from 0 to 80% between 1984 and 1996, 71% of the variability in seasonal productivity was explained by parasitism (Fig. 1A; $F = 24.8$, $df = 1$ and 10,

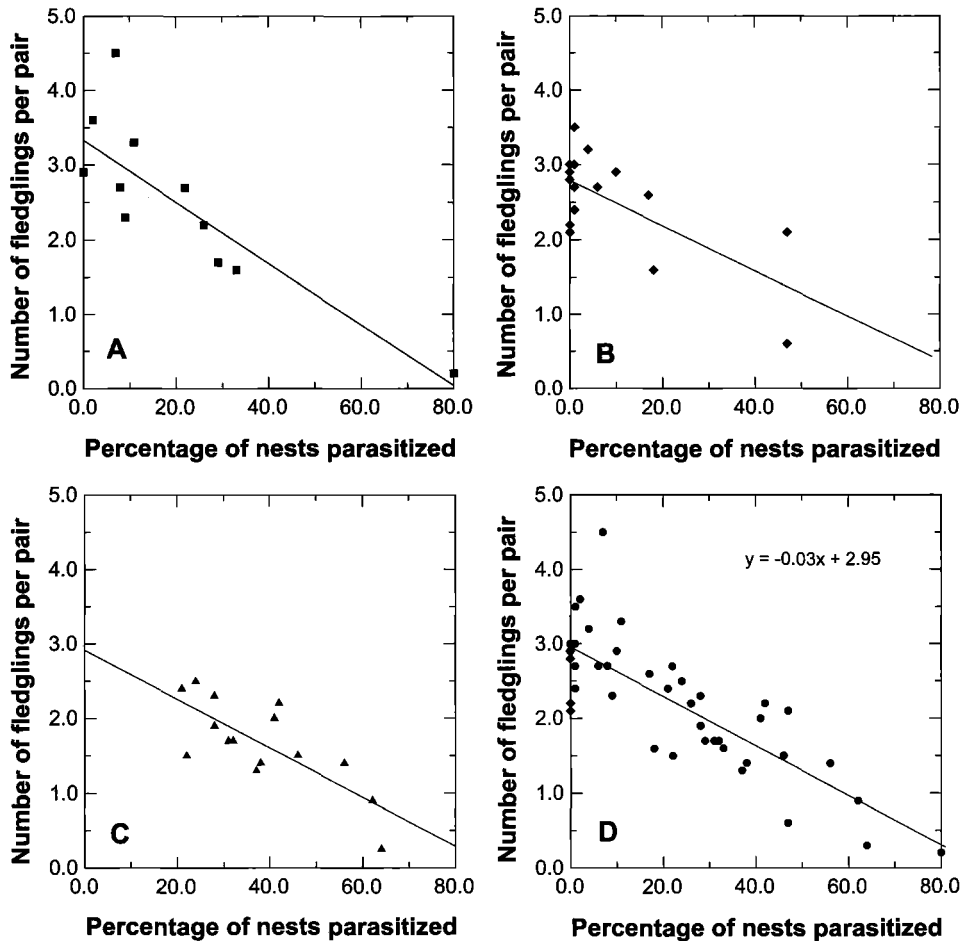


FIG. 1. Seasonal productivity of Least Bell's Vireos as a function of annual parasitism rate at (A) the San Diego River, (B) Camp Pendleton, (C) the San Luis Rey River, and (D) the three sites combined.

$n = 12$ years, $P = 0.001$). The effect of cowbirds on vireo productivity was similar at Camp Pendleton, where parasitism explained 62% of the variability in seasonal production of young between 1981 and 2000 (Fig. 1B; $F = 11.8$, $df = 1$ and 15, $n = 17$ years, $P = 0.004$). Parasitism was considerably higher at the San Luis Rey River than at the other two sites, ranging from 21% to 64% over the 20-year study period; nevertheless, vireo productivity increased with decreasing cowbird parasitism even at these high levels of parasitism (Fig. 1C; $r^2 = 0.58$, $F = 17.9$, $df = 1$ and 13, $n = 15$ years, $P = 0.001$). Finding no significant difference between the slopes of the three regression lines ($F = 0.7$, $df = 2$, $n = 44$ site-years, $P = 0.53$), we combined the data to determine the effect of parasitism on productivity over the full

range of parasitism levels observed throughout the vireo's range, and found that parasitism explained 65% of the interannual variability in production of vireo young (Fig. 1D; $F = 77.7$, $df = 1$ and 42, $n = 44$ site-years, $P < 0.001$). Annual productivity of vireos increased by one young for each drop of 30% in parasitism frequency.

Like vireos, flycatchers at the Kern River exhibited a decline in productivity with increasing parasitism, though the relationship was not quite significant (Fig. 2; $r^2 = 0.23$, $F = 4.0$, $df = 1$ and 13, $n = 15$ years, $P = 0.07$). No parasitism of flycatchers occurred at Camp Pendleton during the study period, and flycatchers fledged 1.5–2.9 young per year (Fig. 2). Data from the Kern show that, over a wide range of parasitism from 0 to nearly 80% of nests, 23% of the annual variability

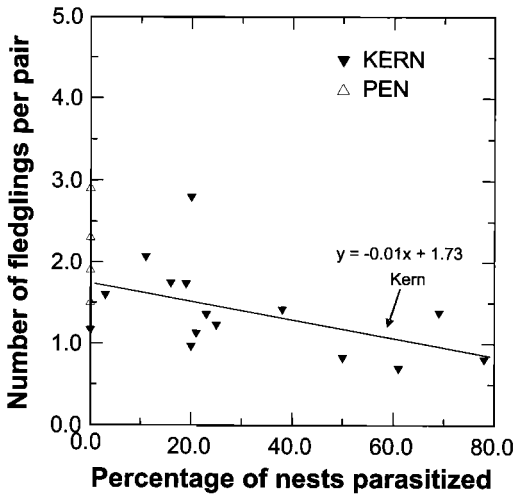


FIG. 2. Seasonal productivity of Southwestern Willow Flycatchers as a function of annual parasitism rate at Kern River (KERN) and Camp Pendleton (PEN).

in flycatcher productivity is attributable to cowbird parasitism. In flycatchers, a difference of 91% in parasitism frequency produces a change in annual productivity of one young.

Response to cowbird control.—Implementation of cowbird control at all four sites significantly reduced the incidence of parasitism of vireo and flycatcher nests (Table 1). Parasitism of vireos at Camp Pendleton dropped from an average of 47% of nests (SD = 0, $n = 2$ years) prior to cowbird trapping to 4% of nests (SD = 6) in the 15 years after trapping was initiated ($t = 9.6$, $df = 15$, $P < 0.001$). At the San Diego River, parasitism of vireo nests dropped from an average of 57% (SD = 33) during the two years before trapping to 11% (SD = 11) after ($t = 4.0$, $df = 10$, $P = 0.001$). Even at the San Luis Rey River, where parasitism has remained high in comparison with the other two vireo sites, between 1988 and 1996, parasitism declined from an average of 63% (SD = 1.4, $n = 2$ years) to 32% (SD = 7.9; $t = 5.3$, $df = 9$, $P < 0.001$). Since 1999 and the cessation of trapping at the San Luis Rey River, average parasitism (39%; SD = 15, $n = 4$ years) has not changed ($t = -1.2$, $df = 11$, $P = 0.13$). Parasitism of flycatcher nests at Kern River declined from 63% (SD = 14) in the 3 precontrol years to 22% (SD = 18) in the 12 postcontrol years ($t = 3.66$, $df = 13$, $P = 0.001$). No parasitism of flycatcher nests at Camp Pendleton has been detected during four years of monitoring since trapping began.

Associated with declines in parasitism were significant increases in seasonal productivity of both species. Vireo pairs at Camp Pendleton increased production of young from 1.4 ± 1.1 year⁻¹ (mean \pm SD) prior to trapping to 2.7 ± 0.5 after ($t = -3.1$, $df = 15$, $P = 0.003$). At the San Diego River, pretrapping productivity of 0.9 ± 1.0 young per pair increased to 2.9 ± 0.8 after trapping ($t = -3.2$, $df = 10$, $P = 0.01$), the highest average productivity recorded at any site with long-term monitoring. Productivity tripled at the San Luis Rey River from 0.6 ± 0.5 young per pair before trapping to 1.9 ± 0.4 in 1988–1996 ($t = -4.0$, $df = 9$, $P = 0.002$). The response of flycatchers to trapping, though less dramatic than that of vireos, was nevertheless significant, with pairs increasing seasonal production of young from 0.8 ± 0.1 before trapping to 1.6 ± 0.5 after ($t = -2.6$, $df = 13$, $P = 0.01$).

Population growth of vireos occurred at all three sites following implementation of cowbird control. At the San Luis Rey River, vireo abundance increased from 24 territories in 1984 to 132 territories in 1999; in the four subsequent years, it leveled off and declined slightly (Fig. 3A). Similarly, vireo numbers at Camp Pendleton increased from 27 territories in 1981 to >1,000 in 1998 (Fig. 3B; note different scale), then declined to an apparent equilibrium of ~800 territories. Vireos at the San Diego River exhibited a modest increase over the 13-year study period from the low 20s to the high 30s.

In contrast, flycatcher numbers at the Kern River grew for a few years post-trapping, reaching a peak of 37 territories in 1997, but then declined steeply to reach the lowest level recorded at the site in 2002 (Fig. 3C). Camp Pendleton flycatchers, in the absence of trapping, have maintained stable numbers of approximately 18–20 territories since 1995.

DISCUSSION

Least Bell's Vireo.—Cowbird control has been effective in reducing the incidence of parasitism and consequently increasing the productivity of vireos, as shown previously by Griffith and Griffith (2000). Our analysis of data collected at several sites during the past 20 years suggests that parasitism is a major determinant of seasonal production of young in vireos, illustrating another connection between cowbird control, parasitism frequencies, vireo nesting success,

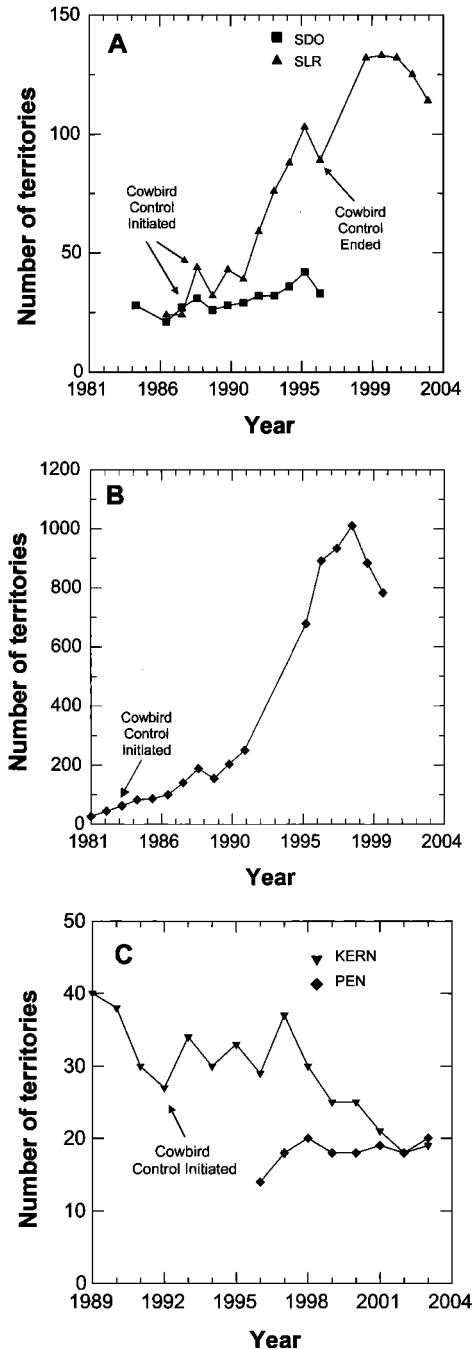


FIG. 3. Population size, between 1981 and 2003, of Least Bell's Vireos at (A) San Diego (SDO) and San Luis Rey (SLR) rivers and (B) Camp Pendleton; and of Southwestern Willow Flycatchers at (C) Kern River (KERN) and Camp Pendleton (PEN). Sources (in addition to those in Table 1): J. C. Griffith and J. T. Griffith unpubl. data.

and population size. The relationship between parasitism and productivity was consistent across several sites and maintained over a wide range of environmental conditions, including periods of drought and of high precipitation. Although other factors influenced annual productivity, parasitism accounted for ~65% of the annual variation in that measure of breeding success.

Reduction or elimination of parasitism over time and a corresponding increase in productivity have resulted in population increases in vireos at all sites where trapping has been employed. Rangelwide, vireo territories now number ~2,500 (B. Kus and L. Hays unpubl. data), >8x the number that existed at the time of listing. However, allowing that trapping is clearly effective as a short-term means of increasing vireo abundance, the perspective afforded by 20 years of monitoring indicates that all of the populations described here may have reached carrying capacity, having exhibited little change during the past five years.

Despite cessation of local population growth, cowbird control is likely still contributing to vireo recovery by promoting the role of these populations as sources of dispersers that are essential for the recolonization of the vireos' historical range and maintenance of populations within an overall metapopulation. Evidence from studies of banded birds indicates that each of the populations discussed here has produced dispersers traveling as far as 250 km from their natal sites to colonize new sites, including areas along the Santa Clara and Ventura rivers in Ventura County (Greaves and Labinger 1997, Griffith and Griffith 2000, B. Kus unpubl. data) that together now support a population of >100 vireo territories (J. Greaves unpubl. data). However, saturation of habitat at vireo breeding sites that 20 years ago were among the largest remaining indicates that we have reached a pivotal point with regard to recovery, where our management priority needs to shift from enhancing numbers at historical sites to ensuring that adequate habitat exists for establishment of new populations.

Cowbird control will remain effective in increasing bird abundance only as long as suitable habitat is available to support population growth. Although no one disputes the critical need for habitat protection in recovering both vireos and flycatchers, translation of that

awareness into action has been slow in coming (USFWS 1998, 2002). Practically speaking, cowbird trapping is a more straightforward and easy form of management for regulatory agencies, resource managers, and mitigants than is habitat protection, which is a complex and costly process often requiring years to accomplish. Protection of unoccupied habitat through acquisition or other agreements and creation of suitable habitat through restoration of degraded sites both present the uncertainty of whether and when sites will be colonized by the species of interest, whereas cowbird control produces immediate results. These challenges often serve as deterrents to aggressive pursuit of habitat protection, yet they underscore the need for planning and investment of resources to meet the future habitat needs of recovering species.

Southwestern Willow Flycatchers.—Unlike vireos, flycatchers have not responded to cowbird control with population increases, at least not with sustained increases. Although a significant determinant of productivity, parasitism has less of an effect on flycatchers than on vireos and minimal detectable effect on population growth, outside of a brief initial increase immediately following implementation of trapping (Whitfield et al. 1999). Today, nearly a decade after listing, flycatcher territories number only ~200 in California (Kus et al. 2003), 20% of the species' population throughout its U.S. range (Sogge et al. 2003). Clearly, factors other than parasitism are currently limiting flycatcher abundance and distribution, and exclusive emphasis on trapping will not aid in identifying or managing these factors. A similar situation was encountered in the use of cowbird trapping to increase populations of Kirtland's Warblers (DeCapita 2000). After two decades of trapping and reduction of parasitism to ~5%, Kirtland's Warbler numbers failed to increase until a wildfire created thousands of hectares of new jack pine (*Pinus banksiana*) nesting habitat, indicating that habitat availability rather than parasitism was the primary factor limiting population growth. It appears unlikely that flycatchers have saturated their existing habitat, given the decline at Kern River and the disparity in numbers of flycatchers and vireos at Camp Pendleton, where they occur sympatrically and are subject to the same management. Ongoing investigations of declining egg hatchability, possibly related to contaminants (M. Whitfield

unpubl. data), and other demographic factors on both the breeding and wintering grounds, should shed light on their roles as possible limiting factors.

Cowbird control.—Cowbird control has affected the recovery of vireos and flycatchers differently. The ways that they differ are instructive when considering cowbird control in management of other species. In vireos, cowbird control has been highly effective in producing a rapid reversal of population decline, and the species is now in the process of recolonizing its historical range. Given that success, it was logical and appropriate that cowbird trapping was initiated to protect flycatchers once they were listed as endangered, and that effort, too, has advanced flycatcher recovery—not by increasing abundance, but by revealing that something other than parasitism is limiting flycatcher populations. In both cases, cowbird control has brought us to a point where a redistribution of management effort is warranted, and becoming complacent because of prior success will likely delay or prevent achievement of full recovery.

Recommendations for cowbird control.—With that in mind, we note that a critical component missing from all the cowbird control programs with which we are familiar is a plan for ending the control. Rothstein and Cook (2000) raised the same concern. Given the growth in our understanding of both the effectiveness and limitations of prolonged cowbird control and the potential for reliance on open-ended control to detract from exploring or implementing other, more appropriate forms of management, we recommend that control programs give consideration to the desired results of the control and specify criteria for ending it.

Reasons for avoiding open-ended control whenever possible include a number of economic, political, and ethical issues (Rothstein and Cook 2000, Rothstein et al. 2003). A possible biological consequence is that cowbird control interferes with the evolutionary processes necessary for establishment of genetically based natural defenses that would allow for the continued existence of host species in the absence of human intervention. We refer not to the appearance of new defenses, but to enhancement of defenses already present and expressed to some degree, a process requiring far less evolutionary time. For example, desertion of parasitized nests followed by successful renesting is a defense

exhibited by many small hosts (Friedmann 1963), including other subspecies of vireos (Kus 2002). Least Bell's Vireos share an evolutionary history with these subspecies, and like them, desert parasitized nests, but at a much lower rate (29% of nests [Kus 1999] as compared with 43–74% of nests [Averill-Murray 1999, Parker 1999, Budnik et al. 2001]) and within an ecological context different from that in the Great Plains portion of the Bell's Vireo's range, where cessation of cowbird breeding 2–3 weeks before vireos stop nesting allows renesters to be successful (Parker 1999, Budnik et al. 2001). The result is that deserting Least Bell's Vireo pairs fledge only half as many young as unparasitized pairs (Kus 2002). However, they produce more young than they would if they failed to desert, creating positive selection for desertion if that behavior is heritable. Cowbird control, done effectively, removes the selective pressure necessary for promoting an increase in such a response.

Nest manipulation is another form of cowbird control that interferes with the evolution of antiparasite behaviors. Removal of cowbird eggs from vireo nests allows rescued pairs (non-deserters with at least one parasitized nest; Kus 2002) to attain seasonal productivity comparable with that of unparasitized pairs, an outcome considered a management success—which it is, in the short term. In fact, vireo young from manipulated nests are twice as likely to survive to breeding age as those from unparasitized nests (B. Kus unpubl. data), which compensates for the reduced number of young fledged from parasitized nests (Kus 1999). Again, cowbird control in the form of nest manipulation reduces the selective costs of heritable behaviors yielding vireo nests vulnerable to parasitism, which could include those involved in nest placement, timing of nest initiation, and activity at the nest. Variability exists in all of these behaviors and, if genetically based, provides the raw material on which natural selection can act given the opportunity.

We recognize that establishing goals and endpoints for cowbird control programs is a formidable challenge requiring a commitment to the practice of adaptive management as we test and evaluate various possibilities. The data summarized here offer a starting point for addressing questions of when, how, and where trapping might be reduced and eventually discontinued.

For example, on the basis of a simple estimate of two young per female as the level of annual productivity needed to maintain a stable population (Franzreb 1989), our analysis indicates that Least Bell's Vireos are apparently able to maintain equilibrium numbers at parasitism frequencies of up to ~30%, supporting the frequencies proposed elsewhere (Smith 1999, USFWS 2002) as a threshold for initiating cowbird control to protect endangered species. That may be a reasonable goal for managing populations that have reached carrying capacity. The increased cost and effort of managing for 0% parasitism as opposed to 20–30% is considerable, and unjustified if unaccompanied by corresponding biological gains. Other sites might be managed as source populations with lower parasitism thresholds, again using existing data to evaluate incremental differences in the cost:benefit ratios of different options. Experimentation with some large populations on number of traps, dates of operation, and annual trapping frequency needed to achieve desired goals will be a necessary part of research on how to minimize unproductive use of cowbird control. Further studies of hosts' natural defenses are needed to establish which are genetically based and, thus, subject to natural selection, followed by analyses combining selection models and host population dynamics to identify management regimes that minimize the risk of extinction while providing conditions under which selection can operate.

CONCLUSION

We believe that cowbird control is an appropriate and effective short-term management tool in recovery of endangered hosts and has been instrumental in preventing extinction of vireo and flycatcher populations in California. It is not a panacea, however, and is effective only so long as parasitism is the primary limitation to population growth. The degree to which that is the case will vary from species to species, as illustrated by differences between vireos and flycatchers in their responses to control, and over time as populations encounter other obstacles to growth. We encourage managers to be mindful of that in the design of recovery-oriented management for these and other species, and to be prepared to adapt management as species' needs change. In particular, we stress the need to consider the potential negative

effects of long-term cowbird control on the ability of species to persist without management intervention, and avoid creating permanent dependence on humans for survival. We encourage research exploring natural defenses in endangered hosts to guide the design of cowbird management that balances the short- and long-term needs of averting extinction and facilitating evolutionary processes necessary for host persistence.

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CHAPTER 3

EFFECTS OF BROWN-HEADED COWBIRD (*MOLOTHRUS ATER*) REMOVAL ON BLACK-CAPPED VIREO (*VIREO ATRICAPILLA*) NEST SUCCESS AND POPULATION GROWTH AT FORT HOOD, TEXAS

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ABSTRACT.—In 1988 at Fort Hood, Texas, after high parasitism (up to 91%) of the endangered Black-capped Vireo (*Vireo atricapilla*) by Brown-headed Cowbirds (*Molothrus ater*) and associated low nest success (<5%), a cowbird control program was implemented. We review and re-assess data related to that program and provide an update on control efforts. Initial control efforts were beneficial but limited. With onset of more intensive control efforts in 1991, parasitism fell below 20%, and Black-capped Vireo nest success rose above 20%. Number of Black-capped Vireo pairs within three study areas at Fort Hood also increased over time. Parasitism and Black-capped Vireo nest success varied with management (i.e. different combinations of trapping, shooting, and cattle grazing) across regions of Fort Hood, but generally decreased and increased, respectively, over time. Because removal techniques were applied simultaneously, it is difficult to determine the magnitude of effect that individual techniques had on parasitism and Black-capped Vireo nest success. A reduction in cattle stocking rate on the East Range of Fort Hood appeared to reduce parasitism during 1997–1998. However, an earlier cattle removal on West Fort Hood had no apparent effect on parasitism. We attribute reductions in parasitism on West Fort Hood primarily to shooting, because trapping efforts there have been minimal. Fort Hood currently meets both local and regional recovery goals for the Black-capped Vireo. We attribute success in meeting those goals primarily to cowbird control.

RESUMEN.—En 1988 en Fort Hood, Texas luego de detectar un alto parasitismo (más del 91%) de *Vireo atricapilla* por parte de *Molothrus ater* asociado a un bajo éxito de nidificación (<5%), se aplicó un programa de control de *Molothrus ater*. Aquí revisamos y reevaluamos los datos relativos a aquel programa y proveemos una actualización sobre la eficacia del control. La eficacia de control inicial fue benéfica pero limitada. Con el inicio de esfuerzos de control más intensos en 1991, el parasitismo cayó por debajo del 20%, y el éxito de nidificación de *Vireo atricapilla* se elevó a más del 20%. El número de parejas de *Vireo atricapilla* en tres sitios de estudio dentro de Fort Hood también se incrementó a lo largo del tiempo. Tanto el parasitismo como el éxito de nidificación de *Vireo atricapilla* variaron con el tipo de manejo (e.j. diferentes combinaciones de trapeo, caza con armas de fuego, y pastoreo de ganado) entre regiones de Fort Hood. En general, el parasitismo disminuyó y el éxito de nidificación se incrementó a lo largo del tiempo. Debido a que las técnicas de remoción de *Molothrus ater* fueron aplicadas simultáneamente, es difícil determinar la magnitud del efecto individual de cada una sobre las tasas de parasitismo y el éxito de nidificación de *Vireo atricapilla*. Una reducción en la carga ganadera en el rango este de Fort Hood aparentemente redujo el parasitismo durante 1997–1998. Sin embargo, una remoción de ganado más temprana en el oeste de Fort Wood no tuvo efecto aparente sobre el parasitismo. Nosotros atribuimos las reducciones en parasitismo en el este de Fort Wood primariamente a la caza con armas de fuego, ya que el esfuerzo de trapeo en dicha área fue mínimo. Fort Hood actualmente cumple tanto con las metas locales y regionales de recuperación de *Vireo atricapilla*. Nosotros consideramos que el éxito logrado en el cumplimiento de dichas metas es debido principalmente al control de *Molothrus ater*.

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BLACK-CAPPED VIREOS (*Vireo atricapilla*; hereafter "vireo") breed in low, shrubby deciduous vegetation irregular in height and distribution, with grassy spaces between small thickets or clumps and with an apron of vegetative cover to ground level (Graber 1961, Grzybowski 1995). Such vegetation is indicative of an early successional stage that follows disturbances, such as fire, or that is maintained by edaphic conditions. Historically, the breeding range of the vireo included north-central Mexico, central Texas, central Oklahoma, and south-central Kansas (Grzybowski 1995). Substantial range reduction has occurred.

The vireo was listed as federally endangered in 1987 (Ratzlaff 1987). Listing was based on population declines, deterioration and loss of habitat, and low productivity associated with high rates of parasitism by Brown-headed Cowbirds (*Molothrus ater*; hereafter "cowbirds"; U.S. Fish and Wildlife Service [USFWS] 1991). Deterioration and loss of habitat have been caused by alteration of natural disturbance regimes (e.g. fire suppression), agricultural practices (e.g. overbrowsing), and urban development (USFWS 1991). Cowbird parasitism can be severe, with local parasitism rates as high as 90%, and result in low reproductive success (<1 young per female per year; USFWS 1991).

The goal of the Black-capped Vireo Recovery Plan is to down-list the vireo from endangered to threatened by 2020 (USFWS 1991). Recovery criteria mandate protection and stabilization of all existing vireo populations. Eight recovery regions have been designated within the vireo's breeding range (USFWS 1991). Viable breeding populations (500–1,000 pairs) should exist in six of those regions and be maintained for at least five consecutive years, with the assurance that they will continue to exist in perpetuity. Management actions mandated to promote recovery of the vireo include the elimination of cowbird parasitism threats (i.e. cowbird removal by trapping and shooting). To mitigate habitat loss and deterioration, practices such as habitat acquisition, easements, and cooperative land-management practices with private land-owners are promoted (USFWS 1991, 1996).

Currently, Fort Hood military reservation in central Texas maintains a population of ~2,000 territorial male vireos, which potentially represents 2,000 pairs (The Nature Conservancy of Texas, Fort Hood, Texas [hereafter "TNC"],

unpubl. data). That population is likely the largest under a single management authority. The primary threat to the population has been cowbird parasitism. In 1987, 90.9% ($n = 33$) of vireo nests found on Fort Hood were parasitized by cowbirds (Eckrich et al. 1999). The maximum parasitism frequency that the population could withstand without declining was estimated to be 16–38% (Tazik and Cornelius 1993). Thus, cowbird control was implemented at Fort Hood in 1988 to promote recovery of the vireo (Eckrich et al. 1999). Biological Opinions issued for Fort Hood (USFWS 1993, 2000) and Fort Hood's Endangered Species Management Plan (Hayden et al. 2001) officially sanction continuation of cowbird control.

The effect of cowbird control on parasitism of vireos at Fort Hood has been reviewed through 1997 (Eckrich et al. 1999, Hayden et al. 2000). Vireo nest success in relation to cowbird control at Fort Hood has been reviewed through 1994 (Hayden et al. 2000). Here, we provide data on cowbird control efforts, parasitism of the vireo, and vireo nest success through 2002. Additionally, we assess the relationship between cowbird control and vireo population growth. Finally, we re-assess the effects that individual management actions (i.e. shooting, trapping, and cattle-grazing manipulations) may have had on reducing parasitism and increasing vireo nest success and population size. Although Eckrich et al. (1999) and Hayden et al. (2000) commented on the possible effects of particular management actions, their assessments were speculative and confounded by the fact that cowbird management actions have often been applied simultaneously at Fort Hood.

STUDY AREA AND METHODS

Study area.—Fort Hood is an active U.S. Army post occupying 88,500 ha within the Crosstimbers and Southern Tallgrass Prairie and Edwards Plateau Ecoregions of Bell and Coryell counties in central Texas (TNC 1997). The Fort Hood acreage is estimated to be 65% perennial grassland and 31% woodland dominated by Ashe juniper (*Juniperus ashei*) and oaks (*Quercus* spp.); the remaining 4% is developed. Although military training is the primary land use on Fort Hood, the post is managed for other uses, including cattle grazing, fish and wildlife habitat, and outdoor recreation. More detailed descriptions of Fort Hood are provided in Eckrich et al. (1999) and Hayden et al. (2000).

Cowbird control.—Cowbird trapping within vireo

nesting habitat during the breeding season (March–June) began in 1988 (Eckrich et al. 1999, Hayden et al. 2000). Beginning in 1991, the majority of traps were moved to cattle pastures where flocks of cowbirds foraged. Trapping effort varied over time (Fig. 1). On average, 31 traps were deployed each year (range = 3–50). Shooting of cowbirds augmented trapping beginning in 1989 (Eckrich et al. 1999, Hayden et al. 2000). Shooting efforts have also varied spatially and temporally at Fort Hood. An average of 87 (SE = 22, range = 0–320) female cowbirds are removed by shooting each year. Since 1997, cowbird control has been conducted under Federal Bird Marking and Salvage Permit 22998 and Texas State Permit SPR-0200-078.

Land use.—Except for grazing, land use at Fort Hood has remained relatively constant over time. Cattle stocking rates have been difficult to estimate at Fort Hood, but have clearly varied over time. A brucellosis outbreak in 1989 and 1990 resulted in removal of approximately half the cattle on the post. No cattle grazed West Fort Hood during 1992–1996. Stocking rates were reduced from 752 to 103 animal units on the north half of the East Range during 1997–1998 (Kostecke et al. 2003). Since 2002, cattle have been generally absent from the West Range.

Black-capped Vireo population monitoring.—Vireos have been monitored at Fort Hood since 1987. To assess population growth, we calculated the mean number of territorial male vireos (i.e. potential pairs)

per hectare within three study areas (Manning 1 [23.2 ha, West Range], Training Area 2 [88.4 ha, East Range], and West Fort Hood [103.3 ha, West Fort Hood]). The process of locating territorial male vireos involved walking the entire study areas at least once per week between April and August. Once we located males, we attempted to capture and fit them with federal and color bands. Territories were defined by (1) a color-banded male, (2) an active nest, (3) an unbanded male singing in the same location on three different days, or (4) a male in the company of a female. After territories were identified, they were visited at least once a week to determine nesting status.

Within our three study areas, after we located nests, we visited them every 3–5 days and documented nest contents. We monitored nests until the young fledged, the nest failed, or the nest was determined to be inactive. Nests were considered to be successful if they fledged ≥ 1 vireo young. We calculated annual overall (incubation and nestling periods) nest survival rates for each study area, and for all study areas combined, using the Mayfield method (1961, 1975). For those calculations, we considered the incubation and nestling periods to last 14 and 11 days, respectively (Grzybowski 1995). Data were not available to calculate Mayfield nest success for 1987 and 1990. Beginning in 1991, cowbird eggs and nestlings were removed from all parasitized nests to minimize the effect of parasitism on productivity. We

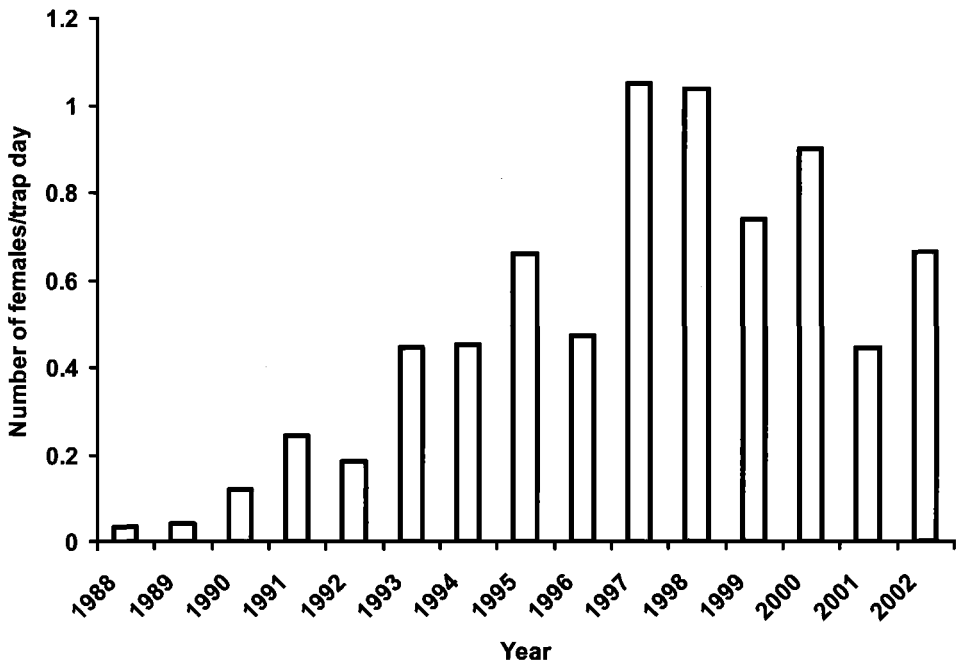


FIG. 1. Brown-headed Cowbird trapping effort (number of females trapped per trap day) at Fort Hood, Texas, from 1988 to 2002.

considered a nest to have failed as soon as a cowbird nestling was present, regardless of whether the cowbird nestling was removed from the nest, because no vireo nest monitored at Fort Hood before 1991 had fledged vireos when a cowbird nestling was present (TNC unpubl. data).

Analyses.—We used simple linear regression (PROC REG; SAS Institute 1999) to assess the relationship between potential vireo pairs per hectare and year. We used the program CONTRAST to compare nest survival rates over time (Hines and Sauer 1989) and G-tests to compare parasitism frequency over time (Sokal and Rohlf 1995). Because multiple comparisons were conducted, we used Bonferroni's correction to maintain the experiment-wise error rate of $P = 0.05$ (Sokal and Rohlf 1995). We present 95% confidence intervals for all parasitism and survival rates (Zar 1999). We used Pearson correlation coefficients calculated using PROC CORR to assess the relationships between nest success and parasitism frequency and between numbers of female cowbirds trapped and parasitism frequency (SAS Institute 1999).

Our parasitism and nest success data differ, in some cases, from data previously presented for Fort Hood (Eckrich et al. 1999, Hayden et al. 2000), because we analyzed data only from three study areas (i.e. Manning 1, Training Area 2, and West Fort Hood), and not from all of Fort Hood. We confined our analyses to those three study areas because annual monitoring efforts within those areas have been relatively constant since 1987, allowing us to assess how vireos have responded to cowbird control over time. Outside of those study areas, monitoring efforts have been opportunistic or temporally variable (TNC unpubl. data).

RESULTS

Mean numbers of territorial male vireos increased over time (adjusted $r^2 = 0.35$; $F = 9.54$, $df = 1$ and 15 , $P = 0.01$; Fig. 2). Nest exposure days per year for the East Range, West Fort Hood, West Range, and overall were (mean \pm SE) 402.25 ± 152.87 , 305.71 ± 195.44 , 318.57 ± 222.47 , and 1026.54 ± 438.70 , respectively. Number of nests per year for the East Range, West Fort Hood, West Range, and overall were 33 ± 12 , 27 ± 14 , 24 ± 14 , and 83 ± 31 , respectively. Nest success was strongly and negatively correlated with parasitism rate on the East Range ($r = -0.70$, $P = 0.006$), West Fort Hood ($r = -0.68$, $P = 0.008$), West Range ($r = -0.71$, $P = 0.005$), and overall ($r = -0.77$, $P \leq 0.001$). As the parasitism rate decreased over time, nest success increased (Fig. 3). By 1991–1992, the parasitism rate fell below 20% and nest success increased above 30%. Parasitism rate was strongly and negatively correlated with number of female cowbirds trapped overall ($r = -0.77$, $P = 0.001$) and in all regions, except West Fort Hood ($r = -0.14$, $P = 0.63$).

However, within regions, nest success (East Range: $\chi^2 = 2105.17$, $df = 6$, $P < 0.01$; West Fort Hood: $\chi^2 = 922.02$, $df = 7$, $P < 0.01$; West Range: $\chi^2 = 566.60$, $df = 4$, $P < 0.01$) and parasitism (East Range: $\chi^2 = 182.82$, $df = 4$, $P < 0.01$; West Fort Hood: $\chi^2 = 144.63$, $df = 8$, $P < 0.01$; West Range: $\chi^2 = 165.14$, $df = 7$, $P < 0.01$) differed across

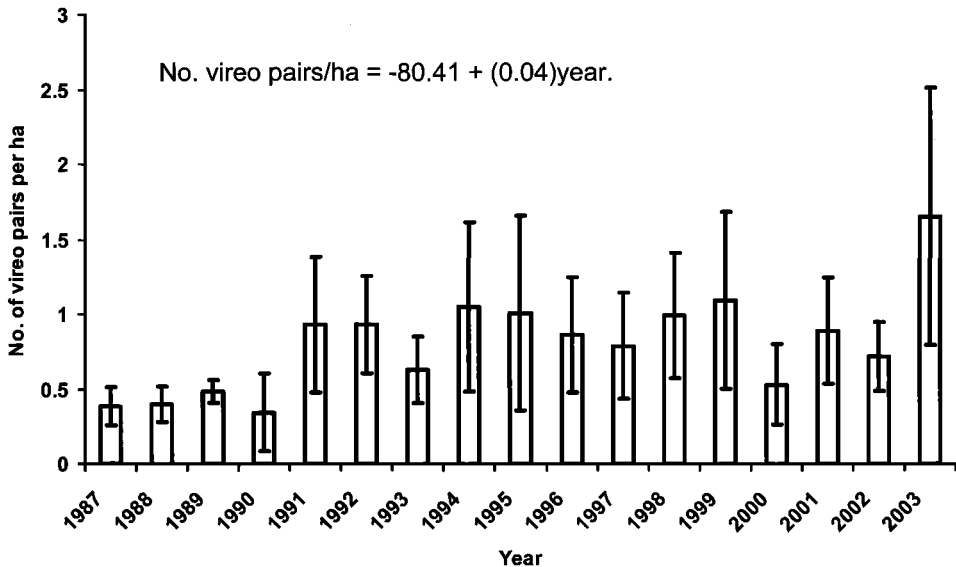


FIG. 2. Mean number of potential Black-capped Vireo pairs per hectare at Fort Hood, Texas, 1987–2003.

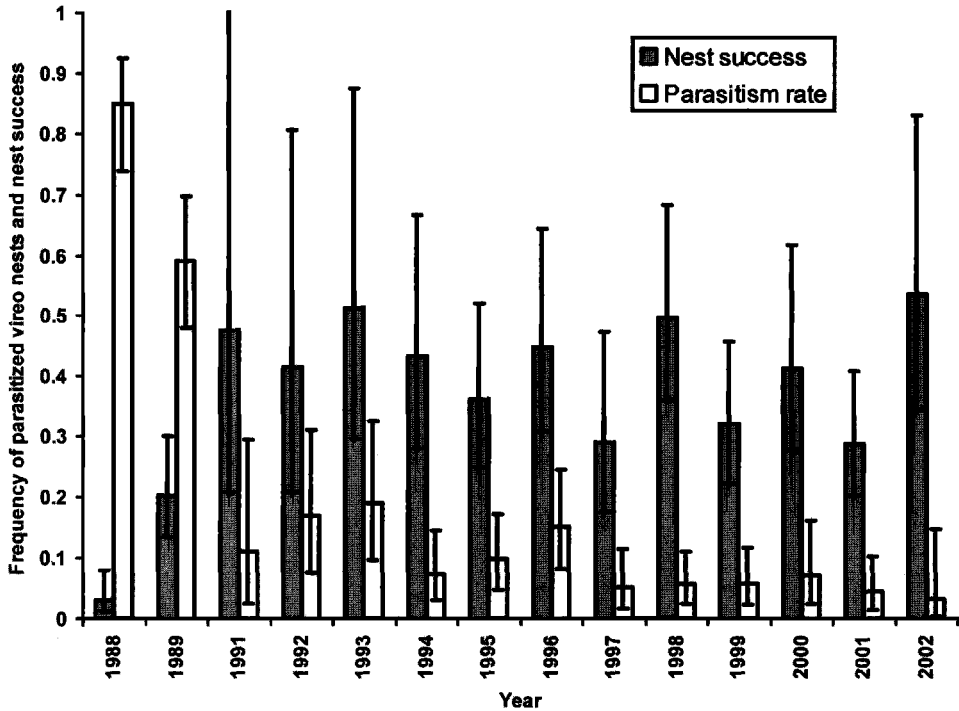


FIG. 3. Overall Black-capped Vireo nest success and Brown-headed Cowbird parasitism of vireo nests at Fort Hood, Texas, 1988–2002.

management regimes (Table 1). Following initial, less-intensive cowbird control efforts, nest success on the East Range was generally highest during 1991–1993 and 2002, periods when trapping and shooting efforts were more widely distributed across the East Range. Nest success was highest on West Fort Hood during 1991 and 1994–2001, years when shooting occurred. Management regimes have not differed greatly over time on the West Range, in that trapping and shooting have been consistently implemented since 1989, but there has been a constant increase in nest success and decrease in parasitism rate. Parasitism rates on the West Range were highest in 1988 and 1989 and lowest during 1991–2002.

DISCUSSION

Vireos are vulnerable to cowbird parasitism and have experienced local and regional population declines, in part, because of cowbird parasitism. Thus, cowbird control was justified at Fort Hood, where annual parasitism frequencies were high (59–91% during 1987–1990, $n =$

24–90 nests). Early cowbird control efforts (1988–1990) decreased parasitism and increased vireo nest success, but it was only with more intensive control in 1991 that parasitism fell to levels less than or equal to 16–38% (Tazik and Cornelius 1993), where it was predicted that a stable vireo population could be maintained (Eckrich et al. 1999, Hayden et al. 2000).

We were more restrictive than Eckrich et al. (1999) and Hayden et al. (2000) regarding nests included in our analyses. The sharper decrease in parasitism, the sharper increase in vireo nest success, and the quicker leveling-off of parasitism and vireo nest success shown by our analyses (Fig. 3) can likely be attributed to that difference in methodology. Regardless of methodology, parasitism decreased to an acceptable level and vireo nest success increased quickly after intensive control was initiated. Vireo pair density has also steadily increased within the three study areas on Fort Hood that have been consistently monitored since 1987.

The annual number of female cowbirds removed has remained high (Eckrich et al. 1999, Hayden et al. 2000, TNC unpubl. data); however,

TABLE 1. Mayfield nest success and parasitism frequency by cowbird management regime within regions at Fort Hood, Texas.

Region	Management regime(s)	Year(s)	Nest success (95% CI)		Parasitism (95% CI)	
East Range	G, T	1988	0.04 ^g	(0.01–0.12)	0.77 ^a	(0.59–0.89)
	RG, S, T	1989	0.26 ^f	(0.17–0.41)	0.59 ^a	(0.41–0.75)
	RG, T	1990	—		0.67 ^a	(0.38–0.88)
	G, S, T	1991–1993	0.54 ^b	(0.50–0.57)	0.07 ^{b,c}	(0.02–0.17)
	G, RS, RT	1994–1996	0.34 ^d	(0.11–0.56)	0.17 ^b	(0.09–0.23)
	RG, RS, RT	1997–1998	0.28 ^e	(0.00–1.00)	0.02 ^c	(0.00–0.08)
	G, RS, RT	1999–2001	0.41 ^c	(0.23–0.60)	0.05 ^{b,c}	(0.03–0.15)
West Fort Hood	G, S, T	2002	0.64 ^a	(0.43–0.94)	0.00 ^{b,c}	(0.00–0.18)
	G	1988	0.03 ^e	(0.01–0.15)	1.00 ^a	(0.83–1.00)
	RG, S	1989	0.15 ^d	(0.07–0.31)	0.55 ^{b,c}	(0.35–0.74)
	RG, T	1990	—		1.00 ^{a,b}	(0.48–1.00)
	G, S, T	1991	0.39 ^a	(0.13–1.00)	0.14 ^{c,d}	(0.00–0.58)
	None	1992	0.21 ^c	(0.08–0.57)	0.47 ^{c,d}	(0.23–0.72)
	T	1993	0.07 ^{d,e}	(0.01–0.47)	0.41 ^{c,d}	(0.15–0.72)
	S	1994–1996	0.45 ^a	(0.25–0.66)	0.08 ^d	(0.03–0.15)
	G, S	1997–2001	0.32 ^b	(0.16–0.47)	0.12 ^d	(0.07–0.16)
	G, S, T	2002	0.15 ^{c,d}	(0.02–0.90)	0.25 ^{c,d}	(0.03–0.65)
West Range	G, T	1988	0.004 ^c	(0.00–0.12)	0.83 ^a	(0.52–0.98)
	RG, S, T	1989	0.15 ^c	(0.06–0.37)	0.65 ^a	(0.43–0.84)
	RG, T	1990	—		0.25 ^{a,b}	(0.01–0.81)
	G, S, T	1991–2001	0.40 ^b	(0.32–0.48)	0.07 ^b	(0.01–0.05)
	S, T	2002	0.56 ^a	(0.40–0.77)	0.00 ^b	(0.00–0.11)

Abbreviations: Management regimes: G = grazing, RG = reduced grazing, RS = reduced shooting, RT = reduced trapping, S = shooting, and T = trapping. Within each region, all treatment combinations are independently assigned a superscript letter for nest success and parasitism frequency, superscript letters that are the same indicate no significant differences between treatment combinations ($P > 0.05$). We tested for differences in nest success using the program CONTRAST (Hines and Sauer 1989) and for differences in parasitism frequency using G-tests (Sokal and Rohlf 1995).

high capture rates do not suggest failure of the cowbird control program at Fort Hood. Capture rates are highest during spring migration (March–May; Eckrich et al. 1999, TNC unpubl. data); therefore, the majority of females captured are likely migrants, not locally breeding individuals. Indeed, recent research suggests that only 25% of the cowbirds removed at Fort Hood are potential local breeders (TNC unpubl. data). We have no data available to assess the magnitude of decrease in the Fort Hood cowbird population.

Undoubtedly, cowbird control has benefited Fort Hood's vireos, but it is difficult to assess the individual effects of trapping, shooting, or cattle-grazing manipulations on parasitism, because those management actions were often applied simultaneously. For example, on the East and West ranges, a combination of trapping and shooting steadily reduced parasitism and increased vireo nest success over time. On the East Range, the only management activity that can be singled out as having a particular effect was reduction in cattle stocking rate,

which apparently reduced parasitism during 1997–1998 (Kostecke et al. 2003). However, that effect, albeit beneficial, occurred after parasitism had already been substantially reduced by trapping and shooting.

In contrast, removal of cattle from West Fort Hood during 1992–1993 had no beneficial effect on parasitism (Hayden et al. 2000), because alternative feeding sites for cowbirds existed within nearby suburban areas that bordered West Fort Hood (Eckrich et al. 1999). Therefore, the ultimate utility of using cattle-grazing manipulations to manage cowbird parasitism at Fort Hood remains clouded. Manipulation of cattle-grazing patterns shows promise as a tool to manage cowbird parasitism in some landscapes (Goguen and Mathews 2001). However, such manipulations may be less effective at small scales or where alternative foraging and congregation sites are available (i.e. outside areas where cattle-grazing patterns can be manipulated; Kostecke et al. 2003).

In contrast to efforts on the East and West ranges, trapping effort was minimal on West

Fort Hood (Eckrich et al. 1999, Hayden et al. 2000). Therefore, we attribute reductions in parasitism at West Fort Hood primarily to shooting. Indeed, parasitism increased on West Fort Hood during all years when shooting was not implemented, regardless of whether trapping occurred or whether there was an absence of cattle. Eckrich et al. (1999) and Hayden et al. (2000) also suggested that decreases in parasitism observed at West Fort Hood could be attributed to shooting. However, Eckrich et al. (1999), in particular, are cautious about using shooting alone to reduce parasitism to acceptable levels. They suggest that "landscape-scale cowbird population density" needs to be reduced to a "low enough" level by trapping before shooting can be effective, but their hypothesis has never been tested.

Contrary to Eckrich et al.'s (1999) suggestion, shooting alone appeared to substantially reduce parasitism at West Fort Hood as early as 1989, when Fort Hood's overall cowbird population was likely at or near its highest level and before traps were deployed at West Fort Hood. That result could have significant management implications. Shooting is a selective removal method, and its success can be attributed to removal of only those cowbirds that might actually parasitize a vireo nest; whereas trapping might remove mostly migrant females or those breeding in habitats not used by vireos. If shooting alone is time efficient and effective in reducing parasitism, trapping efforts could be reduced. However, efficiency will depend on available personnel and scale of removal efforts. Ultimately, trapping is probably more efficient at Fort Hood, because it allows limited personnel to remove cowbirds over a large landscape with less effort than shooting alone. However, reduction of trapping should be considered, when reasonable, given that some of the ethical, legal, and political concerns associated with cowbird trapping (e.g. capture of nontarget birds; Ortega 1998, Hall and Rothstein 1999, Rothstein and Cook 2000) may be reduced with selective removal methods, such as shooting.

Fort Hood currently meets both local (Hayden et al. 2001) and regional (USFWS 1991) recovery goals for the vireo. Approximately 2,000 territorial male vireos (i.e. potentially 2,000 pairs) were documented at Fort Hood in 2003 (TNC unpubl. data). That number is twice

the goal set by Fort Hood's Endangered Species Management Plan (Hayden et al. 2001) and at least twice the goal of 500–1,000 pairs set by the Black-capped Vireo Recovery Plan (USFWS 1991). In addition, a local goal is to maintain cowbird parasitism below a five-year average of 10% (USFWS 2000, Hayden et al. 2001). Overall, the parasitism rate on Fort Hood has been <10% since 1997. We attribute attainment of local and regional recovery goals largely to cowbird control. However, in the absence of ample early-successional habitat, recovery of vireos would likely have had little success.

Although warranted in many instances, removal is often perceived as an open-ended method of managing cowbirds that might not result in an increased and self-sustaining host population (Hall and Rothstein 1999, Rothstein and Cook 2000). Although the Black-capped Vireo Recovery Plan (USFWS 1991) mandates cowbird control in specific instances, it also states that "site-specific cowbird removal, by itself, will not provide for long-term recovery of specific populations" and that "additional methods of reducing the threat from cowbirds need to be investigated." Additional methods of reducing threats from cowbirds include improving, increasing, and protecting host habitat, as well as changing land use to minimize cowbird numbers or affect cowbird activity and movements (e.g. manipulation of cattle-grazing patterns; Goguen and Mathews 2000, Kostecke et al. 2003). However, those alternatives have not been thoroughly investigated (Hall and Rothstein 1999); such research is certainly needed. In the meantime, impetus for cowbird removal remains strong.

Although large-scale habitat restoration and changes in land use are acknowledged as important for recovery of the vireo, assessment and reduction of cowbird parasitism are still recommended as the first consideration for land managers (USFWS 1996). It should be noted that alternatives to removal often have economic and political constraints (Rothstein et al. 2003). In the case of the vireo, ultimate recovery of the species hinges on management of private lands (USFWS 1996). Without economically viable alternatives that are compatible with traditional land uses, and without incentives to implement alternatives, cowbird removal will likely remain the primary means of mitigating cowbird parasitism's threat to vireo populations.

So, why continue cowbird control at Fort Hood?—The vireo population at Fort Hood has substantially increased, and the population of locally breeding cowbirds has probably decreased, given the currently low parasitism rates (<10% annually since 1997). In addition, vireo nest success has been maintained at a relatively high level since 1991. An untested possibility is that per-capita risk of parasitism (Hall and Rothstein 1999, Rothstein et al. 2003) has been reduced sufficiently to allow the vireo population to sustain itself without cowbird removal.

Regardless, Fort Hood is legally obligated to continue cowbird control through 2005 (USFWS 1993, 2000; Hayden et al. 2001). We anticipate that updates to the USFWS Biological Opinion for Fort Hood and to Fort Hood's Endangered Species Management Plan that will take effect after 2005 will continue to mandate cowbird control to enhance vireo productivity and to keep parasitism below 10%.

The negative correlation between number of female cowbirds removed and parasitism has been interpreted (though not tested) as evidence that cessation or reduction of cowbird control would result in increased parasitism (Barber and Martin 1997, Eckrich et al. 1999). However, in our opinion, that correlation can be misleading. Because most cowbirds on Fort Hood are likely migrants, the presence of large numbers of cowbirds may not necessarily result in higher parasitism. The actual relationship between number of female cowbirds removed and parasitism is likely related to an increased probability of removing some unknown number of locally breeding females when greater overall numbers of cowbirds are captured. However, because even small numbers of locally breeding female cowbirds can have large effects on parasitism rates (Stutchbury 1997, TNC unpubl. data), at least at the local level, continuation of cowbird control may be justified, even if only a relatively small number of locally breeding females are being removed.

Additionally, cowbird control appears to be effective in reducing parasitism and maintaining low levels of parasitism. Although potential alternatives to control exist (e.g. manipulation of cattle-grazing patterns), such alternatives have had mixed results in reducing parasitism, at least on Fort Hood. Although cattle-grazing manipulations would likely have positive effects on the

vireo, they could be logistically and politically difficult to implement, both on and off Fort Hood. Thus, there is impetus to continue cowbird control, not only because it has been shown to be an effective tool for managing cowbird parasitism, but also because it is easier to implement.

Finally, although vireo populations have increased at several locations (Grzybowski 1995), the Fort Hood recovery region is one of the few to meet its recovery goals (USFWS 1996). We attribute the attainment of those goals primarily to cowbird control. Ultimately, the fate of the vireo remains uncertain, particularly outside of Fort Hood, where cowbird parasitism likely remains high and where habitat deterioration and loss is more of an issue. Arguably, Fort Hood now contains a source population of vireos and cowbird removal should be continued there to enhance vireo productivity and dispersal off Fort Hood, thus potentially promoting the recovery of vireos in bordering areas.

Because of associated economic, ethical, legal, and political considerations, the initiation and continuation of cowbird removal efforts should not be lightly considered (Ortega 1998, Hall and Rothstein 1999, Rothstein and Cook 2000). Cowbird removal is warranted in many instances and has been effective in mitigating cowbird parasitism threats. However, managers should be flexible, not only in the cowbird removal techniques they apply in a given situation (Hall and Rothstein 1999), but in their criteria for initiating and continuing cowbird removal efforts. Decisions to initiate or continue cowbird removal must be made in light of solid information (Rothstein et al. 2003) and in keeping with local and regional recovery goals and available resources (e.g. personnel). In addition, such decisions need to consider the local management landscape, because it may be difficult or impossible to implement politically demanding alternatives to removal, such as cattle-grazing manipulations or habitat preservation or restoration.

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CHAPTER 4

ECOLOGY AND MANAGEMENT OF SHINY COWBIRDS (*MOLOTHRUS BONARIENSIS*) AND ENDANGERED YELLOW-SHOULDERED BLACKBIRDS (*AGELAIUS XANTHOMUS*) IN PUERTO RICO

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ABSTRACT.—Historically, the Shiny Cowbird (*Molothrus bonariensis*; hereafter “cowbird”) was confined to South America, Trinidad, and Tobago. Within the past century, cowbirds have expanded their range into the West Indies, bringing them into contact with avian communities that have never experienced brood parasitism. Because of their small populations, high degree of isolation, and lack of experience with cowbirds, West Indian birds are at greater risk of harm from cowbird contact than mainland birds. Cowbird parasitism was the single most important factor in the reduced reproductive output of the endangered Yellow-shouldered Blackbird (*Agelaius xanthomus*; hereafter “blackbird”), a Puerto Rican endemic. Roost counts estimated that the blackbird population declined in southwestern Puerto Rico from 1,663 individuals (1974–1975) to 266 (1981–1982). Cowbird trapping in upland areas near blackbird nesting areas in mangroves and cowbird feeding areas has proved successful in managing cowbirds and increasing blackbird populations. Removal of cowbird eggs and nestlings from artificial nesting structures has resulted in fewer parasitized blackbird nests. As a result of those measures, cowbird parasitism of blackbirds has fallen from 95% (1973–1983) to <3% (2000–2003) and, judging from roost counts in 2004, the blackbird population has increased to 800 individuals in southwestern Puerto Rico. Cowbird management programs have excellent potential to reduce the adverse effects of cowbird parasitism; however, trapping within nesting areas is not recommended, because it may increase the probability of capturing and stressing breeding blackbirds.

RESUMEN.—Históricamente, *Molothrus bonariensis* estaba confinado a Sudamérica, Trinidad, y Tobago. A lo largo del siglo pasado, *Molothrus bonariensis* ha expandido su área a las Indias Orientales, lo que los ha puesto en contacto con comunidades de aves que nunca antes habían experimentado el parasitismo de cría. Debido a su pequeño tamaño poblacional, alto grado de aislamiento, y falta de experiencia previa con *Molothrus*, las aves de las Indias Orientales están en un mayor riesgo de daño causado por los tordos que las especies continentales. El parasitismo por el *Molothrus bonariensis* fue el único y más importante factor responsable de la reducción del éxito reproductivo de *Agelaius xanthomus*, una especie en peligro endémica de Puerto Rico. Mediante conteos en dormideros se estimó que la población *Agelaius xanthomus* disminuyó en el sudeste de Puerto Rico de 1,663 individuos (1974–1975) a 266 (1981–1982). El trampeo *Molothrus bonariensis* en zonas altas cercanas a las áreas de nidificación de *Agelaius xanthomus*, zonas de manglares y áreas de alimentación de *M. bonariensis* demostró ser exitoso en manejar a los *M. bonariensis* e incrementar las poblaciones de *A. xanthomus*. La remoción de huevos y pichones de *M. bonariensis* de las estructuras de nidificación artificiales se tradujo en un menor número de nidos de *A. xanthomus* parasitados. Como consecuencia de dichas

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medidas, el parasitismo del *M. bonariensis* sobre la *A. xanthomus* cayó del 95% (1973–1974) a <3% en (2000–2003) y, basándonos en los conteos en dormitorios durante 2004, la población de *A. xanthomus* en el sudeste de Puerto Rico, habría aumentado a 800 individuos. Los programas de manejo del *M. bonariensis* tienen un excelente potencial de reducir los efectos adversos del parasitismo. Sin embargo, el trapeo dentro de las áreas de nidificación debería evitarse ya que aumenta la probabilidad de capturar y provocar estrés en los *A. xanthomus* nidificantes.

ORIGINALLY CONFINED TO northern South America, Trinidad, and Tobago, the Shiny Cowbird (*Molothrus bonariensis minimus*; hereafter “cowbird”) has expanded its range into the West Indies within the past 100 years (Cruz et al. 1985) and is now moving into Florida and other areas of the United States and Middle America (Cruz et al. 1989, 2000; Ortega 1998; Lowther and Post 1999).

Because of the small population sizes and degree of isolation of the West Indian avifauna, contact with cowbirds is potentially more detrimental than in other habitats, where new contact between species occurs more gradually and over a wider area (Cruz et al. 1998). Not only are many West Indian species and subspecies restricted in range, but until the arrival of cowbirds, they had no contact with brood parasites—factors that potentially make them more vulnerable to the negative effects of parasitism (Cruz et al. 1989, Woodworth 1997, Nakamura and Cruz 2000). In Puerto Rico, cowbird parasitism was the most important factor in reduced reproductive output of the endangered Yellow-shouldered Blackbird (*Agelaius xanthomus*; hereafter “blackbird”; U.S. Fish and Wildlife Service [USFWS] 1976, Wiley et al. 1991, Lowther and Post 1999, Nakamura and Cruz 2000).

In 1980, the Department of Natural and Environmental Resources (DNER) of Puerto Rico and the USFWS established a management plan for blackbirds that included cowbird control, removal of cowbird eggs, and construction of artificial nesting structures (USFWS 1996). Here, we summarize the results of the management and conservation efforts to reduce cowbird parasitism and to increase the numbers of blackbirds in the remaining population stronghold in southwestern Puerto Rico. The present study is based on an extensive literature review and on fieldwork conducted from 2000 to 2004. The last published study on Shiny Cowbird–Yellow-shouldered Blackbird interactions was that of Lopez-Ortiz et al. (2002), covering the

1996–1999 nesting period. The blackbird, of all the threatened species in the West Indies, has possibly the best chance of recovery. Success with this species could serve as an example of what can be accomplished in the West Indies with an aggressive conservation program (Wiley et al. 1991).

HISTORICAL BACKGROUND

The endemic blackbird was formerly common and widespread on Puerto Rico and Mona Island (Wetmore 1927, Post and Wiley 1977, Post 1981, Wiley et al. 1991). Since the 1940s and 1950s, the population has sharply declined and is now primarily restricted to southwestern Puerto Rico and Mona Island (Post 1981, USFWS 1996, Lopez-Ortiz et al. 2002). In 1976, the species was listed as endangered and critical habitat was designated, pursuant to the Endangered Species Act of 1973 (USFWS 1976). Several factors contributed to the blackbird’s decline, including disease, loss of feeding and nesting habitats, and nest predation (Post and Wiley 1976, 1977; Post 1981; Wiley et al. 1991, USFWS 1996; Lopez-Ortiz et al. 2002; A. Cruz and T. Nakamura unpubl. data). However, cowbird parasitism was the primary factor.

Between 1974–1975 and 1981–1982, the blackbird population in southwestern Puerto Rico decreased by ~80%. In contrast to the 2,000 individuals estimated in 1976, only ~300 were present in 1982 (Post and Wiley 1976, Wiley et al. 1991). Cowbirds have not become established on Mona Island; consequently, blackbird populations there (ranging between 467 and 908) have not been affected by parasitism (E Hernandez-Prieto and A. Cruz unpubl. data).

In the Boquerón Commonwealth Forest (BCF) of southwestern Puerto Rico, 94.6% of blackbird nests (246 of 260) were parasitized between 1973 and 1983 (Table 1; Wiley et al. 1991) and produced fewer chicks than nonparasitized nests. Failure of parasitized nests results mainly from nest

TABLE 1. Change in Shiny Cowbird parasitism rate and number of active Yellow-shouldered Blackbird nests in Boquerón Commonwealth Forest, Puerto Rico, 1973–2003.

Year ^a	Number of active nests	Number of nests parasitized	Percentage of nests parasitized
1973–1983	260	246	94.6
1985	8	2	25.0
1986	32	21	65.6
1987	41	6	14.6
1988	61	23	37.7
1989	42	5	11.9
1990	79	6	7.6
1991	68	8	11.7
1992	125	30	24.0
1993	187	0	0
1994	97	18	18.6
1995	229	11	4.8
1996	224	0	0
1997	145	0	0
1998	271	22	8.1
1999	210	1	0.5
2000	296	0	0
2001	325	12	3.7
2002	282	0	0
2003	306	17	5.6

^a Data from Wiley et al. 1991, USFWS 1996, DNER unpubl. data, and A. Cruz and T. Nakamura unpubl. data.

abandonment, multiple parasitism, and female cowbirds puncturing and breaking host eggs. The frequency of egg puncture in blackbirds increased from 2.8% in 35 clutches in 1975 (Post and Wiley 1977) to 19.6% in 194 clutches in 1988 in the BCF (Nakamura and Cruz 2000).

Between 1982 and 1988, all punctured eggs (47 of 609 eggs, or 7.7%) failed to hatch. Egg puncture was associated with a greater incidence of nest abandonment. Within three days, clutches with punctured eggs were abandoned (Nakamura and Cruz 2000). Egg puncture may be positively correlated with cowbird numbers, given that the incidence of egg puncture increased during the 20-year period following the invasion of southwestern Puerto Rico by cowbirds (Nakamura and Cruz 2000).

Multiple parasitism (i.e. clutches containing two or more cowbird eggs) was also prevalent, with 78.1% of 114 parasitized nests containing ≤ 15 cowbird eggs nest⁻¹ between 1982 and 1988 (Nakamura and Cruz 2000). The combined reproductive consequences of egg puncture and multiple parasitism significantly reduced hatching success in blackbirds, underscoring

the importance of reducing cowbird numbers in blackbird nesting areas.

METHODS

STUDY AREA

Our study area comprises the BCF and surrounding areas in southwestern Puerto Rico. The BCF site is ~1 km wide and extends 15 km from La Parguera to Pitahaya on the eastern shore of Bahía Sucia. The area is composed mainly of mangrove forests—black mangrove (*Avicennia germinans*), white mangrove (*Laguncularia racemosa*), button mangrove (*Conocarpus erectus*), and red mangrove (*Rhizophora mangle*)—and salt flats (salinas), which border arid scrub and savanna. The abandoned salinas and mud flats in the coastal mangrove zone are the most important nesting habitat for blackbirds (Post and Wiley 1976). For a description of the area, see Wiley (1985), Nakamura and Cruz (2000), and Lopez-Ortiz et al. (2002).

COUNTS

From 1990 to 2004, we counted blackbirds in late afternoons as they entered offshore mangrove cay roosts in BCF. The areas surveyed and efforts invested in those counts have been similar since 1990 (Wiley et al. 1991). Two or more persons counted birds, while another recorded data from locations where flight lines into the roost could be seen (La Parguera, Pitahaya, Bahía Sucia, and Boquerón).

COWBIRD CONTROL

Starting in 1980, USFWS conducted cowbird removal experiments at BCF (Wiley et al. 1991). In 1983, the blackbird program was transferred to DNER and has since been conducted under their Section 6 Endangered Species Program.

We captured cowbirds in portable, walk-in decoy traps (a smaller version of decoy traps used for cowbird control in Michigan; Shake and Mattson 1975). Traps were placed on dry ground or on elevated (1 m) wooden platforms over water and were baited with cracked maize (*Zea mays*) and water. Cowbirds were attracted to decoys (live cowbirds) inside traps. The trapped cowbirds were killed, and nontarget species were released (Wiley et al. 1991).

From 1993 until present, 5 to 11 traps were strategically distributed in Pitahaya (a sector within the BCF; the main blackbird breeding ground) and the main feeding grounds of cowbirds around the BCF. Starting in 2000, the program activated traps only within the cowbird feeding grounds from September to April (nonbreeding season) to avoid trapping blackbirds.

ARTIFICIAL NESTING STRUCTURES

Cowbird control was complemented by use of artificial nesting structures (ANS) to improve blackbird reproductive success by preventing predation and parasitism (Lopez-Ortiz et al. 2002). Wooden nest boxes ($n = 189$) were placed on fence posts in nesting areas at BCF from 1977 to 1982 (Wiley et al. 1991). Nest boxes were irregularly spaced in mud flats and salinas surrounded by mangrove forests. That allowed the creation of nesting habitat in areas where management activities could be undertaken. The boxes were used by blackbirds but were also parasitized by cowbirds.

In 1984, DNER continued the ANS program (Lopez-Ortiz et al. 2002). The current nest-box design consists of a polyvinyl chloride (PVC) post with a 10-cm (diameter) PVC elbow attached at the top. The PVC nest structures are more resistant to weathering than the wooden nest boxes, and their slippery surface reduces rat predation. They also prevent nest piracy by the Caribbean Martin (*Progne dominicensis*) (Hirsch 1990, USFWS 1996, Lopez-Ortiz et al. 2002). The current number of ANS is ~200. There are 10 nesting areas where ANS are located. Nests are checked once or twice a week; if the nests are parasitized, cowbird eggs and chicks are removed to enhance reproductive success of blackbirds.

RESULTS OF THE MANAGEMENT PROGRAM

COWBIRD REMOVAL PROGRAM

During 1985 through 2003, ~30,000 cowbirds were captured (Table 2; USFWS 1996, DNER pers. comm.). As representative of the trapping protocol, we describe the 2000–2003 trapping efforts. Five traps were used from September 2001 to March 2002 (2002 trapping period). In 140 capture days, 1,107 cowbirds were captured (402 females and 705 males). Total cowbirds captured was the same as during September 2000 to March 2001, but 66% higher than September 1999 to March 2000 capture data (575 cowbirds). From September 2002 to March 2003, six traps were active. In 100 capture days, 533 cowbirds were captured (241 females and 292 males).

PARASITISM AND EGG PUNCTURE FREQUENCY

Since cowbird control was initiated, the percentage of parasitized blackbird nests has decreased from 95% between 1973 and 1983 to <10% since 1995 (Table 1) with particularly low (<2.5%) mean parasitism frequency since 1995. Additionally, the numbers of blackbird nests

TABLE 2. Shiny Cowbirds captured in southwestern Puerto Rico, 1985–2003.

Year ^a	Number of cowbirds captured		
	Females	Males	Total
1985	748	568	1,316
1986	511	502	1,013
1987	908	999	1,906
1988	669	1,831	2,500
1989	1,549	767	2,316
1990	1,387	1,239	2,626
1991	1,878	1,129	3,007
1992	1,104	919	2,004
1993	1,650	871	2,521
1994	1,513	880	2,393
1995	572	502	1,074
1996	694	659	1,353
1997	519	822	1,341
1998	408	589	977
1999	107	186	293
2000	173	402	575
2001	472	635	1,107
2002	402	705	1,107
2003	241	292	533
Total	15,505	14,476	29,981

^aData from Wiley et al. 1991, USFWS 1996, A. Cruz and T. Nakamura unpubl. data, and DNER unpubl. data.

containing one or more punctured eggs have decreased dramatically (1982–1988: 19.6%, 38 of 194 nests; 1991: 10.3%, 7 of 68 nests; 1992: 1.6%, 2 of 125 nests; 1993: 3.7%, 7 of 187 nests; and 2002–2003: 0%, 0 of 588 nests; Nakamura and Cruz 2000, DNER unpubl. data).

NUMBER OF NESTS AND ARTIFICIAL NEST STRUCTURES

Not only has the number of parasitized nests decreased, but the number of active blackbird nests has increased from 8 in 1985 to 306 in 2003 (Table 1). Number of ANS placed in the nesting area doubled between 1986 and 1990 (USFWS 1996). The proportion of active nests in ANS increased from 20% in 1986 to 98.7% in 1988. From 1989 to 1995, almost every blackbird nest was in ANS, and few nests occurred in natural substrates (Lopez-Ortiz et al. 2002).

The DNER management program controls effects of parasitism on blackbird nesting in ANS by removing all cowbird eggs at the end of the incubation period and prior to hatching. From 1991 until present, every cowbird egg has been removed from nests in ANS. In 2003, 21 cowbird eggs were removed from ANS.

Use of ANS has allowed creation of nesting habitat in areas, such as open salt flats, where management activities (e.g. cowbird egg removal) could be undertaken. In 2002, for example, 193 of 200 ANS were used (97%; DNER unpubl. data). Some of the ANS were used more than once, and a total of 280 nests were constructed, of which 254 (91%) were active and 146 (57%) were successful.

NATURAL NESTS

A positive, more recent outcome has been the greater use of natural nests as a result of increasing populations (Lopez-Ortiz et al. 2002). The use of natural substrates increased from 2% (5 of 243) in 1996 to 31.5% (79 of 251) in 1999. In 2001, 123 natural nests were found, of which 66 (55.9%) were active. Almost every nest in natural substrates was an open-cup nest. The increase in use of natural substrates is a favorable trend for recovery of the species, and it is directly related to the success of the management program.

PARASITISM IN MANAGED AND NONMANAGED AREAS

As a result of the management activities undertaken in BCF, new blackbird colonies have become established outside BCF where there is no cowbird control. That development provides the opportunity to compare parasitism frequency between managed and nonmanaged areas. In a three-year period (2000–2001, and 2003), parasitism frequency in the nonmanaged area (~90 km east of BCF) was higher (52.4%, 11 of 21) than in the managed area (3.1%, 29 of 927) (paired *t*-test: $t = -4.410$, $df = 2$, $P = 0.048$).

POPULATION COUNTS

Roost counts in BCF show that the blackbird population is increasing (Fig. 1). In contrast to the estimated population of 300 individuals in 1982, we estimated the 2004 population in southwestern Puerto Rico to be >800.

CONCLUSIONS AND RECOMMENDATIONS

The lower parasitism rates and increase in the blackbird population in managed areas can

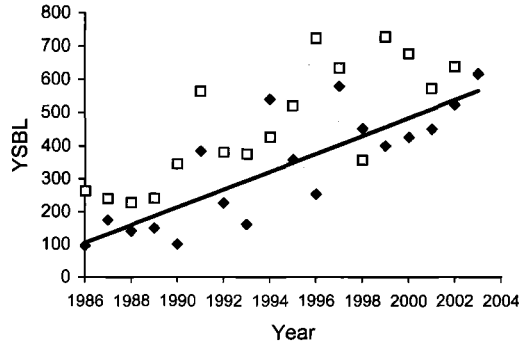


FIG. 1. Yellow-shouldered Blackbird (YSBL) roost counts in Boquerón Commonwealth Forest, Puerto Rico, 1986–2003. Diamonds represent prebreeding counts in spring, and squares represent postbreeding counts in fall.

be attributed to a decrease in the local cowbird population due to trapping and egg removal. As a result, blackbirds are now establishing populations in habitats outside the managed areas. That is encouraging, because it suggests availability of suitable breeding habitat outside of BCF. However, higher rates of parasitism as compared with those in managed areas suggest that cowbirds still pose a threat to blackbird populations.

Although the focus of the cowbird control program has been on blackbirds, other heavily parasitized species in BCF should also share beneficial effects. For example, parasitism levels have declined in Yellow Warbler (*Dendroica petechia*) populations in BCF. Rates of parasitism on the Yellow Warbler decreased from 80% between 1975 and 1977 to 36.9% between 2000 and 2003. In contrast, parasitism rates in nonmanaged areas were 85% (Lopez-Ortiz et al. unpubl. data). Other species that may benefit from cowbird control include Puerto Rican Vireos (*Vireo latimeri*) and Black-whiskered Vireos (*V. altiloquus*); 87% and 73%, respectively, were parasitized between 1982 and 1988 (Nakamura and Cruz 2000). Faaborg et al. (1997) felt that the decline in Puerto Rican Vireos observed at Guánica Commonwealth Forest, southwestern Puerto Rico, was attributable to parasitism; and Woodworth (1997) recorded an 83% parasitism rate for this species in Guánica.

There is almost no possibility that cowbirds can be eliminated from the entire island, because they are abundant and use several host species (Cruz et al. 1985, Wiley 1985, DNER unpubl.

data). However, cowbird trapping appears to be the best available strategy for reducing the effects of parasitism in small, geographically restricted host populations, such as Yellow-shouldered Blackbirds. Populations of endangered species that have low productivity as a result of high levels of parasitism are candidates for intensive cowbird control efforts (Robinson et al. 1993, Rothstein and Cook 2000).

Cowbird control is an important component of blackbird breeding-area management. Other components of blackbird management include ANS, removal of cowbird eggs, control of ectoparasites, reduction of nest piracy and predation, prevention of habitat loss, and patrolling the area to prevent human disturbance (Wiley et al. 1991, USFWS 1996, Lopez-Ortiz et al. 2002).

The increase in the use of natural substrates for nesting by blackbirds is an encouraging trend, and it is directly related to the increase in blackbird numbers in BCF. However, given that nesting success was 17% higher in ANS than in natural substrates as a result of higher predation rates in natural nests, continued use of ANS will be needed to further augment the population (Lopez-Ortiz et al. 2002).

We recommend continuation of the cowbird management program until recovery goals of the blackbird program are met—that is, downlisting of the species from endangered to threatened in response to increasing population levels (USFWS 1996). Recovery goals include (1) monitoring blackbird and cowbird populations, (2) trapping and destroying cowbirds found in areas adjacent to blackbird nesting areas, (3) continued installation of ANS, (4) monitoring blackbird reproductive success in ANS and natural nests, (5) removing and destroying all cowbird eggs found in blackbird nests, (6) characterizing existing nesting habitat, and (7) surveying for populations outside of BCF. We estimate that >90% of the blackbird population in the southwest consists of individuals nesting in BCF. Further investigations should address population dynamics parameters, such as population growth rate and fledgling survival probability. Although nesting success data are available from BCF, nesting data need to be gathered in areas outside BCF. In particular, data on the effects of parasitism on those populations; investigation should begin with remnant populations within the municipalities of Guayama and Salinas. Blackbird

productivity levels outside of BCF need to be assessed to gain insights on the long-term recovery prospects for this species (Collazo et al. unpubl. data).

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CHAPTER 5

COWBIRD (*MOLOTHRUS* SPP.) ECOLOGY: A REVIEW OF FACTORS INFLUENCING DISTRIBUTION AND ABUNDANCE OF COWBIRDS ACROSS SPATIAL SCALES

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ABSTRACT.—Brown-headed Cowbirds (*Molothrus ater*; hereafter “cowbirds”) provide one of the best case studies for demonstrating the need to consider multiple spatial scales in managing a species and designing conservation strategies. An adaptive management program to reduce cowbird parasitism levels through reduction of cowbird abundance should mirror the multiple spatial scales to which cowbirds respond. At the continental scale (>50 km), cowbirds are widespread across most of North America, and their abundance declines with distance from the center of their distribution in the Great Plains and Midwest. Generally, cowbird parasitism frequency is highest in, and declines with distance from, the Midwest; however, abundance at that broad scale is by no means indicative of parasitism frequency at the local level, because regional, landscape, and local factors play a significant role in cowbird abundance, distribution, and parasitism levels. At the regional scale (10–50 km), cowbird abundance and cowbird:host ratio decline with increasing forest cover, resulting in lower parasitism levels in the Midwest, where most of the relevant research has been conducted. Studies from forested regions of the East and Far West and from nonforested systems are under-represented; nevertheless, it is clear that increasing the spatial extent of contiguous habitat for host species is a key priority in cowbird management. Within the landscape scale (<10 km), density and dispersion of feeding sites strongly influence cowbird distribution and abundance. Cowbirds are known to commute >10 km between feeding and breeding habitats; removal of feeding opportunities for cowbirds near targeted management areas is a key control measure. Removal of livestock-centered feeding sites has traditionally been a management focus. However, cowbirds use agricultural fields, residential backyards, and recreational areas, too, and those feeding opportunities need to be considered in land-use planning and zoning. Locally, cowbird breeding abundance and distribution are strongly influenced by habitat type, vegetation structure, and passerine species richness; however, variation in regional or local cowbird abundance may affect local cowbird distribution. Local management should strive to protect habitat for large host populations while reducing habitat edges and, in grasslands, known cowbird perching sites. Comparative studies of cowbird breeding-site use are needed in most regions, and future comparisons would benefit if field researchers used a consistent, standardized protocol for vegetation measurement.

RESUMEN.—*Molothrus ater* provee de uno de los mejores estudios de caso que demuestran la necesidad de tener en cuenta distintas escalas para el manejo de la especie y el diseño de estrategias de conservación. Un programa de manejo adaptativo que busque reducir los niveles de parasitismo del *M. ater* por medio de la reducción de su abundancia debería reflejar las

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distintas escalas espaciales a las cuales los *M. ater* responden. A una escala continental (>50 km), los *M. ater* están extendidos a lo largo de prácticamente toda Norteamérica, y su abundancia disminuye con la distancia del centro de su distribución (Grandes Planicies y Medio Oeste). Generalmente, la frecuencia de parasitismo por *M. ater* es mayor en el Medio Oeste, y disminuye con la distancia al mismo. Sin embargo, su abundancia a una escala mayor de ninguna manera es indicativa de las tasas de parasitismo a nivel local, porque los factores a nivel regional, paisaje, y locales juegan un rol significativo sobre la abundancia y distribución de los *M. ater*, y los niveles de parasitismo. A una escala regional (10–50 km), la abundancia de *M. ater* y la relación *M. ater*:hospedero disminuye con el incremento de la cobertura por bosques, implicando un menor nivel de parasitismo en el Medio Oeste, lugar donde se llevaron a cabo la mayoría de los estudios relevantes. Estudios realizados en áreas boscosas del Este y Lejano Oeste, y de sistemas no boscosos están sub-representados. Sin embargo, es obvio que en estos sistemas un incremento en la extensión del hábitat continuo apto para las especies hospederas es una prioridad clave en el manejo de *M. ater*. Dentro de la escala a nivel paisaje (<10 km), la densidad y dispersión a sitios de alimentación influye marcadamente sobre la distribución de *M. ater* y su abundancia. Se sabe que los *M. ater* pueden moverse a >10 km entre hábitats de alimentación y reproducción en cosecuencia, la remoción de oportunidades de alimentación cercanas a zonas-objetivo de manejo, es una medida clave para su control. Sin embargo, los *M. ater* también usan campos agrícolas, parques residenciales, y áreas recreativas, por lo que aquellas oportunidades de alimentación deberían ser consideradas dentro de las planificaciones de uso y zonificación. Localmente, la abundancia de los *M. ater* reproduciéndose y su distribución está altamente influenciada por el tipo de hábitat, la estructura de la vegetación, y la riqueza de Paseriformes. Sin embargo, la variación regional o local de la abundancia de *M. ater* puede afectar su propia distribución. Las personas a cargo del manejo local deberían procurar protección de hábitats que mantuvieran grandes poblaciones de hospederos, junto con la reducción de sus bordes y, en los pastizales, la reducción de sitios usados por *M. ater* como percha. En la mayoría de las regiones es necesario llevar a cabo estudios comparados sobre el uso de sitios reproductivos por parte del tordo, y las futuras comparaciones se beneficiarían si los estudios de campo se basaran en el uso de protocolos consistentes y estandarizados de las medidas vegetación.

UNDERSTANDING DISTRIBUTION AND abundance of Brown-headed Cowbirds (*Molothrus ater*; hereafter “cowbirds”) is an important first step in developing management plans to reduce the effects of brood parasitism on host populations. The topic has generated considerable interest, because cowbirds present a conservation problem in many regions (e.g. Lowther 1993; Rothstein and Robinson 1994, 1998; Thompson 1994; Robinson et al. 1995a; Donovan et al. 2000; Smith et al. 2000). Cowbirds also demonstrate the need to consider multiple spatial scales in species management and design of conservation strategies (Robinson 1999). Cowbirds routinely commute ≤ 15 km between breeding, feeding, and roosting sites, which are often in very different habitats. Generally, cowbirds lay eggs in host nests in forests, forage in open areas among livestock, and roost communally in large trees.

Here, we summarize the most recent information on factors influencing cowbird distribution and abundance across continental (>50 km), regional (10–50 km), landscape (1–10 km), and local (within-site) scales. We finish our review specifically with the resource manager and

land-use planner in mind, addressing practical aspects of cowbird management in the context of spatial ecology.

FACTORS AFFECTING COWBIRD DISTRIBUTION AND ABUNDANCE AT THE CONTINENTAL SCALE

Cowbirds are widespread across North America and most abundant in the Great Plains (Fig. 1). Although it is generally presumed that the Great Plains was the historical center of cowbird distribution and that cowbirds were historically absent west of the Rocky Mountains (Friedmann 1929, Mayfield 1965), bison, and presumably cowbirds, were more widespread west of the Great Plains than previously believed (Chace and Cruz 1999), albeit at much lower densities than on the Great Plains. Cowbirds became widespread in the eastern United States by 1800 (Bendire 1895) and in the far West by the 1920s (Rothstein 1994, Ward and Smith 2000). During the 1900s, cowbirds invaded the Maritime Provinces of Canada and the southeastern United States (Cruz et al. 2000).

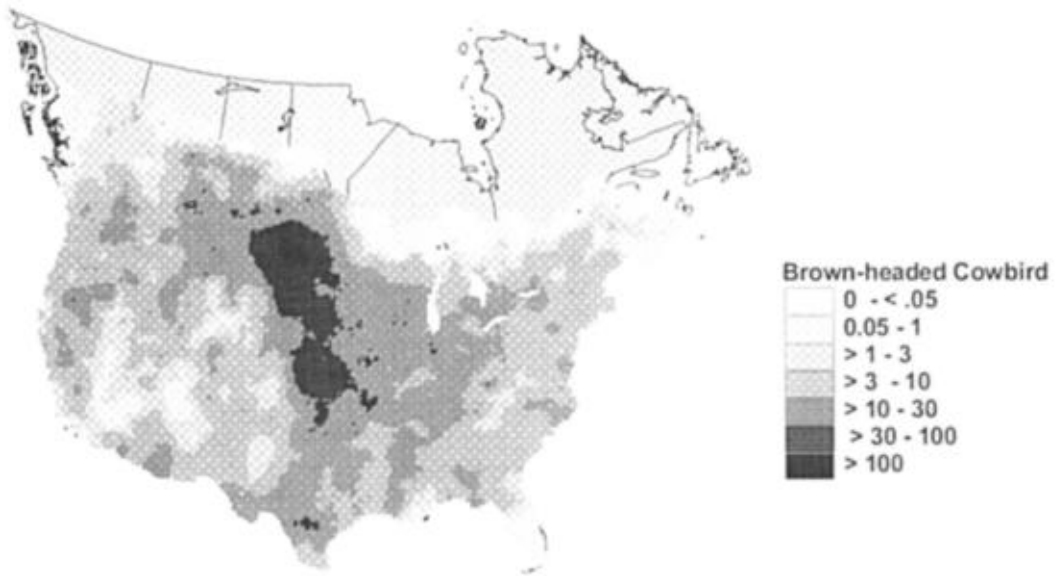


FIG. 1. Breeding distribution and mean abundance of Brown-headed Cowbirds per Breeding Bird Survey (24.5 mile) roadside route, 1966–1996.

Since the beginning of the Breeding Bird Survey (BBS) in 1966, cowbirds have been declining across the BBS region (Sauer et al. 2003), primarily at the fringes of the distribution (Peterjohn et al. 2000, Wiedenfeld 2000, Sauer et al. 2003), including areas of southeastern Canada and the northeastern United States that have had significant levels of reforestation over the past 100 years (Askins 1993). However, cowbirds are increasing in several areas of the far West—for example, in the Central Valley of California (Wiedenfeld 2000), a recently invaded region (Rothstein 1994). Cowbirds are also increasing in Florida, an area where they were declining until the past decade and where cowbird populations are still very low. The BBS is designed to detect population change at large spatial scales and temporal patterns; it is not designed to measure change at the smaller spatial scales at which productivity and survivorship are most strongly influenced.

In general, parasitism frequency on most host species reflects the current continental pattern of cowbird abundance, declining with distance from the center of cowbird abundance in the northern Great Plains (Hoover and Brittingham 1993, Smith and Myers-Smith 1998). Among grassland birds, for example, parasitism (which

is often rare; Peer et al. 2000), is higher in the northern Great Plains than in the Midwest (i.e. Minnesota south to Missouri and east to Ohio; Davis and Sealy 2000, Koford et al. 2000). Likewise, Wood Thrush (*Hylocichla mustelina*) parasitism levels are higher in Illinois (80–100%; Robinson 1992, Hoover and Brittingham 1993, Robinson et al. 2000) than in Maryland (<25%; Dowell et al. 2000, Petit and Petit 2000). At the continental scale, cowbird abundance is a good predictor of parasitism levels; however, regional, landscape, and local factors can very strongly influence cowbird abundance and parasitism pressure on host species.

FACTORS AFFECTING COWBIRD DISTRIBUTION AND ABUNDANCE OF AT THE REGIONAL SCALE

The regional (10–50 km radius) scale is relevant for studies of cowbird distribution, because it encompasses the species' large home range. The cowbird's maximum recorded daily travel distance is 15 km (Curson et al. 2000). That maximum distance presumably explains why cowbirds are absent in extensively forested habitats that lack feeding areas (e.g. Holmes et al. 1992, Coker and Capen 2000). To exclude cowbirds from forest habitat, forest tracts must

be >700 km², which is generally not feasible in terms of land management. However, cowbirds' responses to landcover at the regional scale can be used to guide management aimed at reducing, though not eliminating, cowbird parasitism.

At the 10-km-radius scale, cowbird abundance and parasitism show a consistent negative relationship to the proportion of forest cover surrounding the study site (Robinson et al. 1995b, Donovan et al. 2000, Thompson et al. 2000). Cowbird abundance can be positively correlated with host density (Gates and Gysel 1978, Rothstein et al. 1986), forest perimeter:area ratio, and forest–nonforest edge density; and negatively correlated with forest-tract size and forest core area. However, those variables are often intercorrelated, making them hard to separate from the proportion of forest cover. Results of relevant studies are as follows. Parasitism-induced nest failure for three forest-breeding host species was higher in a fragmented landscape (mean 31% forest cover) than in a nonfragmented landscape (mean 93% forest cover), decreased with increased forest-patch size and forest core area, and increased with edge density (see tables 1 and 4 in Donovan et al. 1995). Parasitism decreased monotonically as forest cover at a 10-km radius increased from a low of 6% to a high of 95% (Robinson et al. 1995b). The trend was significant for five of nine host species and overall. Cowbird abundance and nest parasitism levels decreased with mean forest-tract size and with increasing proportion of forest cover and core area (Thompson et al. 2000). Cowbird abundance generally increased with edge density (meters per hectare). Cowbird abundance decreased significantly with increasing forest cover (20–92%), and increased significantly with increasing forest perimeter:area ratio (Donovan et al. 2000). When the relationship between scale of forest cover and cowbird abundance was explicitly examined across 1- to 10-km radii, the most significant relationships occurred for male and female cowbirds combined at the 10-km radius, and for female cowbirds only at 3- to 5-km radii (Donovan et al. 2000).

A limitation of the studies discussed above is that they were all conducted in the Midwest and shared some of the same data. To address the relationship between forest cover and cowbird parasitism in other geographic areas,

Hochachka et al. (1999) used nest records from the BBIRD database (see Acknowledgments) for 26 sites across the United States to investigate the relationship between percentage of forest cover at a 10-km radius and the proportion of host nests parasitized. Across a range of forest cover (5–99%), they found a small but significant decrease in parasitism with increasing forest cover: a 10% increase in forest cover reduced parasitism by ~1%. It is not clear whether the weaker effect found by Hochachka et al. (1999) reflects regional differences in patterns of cowbird abundance or differences in methodology.

Only two studies have considered the relationship between cowbird abundance and forest cover at spatial scales larger than a 10-km radius. As suggested by Hochachka et al. (1999), scales exceeding the cowbirds' daily travel distance could be relevant to explaining cowbird abundance if cowbirds show a numerical as well as a functional response to landcover. Results at the 50-km radius are ambiguous; however, cowbird parasitism was positively but nonsignificantly related to percentage of forest cover (Hochachka et al. 1999). At an intermediate scale (864-km² hexagons, or ~2.7× the 10-km radius), cowbird abundance decreased significantly as forest cover increased (Donovan et al. 1997). Given the limited number of studies, it is not possible to identify the scale most strongly related to cowbird abundance, but it is probably greater than the 3-km radius and less than the 50-km radius.

Two studies, both done at the 10-km radius, have examined how the ratio of cowbirds to hosts changes with increasing forest cover. The cowbird:host ratio is difficult to interpret, because species vary widely in their quality as cowbird hosts (Winfree 2004), making the binary classification of "host" and "nonhost" problematic. Nonetheless, the ratio is of interest, because it roughly assesses the degree of parasitism pressure per host individual. The cowbird:host ratio decreased with increased mean forest-patch size (Thompson et al. 2000) and with increasing proportion of forest cover (see fig. 5 in Donovan et al. 1997). Those results suggest that breeding cowbirds do not track their hosts perfectly in more-forested landscapes, presumably owing to the energetics of commuting long distances from feeding sites.

The single study examining survival of cowbird offspring as a function of forest cover found

a significant positive relationship, attributable to lower nest-predation in more-forested landscapes (Donovan et al. 2000). That result suggests that, although the total number of breeding cowbirds decreases with increasing forest cover, per-capita reproductive success may increase.

In conclusion, all studies done at the 10-km-radius scale have found that cowbird abundance, parasitism of forest-breeding hosts, and cowbird:host ratio all decrease with increasing forest cover. Those results should be robust, because they reflect virtually the entire forest-cover gradient, from <5% to >95%. There is no evidence at the 10-km scale for a nonlinear response to forest cover by cowbirds, as would be expected if cowbirds were limited by feeding-site availability at the high end of the forest-cover gradient and by host availability at the low end. Responses may be nonlinear, however, at smaller spatial scales (e.g. Gustafson et al. 2002). An important role of landcover at the 10-km scale is that it may determine the strength of edge effects at smaller scales. For example, in highly fragmented landscapes saturated with cowbirds, edge effects may not occur, but as forest cover at the landscape scale increases, cowbirds may be limited to forest edges.

Our understanding of cowbird responses to landcover at the regional scale would benefit from several lines of future research. First, some of the scatter in existing relationships may be attributable to use of low-resolution landcover data. Many studies used 1-km² grid cells, which would miss many openings that could provide feeding or parasitism opportunities for cowbirds (e.g. Chace and Cruz 1999). Second, studies are needed in the eastern and western parts of the continent to find out whether patterns observed in the Midwest are found in other regions. Finally, all studies to date have focused on forest-breeding host communities. The effect of surrounding land use on parasitism of hosts in other habitats is an interesting and understudied question.

FACTORS AFFECTING COWBIRD DISTRIBUTION AND ABUNDANCE AT THE LANDSCAPE SCALE

At the landscape scale, cowbird distribution and abundance are determined primarily by relative spatial distribution of preferred foraging habitat and breeding habitat. Cowbirds are unusual among passerines in using distinct

habitat types for foraging and breeding and establishing spatially separate home ranges for those two activities. Cowbirds are ground-foragers and require open habitats for feeding, often exploiting a wide variety of feeding sites across anthropogenic landscapes: grazed grassland, agricultural fields, row crops, livestock corrals, lawns, and campgrounds (Friedmann 1929, Mayfield 1965, Ortega 1998). Cowbirds are well known for their commensal relationship with livestock. Large ungulates provide foraging opportunities for cowbirds via mechanisms including creation of feeding microhabitats, increased insect abundance, and flushing of insects while grazing (Goguen and Mathews 1999).

For breeding, however, cowbirds prefer to use habitats with more complex structure, such as forest, savannah, shrublands, and old fields. Where direct comparisons have been made, parasitism frequencies are higher in such habitats than in adjacent grasslands (Hahn and Hatfield 1995, Strausberger and Ashley 1997, Robinson et al. 1999). That habitat preference is most likely attributable to higher densities of hosts in more-structured habitats and the presence of elevated perches from which cowbirds can search for host nests.

COMMUTING BEHAVIOR: THE LINK BETWEEN BREEDING AND FEEDING SITES

An important consequence of the spatial separation of cowbird breeding and feeding locations is that abundance of cowbirds at any location depends not only on quality of the habitat at that location but also on characteristics of the surrounding landscape. To predict cowbird abundance in breeding areas where hosts are most exposed to the effects of parasitism, we must consider the surrounding distribution of cowbird feeding sites. The most important factors for cowbird breeding distribution at the landscape scale are likely to be (1) distance to nearest feeding site, (2) density of feeding sites, and (3) cowbird feeding-site preference.

In landscapes where feeding and breeding habitats are spatially separated, cowbirds commute daily between the two, maintaining regular home ranges in each throughout the breeding season (Rothstein et al. 1984, Thompson 1994, Gates and Evans 1998, Goguen and Mathews 2001). Radiotelemetry studies of

cowbirds at widely separated sites across North America have revealed a typical daily behavior pattern, consisting of morning breeding activity in forested habitats and afternoons spent foraging at livestock corrals and feeders (Rothstein et al. 1984), agricultural land and feedlots (Thompson 1994, Gates and Evans 1998), or grazed prairie (Goguen and Mathews 2001).

Distance to nearest feeding site.—Distance commuted between morning breeding sites and afternoon foraging sites appears to depend on the landscape context. Where breeding and feeding opportunities are tightly interspersed, many cowbirds have overlapping home ranges for those activities (Dufty 1982, Raim 2000) and thus do not commute daily. Where cowbirds commute, mean breeding-to-feeding distances tend to be 1–3 km: 1.2 km in Missouri and Illinois (Thompson 1994), 2.27 km in the Appalachians of western Maryland (Gates and Evans 1998), 4.1 km in the Sierra Nevada of California (Rothstein et al. 1984), and 1.47 km at a sharp forest–prairie interface in New Mexico (Goguen and Mathews 2001). In unfragmented forest in New Mexico, female cowbirds trapped at breeding areas in the forest interior commuted 9.3–13.2 km to foraging sites in the nearest available grazed prairie (Curson et al. 2000). Two factors account for the long commutes observed in New Mexico: the unfragmented forest contained large areas of suitable breeding habitat distant from the nearest available feeding habitat, and the cowbirds studied were trapped in that breeding habitat and did not represent a random sample of the local population (Curson et al. 2000).

Cowbirds are restricted in their choice of breeding areas to those within commuting distance of suitable foraging habitats. In severely fragmented landscapes, such as the Midwest, where cowbirds are abundant and forest exists only as small remnants, cowbirds parasitize host nests throughout the patch (Robinson et al. 1995b). However, in landscapes containing larger forest blocks, the result of cowbird commuting behavior is an edge effect at the landscape scale, with greater cowbird abundance and parasitism frequency observed near agricultural edges where cowbirds forage (Thompson et al. 2000).

That large-scale edge effect has been demonstrated by studies that measured a decline in cowbird abundance with increasing distance from cowbird feeding habitat. Studies from

the Intermountain West have measured such declines across distances of 4 km (Tewksbury et al. 1999), 5 km (Chace et al. 2003), 8–12 km (Goguen and Mathews 2000), and >20 km (Young and Hutto 1999). Chace et al. (2003) and Goguen and Mathews (2000) found corresponding gradients in parasitism of a major cowbird host, Plumbeous Vireo (*Vireo plumbeus*), and one study east of the Great Plains described a declining gradient in parasitism of a forest-dwelling host, Kentucky Warbler (*Oporornis formosus*), across a distance of 2 km from an agricultural edge (Morse and Robinson 1999). Distance from feeding sites appears to be one of the most important determinants of cowbird breeding abundance, having greater influence than forest type or host density in multivariate models (Tewksbury et al. 1999, Young and Hutto 1999, Goguen and Mathews 2000).

It is important to recognize that the landscape-scale edge effect discussed here is distinct from the more widely reported edge effects resulting from cowbirds' preference for nest-searching near structural edges (e.g. Brittingham and Temple 1983, Hahn and Hatfield 1995, Donovan et al. 1997); this effect differs in both scale and cause.

Density of feeding sites.—Cowbird abundance depends not only on distance to the nearest feeding site, but also on number of feeding sites within a given radius corresponding to the local commuting distance. In the Green Mountains of Vermont, where cowbird densities are low, cowbird occurrence in forest openings was positively related to number of livestock areas within 7 km but not influenced by distance to the nearest livestock area (Coker and Capen 1995). That may be attributable to low cowbird densities in the area. Where individual sites support low numbers of foraging cowbirds, number of feeding sites may be more important than distance to the nearest feeding site. A number of studies have related cowbird abundance or parasitism to the proportion of potential cowbird feeding habitat in the landscape at scales of 1.3 km (Hejl and Young 1999), 3 km (Stribley and Haufler 1999), and 7 km (Coker and Capen 1995). Cowbird abundance or parasitism increased with the proportion of open land (grassland and agriculture; Hejl and Young 1999) and agriculture (Stribley and Haufler 1999) in the landscape, and was negatively correlated with forest area at spatial scales >3 km (Donovan et al. 2000).

Feeding-site preference.—Distribution of feeding cowbirds at the landscape scale is determined not only by the presence of potential feeding sites but by the quality of those sites. Knowledge of cowbirds' feeding-site preferences is thus essential for understanding patterns of cowbird abundance. Cowbirds forage primarily with livestock, in agricultural fields, or in urban areas.

Livestock.—There is no doubt that cowbirds show a strong preference for foraging with livestock. The best quantitative data on foraging location are provided by the relatively unbiased sampling method of radiotelemetry. In a Midwestern landscape offering alternative feeding sites, such as row crops and ungrazed grassland, 57% of foraging observations were with cattle (Thompson 1994). In short-grass prairie in New Mexico, 98% of foraging observations of radiotagged cowbirds occurred with either pastured or corralled livestock (Goguen and Mathews 2001).

An understanding of the role of livestock in determining cowbird distribution and abundance is crucial to the success of management efforts to reduce parasitism in landscapes where cattle-grazing is a predominant land use, such as the western United States. For example, we do not know if presence of livestock increases cowbird populations at a landscape scale or merely redistributes cowbirds to the vicinity of grazing herds that act as foci for cowbird feeding activity. A more specific question is this: how do cowbirds respond to altered distribution of livestock?

Because cowbirds may not commute when food and breeding habitat are near each other (C. P. Ortega pers. comm.), removing the food source is the most prudent first management step. That strategy is used by federal agencies to protect the endangered southwestern Willow Flycatcher (*Empidonax traillii*) during the breeding season (Goguen and Mathews 1999). The idea behind the strategy is that removal of cowbirds' preferred foraging opportunities will force them to abandon their breeding areas. Unfortunately, it is difficult to evaluate the success of such measures, because they are generally carried out in conjunction with cowbird trapping programs (Finch and Stoleson 2000). Exclusion of cowbirds from host breeding areas requires removing their food sources so they are outside the maximum cowbird commuting distance of 15 km (Curson et al. 2000).

Two lines of evidence suggest that once the breeding season has begun, cowbirds' attachment to their breeding areas may be difficult to break by removing livestock. First, in New Mexico, cowbirds responded to livestock movements by adjusting the length of their commuting flights to reach livestock at locations farther from breeding areas, increasing mean commutes from 1.47 km to 3.14 km when cattle were moved in early July (Goguen and Mathews 2001); at another site, they responded by repeatedly altering commuting length through the breeding season, according to the location of free-ranging bison (Goguen et al. 2005). Second, when few bison were within 10 km of cowbird breeding areas, cowbirds responded by commuting similar distances but feeding without ungulates (Goguen et al. 2005).

Management strategies that force cowbirds to extend commuting flights may reduce parasitism levels by lowering the fecundity of individual cowbirds. Curson and Mathews (2003) found that female cowbirds commuting ~12 km between breeding and feeding areas laid 50% fewer eggs in a five-day period than females with breeding-feeding commutes of ~2 km. Cowbirds meet the energetic need for egg production with their daily dietary intake (Ankney and Scott 1980), so egg production and commuting compete for physiological energy resources.

Removing livestock to outside the radius within which cowbirds are likely to commute might sever the commuting link between breeding areas and feeding sites. Recent research suggests that the distance can be ≥ 10 km and perhaps >15 km (Curson et al. 2000), requiring removal of all livestock within 300–700 km². That may be unrealistic in many cases, but it might be possible to deter cowbirds from establishing breeding territories at target locations if livestock are moved 10–15 km during the start of the breeding season. However, we know nothing about the extent to which cowbirds use distributions of livestock as cues to assess feeding-site quality when they are establishing breeding territories. There is a need for studies that evaluate the influence of such factors on efficacy of livestock removal programs within a sound scientific framework, using control sites and monitoring before and after removals occur. Ideally, the behavioral response of female cowbirds should be measured using

radiotelemetry in addition to parasitism levels on target hosts.

Agriculture.—Cowbirds do not feed exclusively with livestock. They regularly feed in agricultural habitats, including row crops, plowed fields, ungrazed grassy fields, and livestock corrals, as well as in lawns, at bird feeders, and on campgrounds (Mayfield 1965, Rothstein et al. 1980, Verner and Ritter 1983, Thompson 1994). Few studies have compared cowbird feeding preferences among open habitat types (Gates and Evans 1998, Morris and Thompson 1998, Thompson and Dijak 2000). In Missouri, Morris and Thompson (1998) found grazing, invertebrate density, and grass height to be important predictors of cowbird foraging abundance. Cowbirds preferred grazed over ungrazed grassland, and short grass over long grass. Cowbird numbers were positively related to invertebrate density (Morris and Thompson 1998), probably because female cowbirds require a high-protein diet to support their high levels of egg production (Ankney and Scott 1980). Short grass may be preferred because it may enhance cowbirds' detection of food or detection of predators (Morris and Thompson 1998). Row crops appear to be of relatively low importance, yielding 2.4% of foraging observations in Maryland (Gates and Evans 1998) and 0–23% of observations in Missouri and Illinois (Thompson and Dijak 2000). Yet, in areas with few cattle, row crops may be relatively important feeding areas. Robinson (unpubl. data) has found that cowbirds make extensive use of late-planted, recently tilled soybean fields in Illinois, where beans are planted up to a month later than corn. Thus, long after the cornfields have grown to the point where they are rarely used by cowbirds, bean fields may continue to provide the bare-ground conditions favored by cowbirds. Therefore, subtle details of agricultural practices may strongly affect the distribution of cowbirds.

Urbanization.—Urban and suburban habitats and small areas of human development constitute important feeding habitat for cowbirds in many regions. Cowbird abundance is positively associated with new suburban development in rural regions of Vermont (Coker and Capen 2000), Wisconsin (Lindsay et al. 2002), and Maryland (Aldrich and Coffin 1979). Cowbirds are “suburban adaptable” (Blair 1996) and are known to exploit the resources of

urban environments—in Arizona (Germaine et al. 1998), Ohio (Blair 2001), and California (Blair 1996)—from which, presumably, they commute to parasitize host nests.

It is fairly well established that urban and suburban areas provide foraging opportunities for cowbirds, yet few studies have examined the effects of brood parasitism within that context. In Boulder, Colorado, cowbirds use the urban environment for feeding and roosting, and move to undeveloped forests to parasitize hosts (Chace 2001, Chace et al. 2003). Abundance of cowbirds and parasitism frequency on Plumbeous Vireos drop off dramatically with increasing distance from the urban–wildland boundary (Chace et al. 2003). Likewise, parasitism of Warbling Vireos (*V. gilvus*) is higher in lower-elevation riparian drainages close to the city of Boulder than among Warbling Vireo nests far (>10 km) from the urban boundary (J. Walsh pers. comm.). In Sierra Vista, Arizona, Bronzed (*M. aeneus*) and Brown-headed cowbirds feed and roost on golf courses and in cemeteries and urban backyards and move ≤6 km to forested foothills and riparian drainages, regions of high host abundance (Chace 2001).

FACTORS AFFECTING COWBIRD DISTRIBUTION AND ABUNDANCE AT THE LOCAL SCALE

Understanding the factors that influence distribution and abundance of cowbirds at the local scale is challenging, because of factors operating at larger spatial scales. Locally, cowbird distribution and abundance is influenced by spatial and temporal variation and interaction among (1) habitat type, (2) vegetation structure, and (3) host abundance and diversity. Various studies have found that cowbird breeding habitat is characterized by different, and sometimes contradictory, combinations of those factors (Table 1). One reason for the apparent variation is that those studies were conducted across disparate habitats scattered widely throughout the continent. Additionally, habitat type, vegetation structure, and avian diversity are all inter-related, so it is difficult to determine whether cowbirds are using hosts or vegetation as cues for potential breeding sites. Temporal variation further obscures patterns, because habitat type, vegetation structure, host community composition, and local cowbird population change within and between breeding seasons;

TABLE 1. Avian influences on Brown-headed Cowbird distribution. Each study examined a different subset of species richness (R) and abundance (A) at the three community levels. The studies were in a range of habitats across the continent, so inter-relationships among local, landscape, regional, and continental factors change across studies (see text). Results are indicated as follows: ++ = most significant positive predictor of cowbird distribution (used only if multiple avian community levels were analyzed); + = positive relationship; 0 = examined, nonsignificant; - = negative relationship; (blank) = not examined.

Study	Location	All avian species		Passerine species		Host species ^a		Individual species ^b
		R	A	R	A	R	A	
Chace 2004	Southeastern Arizona			+			0	
Donovan et al. 1997	Illinois, Indiana, Missouri						+/- ^c	
Donovan et al. 2000	Missouri						+ / 0 ^c	
Evans and Gates 1997	Western Maryland	0	+			0	0	
Farmer 1999a	Coastal southern California	+	+	+	++	++	0	++
C. Farmer and J. C. Uyehara unpubl. data	Southern California	+	+	++	+	+	+	
Goguen and Mathews 2000	Northeastern New Mexico						0	
Hahn and Hatfield 1995	Eastern New York					+	0	
Hahn and O'Connor 2002	United States					+		
Lowther and Johnston 1977	Eastern Kansas					0	+	
Purcell and Verner 1999	Southern Sierra Nevada			++	+	+	+	
Robinson et al. 2000	Illinois						0	
Tewksbury et al. 1999	Western Montana						+	
Thompson et al. 2000	Illinois, Indiana, Missouri, Wisconsin						+	
Verner and Ritter 1983	Southern Sierra Nevada							-
Ward and Smith 2000	British Columbia					0	0	
Young and Hutto 1999	Northern Rocky Mountains			+	+	++	+	

^a Different definitions of host species were used in each study.

^b Farmer 1999: Yellow Warbler; Verner and Ritter 1983: Warbling Vireo.

^c Influence of hosts changed, depending on fragmentation and forest-tract size.

therefore, the relative importance of those cues change over short intervals (Wolf 1987, Farmer 1999a).

Further complicating any attempt to understand local factors affecting cowbird distribution and abundance is that most studies focus on influences on host parasitism frequency, which provides limited data on cowbird distribution patterns. Numerous studies have examined the relationship between host characteristics (e.g. abundance, defense, and nest location) and parasitism frequency (Smith and Arcese 1994, Uyehara and Narins 1995, Burhans 1997, Ortega 1998, Staab and Morrison 1999, Robinson and Smith 2000). However, local community composition and vegetation can dramatically alter individual species' parasitism frequencies, without altering cowbird distribution or abundance (Clark and Robertson 1979, Freeman et al. 1990, Barber and Martin 1997, Burhans 1997, Dufty 2000, Strausberger 2001). It is difficult to generalize cowbird preferences using results from multiple study sites,

because of differences in vegetation, habitat structure, and relative abundances of hosts and cowbirds (see below; Wolf 1987, Briskie et al. 1990, Barber and Martin 1997, Ortega 1998, Spautz 1999, Robinson et al. 2000, Robinson and Smith 2000). Even when community parasitism levels are obtained, projecting from parasitism frequencies to local cowbird distribution and abundance is not always straightforward (Robinson et al. 2000, Robinson and Smith 2000, Thompson et al. 2000, Winslow et al. 2000). Those studies refute the earlier assumption that cowbird parasitism is directly related to cowbird density (e.g. McGeen 1972, Mayfield 1977, Brittingham and Temple 1983). Furthermore, recent work suggests that female cowbirds may have (1) a much lower fecundity than previously reported and (2) variable commuting behavior that alters egg-laying patterns (Hahn et al. 1999, Curson and Mathews 2003, Woolfenden et al. 2003). Therefore, the validity of correlating cowbird abundance with parasitism frequency is questionable.

The effect of parasitism is frequently the ultimate factor of concern (e.g. Trine et al. 1998, Rothstein and Cook 2000, Morrison and Hahn 2002), and reducing cowbird numbers to reduce the parasite pressure is often a management objective (Kostecke et al. 2005). Below, we concentrate on explicit studies of distribution and abundance of cowbirds at the local scale, focusing on the primary local factors of (1) habitat type, (2) vegetation structure, and (3) host abundance and diversity.

HABITAT INFLUENCES

Cowbirds breed in nearly every major habitat in North America (Rothstein 1994, Robinson et al. 1995a). Availability and proportion of habitat types and vegetation structure vary tremendously across the continent, so cowbirds' local habitat preferences have to be interpreted in the context of habitat availability. Habitat preference, rather than habitat use, is demonstrated by explicit comparison of cowbird abundances or parasitism rates among the alternative habitats available at the landscape scale (e.g. Braden et al. 1997, Davis and Sealy 2000, Hejl et al. 2002). Habitat heterogeneity varies regionally; in the East and Midwest, small fragments of relatively unaltered habitat embedded in a matrix of heavily human-modified habitat limits breeding-habitat types available to cowbirds at the local scale (George and Dobkin 2002). The majority of the West has a much higher natural heterogeneity, such that numerous habitat types are often contained within the range of one cowbird (George and Dobkin 2002), allowing for more local-scale comparative studies. Differences in natural heterogeneity could lead to differences in cowbird responses to edge-effect (*sensu* Gates and Gysel 1978); therefore, we re-examine the conventional wisdom concerning cowbird responses to habitat edges. Given that patterns of natural and unnatural habitat heterogeneity have broad regional differences, we will discuss habitat preferences in three regional sections: the eastern, central, and western United States (Hochachka et al. 1999).

Edge effects.—We will focus on “hard” edges, where a sharp boundary exists between two very different habitats—a pattern known to increase nest predation and brood parasitism in some areas, with effects typically <300 m from the habitat discontinuity (Paton 1994).

Results of parasitism studies within edge habitats are mixed. The preponderance of research suggests that cowbirds are an edge species, in that parasitism frequency decreases with increasing distance from edge habitats in forests (Gates and Gysel 1978, Chasko and Gates 1982, Brittingham and Temple 1983, Gates and Giffin 1991, Coker and Capen 1995, Evans and Gates 1997, Morse and Robinson 1999, Chace et al. 2000); however, some studies have found no effect of habitat edges on parasitism frequency (Robinson and Wilcove 1994, Hahn and Hatfield 1995, Thompson et al. 2000).

Habitat edges can elevate parasitism frequencies without significant increases in cowbird abundance (Donovan et al. 1997, 2000; Winslow et al. 2000). At the continental scale, fragmentation resulted in increased parasitism frequency east of the Rocky Mountains but had no effect in the West (Cavitt and Martin (2002). Cowbird habitat preference is a function of greater habitat heterogeneity and concurrent frequency of edge habitat (e.g. in riparian habitat of the Southwest; George and Dobkin 2002, C. Farmer and J. F. Chace pers. obs.). The cowbird's edge “preference” appears to be a function of larger-scale (>10 km) factors.

Eastern habitat preferences.—The eastern U.S. cowbird population has declined simultaneously with an increase in forest cover (Askins 1993, Robinson et al. 1995a, Peterjohn et al. 2000, Wiedenfeld 2000). Most research has focused on within-habitat studies of fragmentation and edge issues; among-habitat patterns have received less attention. In three eastern locations, three different, mutually exclusive results emerge. In Maryland (Gates and Giffin 1991, Evans and Gates 1997, Gates and Evans 1998), cowbirds were detected most often in stream bottomlands with home ranges that include brush and deciduous forest habitats. In southern New York, cowbirds preferred forest interior adjacent to old-field edges between the habitat types (Hahn and Hatfield 1995, 2000). Research in northern New England (Coker and Capen 2000, Yamasaki et al. 2000) suggests that cowbirds prefer breeding sites with higher proportions of residential or agricultural fields within 1,000 m.

Midwestern and Great Plains habitat preferences.—Cowbirds are most abundant in the tallgrass prairies of the Great Plains and Midwest, where they appear to saturate all potential breeding

sites, making identification of important local factors difficult (Robinson and Wilcove 1994, Robinson et al. 2000, Thompson et al. 2000). Parasitism frequencies in forested habitats were higher than in shrubland or grassland throughout Illinois (Strausberger and Ashley 1997; Robinson et al. 1999, 2000), though parasitism frequency can be high within some grassland communities (Elliott 1978, Robinson et al. 1995a, Davis and Sealy 2000, Herkert et al. 2003). Abundance of cowbirds and female cowbird morning activity were highest in forests and lowest in grasslands (Thompson 1994, Robinson et al. 1999). Cowbird abundance in Midwestern forest tracts was independent of tract size, but parasitism frequencies were lower in larger forest tracts (200–3,000 ha; Robinson et al. 2000). Perhaps at very large scales (>30,000 ha), interior forest habitats are too remote for cowbirds, thereby protecting hosts from parasitism (see below; Robinson et al. 1995b).

Western habitat preferences.—The West has much greater habitat heterogeneity than the East or Midwest, because of variable rainfall, aridity, influence of fire, and topographic diversity (George and Dobkin 2002). Willow–cottonwood riparian corridors are often bordered by oak woodland, manzanita, sagebrush, juniper, grasslands, or a combination of those vegetation types on the slopes or uplands. Natural fragmentation makes testing for local habitat factors easier than in other parts of the continent. Comparative studies among habitats suggest that cowbirds favor riparian vegetation in southern California (Farmer 1999b), Arizona (Chace 2004), and Idaho (Tewksbury et al. 1999), but use a wide range of habitat types (Lynn et al. 1998), including upland pine and fir forest (Ward and Smith 2000, Chace 2004). In the Sierra Nevada and Rocky Mountains, cowbirds use grasslands, coniferous forest, and riparian habitat (Verner and Ritter 1983, Rothstein et al. 1984, Hejl and Young 1999, Young and Hutto 1999). Comparison within western regions shows that cowbird abundance in some riparian habitat is lower than in fir forest, pinyon–juniper, shrubsteppe, or coastal sage-scrub habitats (Braden et al. 1997, Ellison 1999, Farmer 1999a, Goguen and Mathews 1999, Vander Haegen and Walker 1999).

Topography and elevation are additional, related factors that affect cowbird distribution in the West. Vegetation, avian community, and landscape context change in association with

topography and elevation, so it is difficult to discriminate among those factors. Cowbirds were detected significantly less often in the canyons of western Montana (Tewksbury et al. 1999) and narrow riparian canyons of coastal southern California (Farmer 1999a). Cowbird abundance is lower at high elevations in the northern Rocky Mountains (Hejl and Young 1999, Young and Hutto 1999) and Sierra Nevada (Rothstein et al. 1980, Verner and Ritter 1983, Lynn et al. 1998, Purcell and Verner 1999); however, Finch (1989) found that cowbird habitat use was independent of elevation in Wyoming.

Current knowledge suggests that cowbirds prefer breeding in riparian habitat of the arid Southwest, but that preference is not as strong in the Mountain West and Northwest. Cowbirds avoid deep, narrow, and arid canyons and have a weak preference to breed at lower elevations in the Intermountain West. Future studies should explicitly evaluate the influence of topography and elevation on cowbird habitat use, abundance, and parasitism frequency to resolve potentially confounding influences in cowbird habitat-selection models.

VEGETATION STRUCTURE

Vegetation structure can both influence a cowbird's ability to find a host nest and serve as an indicator of future host breeding. Research has focused on discriminating vegetation structure (1) used by cowbirds (e.g. Evans and Gates 1997, Farmer 1999a), (2) between parasitized and unparasitized nests (e.g. Brittingham and Temple 1996, Burhans 1997, Chace and Cruz 1999), and (3) among members of the avian community (e.g. James 1971, Staab and Morrison 1999). A problem is that each researcher tends to collect different microhabitat data, making it difficult to determine how cowbirds use vegetation structure as settlement cues. Therefore, we urge researchers in the future to use established protocols (e.g. BBIRD; see Acknowledgments) to facilitate comparative studies.

Two aspects of vegetation structure have been examined in multiple studies of cowbird use: perch availability and nest-concealment vegetation volume. Cowbirds use high perches in trees to detect host nests (Friedmann 1963, Payne 1973, Norman and Robertson 1975, Gates and Gysel 1978), and nests near elevated perches have higher parasitism frequencies

(Anderson and Storer 1976, Freeman et al. 1990, Uyebara 1996, Clotfelter 1998, Averill-Murray et al. 1999, Hauber and Russo 2000; but see Staab and Morrison 1999). It seems unlikely that trees and perches would be a limiting factor or an important cue underlying cowbird distribution, except perhaps in open Midwestern grasslands. Jensen (2003) experimentally tested that hypothesis by increasing perch sites in a Kansas tallgrass prairie and found no increase in cowbird abundance or parasitism frequency. Furthermore, cowbirds can use alternative methods of nest detection, such as walking, host flushing, and host defenses (Norman and Robertson 1975, Smith et al. 1984, Smith and Arcese 1994, Uyebara and Narins 1995, Clotfelter 1998, Hahn and Hatfield 2000).

Several studies that have used multivariate techniques to partition habitat use of an entire avian community suggest that cowbirds are habitat generalists whose distribution is influenced by plant species diversity, tree density, and vegetation volume or cover at various height classes (James 1971, Johnston 1977, Whitmore 1977, Rice et al. 1983, Finch 1989, Saab 1999). In western Maryland, cowbirds prefer breeding sites with high numbers of saplings (<7.5 cm diameter at breast height [DBH]), large snags (>22.5 cm DBH; Gates and Evans 1998), higher vegetation volume (0–3 m), and snag basal area (Evans and Gates 1997). In southern California, cowbirds were more frequent at sites with an open upper and lower canopy, few tree species, and high grass-forb cover (Farmer 1999a).

Many studies have examined how vegetative concealment of host nests affects parasitism frequency. Some studies have found no difference in vegetative concealment between parasitized and unparasitized nests (Anderson and Storer 1976, Best 1978, Best and Stauffer 1980, Smith 1981, Robinson et al. 1995a, Barber and Martin 1997). However, most of those studies were in the Midwest; some recent studies in the West have found that parasitized nests had less vegetative concealment (Averill-Murray et al. 1999, Spautz 1999, Staab and Morrison 1999, Ortega and Ortega 2001) and lower-density understory (Whitfield 1990, Uyebara and Whitfield 2000) than unparasitized nests. Habitat context further complicates the effect of nest concealment. Burhans (1997), for example, found that high levels of nest concealment among Indigo Buntings (*Passerina cyanea*) reduced parasitism in old

fields, but not in forests; whereas concealment had no effect on parasitism frequency in Field Sparrows (*Spizella pusilla*) in old fields. For some host species, risk of parasitism depends more on nesting location in the vegetation layers than on nest concealment (Briskie et al. 1990). Conflicting results from nest concealment studies suggest that cowbirds use the environment at scales larger than the microhabitat. Research into the effects of mesoscale habitat and host factors will be more productive in understanding cowbird distribution patterns (Dufty 1982, Rothstein et al. 1984, Teather and Robertson 1984, Gates and Evans 1998, Thompson and Dijak 2000). Conflicting conclusions from nest concealment studies may result from different methods (Ortega et al. 2002) but may also suggest that cowbirds use the environment at scales larger than the microhabitat or that they rely more on host behavior to find nests.

AVIAN INFLUENCES

Many studies suggest that distribution of cowbirds at the local level is determined by distribution of their hosts (McGeen 1972; Elliott 1980; Chasko and Gates 1982; Rothstein et al. 1984, 1986; Gates and Giffin 1991; Thompson 1994; Robinson et al. 1995a; Evans and Gates 1997). Cowbirds could use four levels of the avian community as cues for settlement: (1) all bird species, to (2) all passerine species, to (3) all host species, to (4) an individual host species; researchers generally analyze relative abundance or richness within each level (Table 1).

All avian and all passerine species.—Avian abundance (Evans and Gates 1997) and richness (Farmer 1999a) have been found to be significantly higher at sites where cowbirds were detected. Passerine species richness was a better predictor of cowbird occurrence than passerine or host abundance in the southern Sierra Nevada (Purcell and Verner 1999), southeastern Arizona (Chace 2004), and southern California (C. Farmer and J. C. Uyebara unpubl. data). Farmer (1999a) found that passerine abundance was the best predictor of cowbird distribution in coastal southern California. Young and Hutto (1999) determined that both passerine richness and abundance had a positive significant relationship with cowbirds in Montana, but host species richness was the strongest predictor of cowbird distribution.

Host species.—Cowbirds have parasitized 228 species, but only 132 successfully raise cowbirds (DeGeus and Best 1991, Ortega 1998). Continental and regional variation occurs in both abundance and parasitism frequency of some host species, with suitable hosts (e.g. Red-winged Blackbirds; *Agelaius phoeniceus*) not parasitized in some locations (e.g. Hoover and Brittingham 1993, Winslow et al. 2000). Cowbirds sometimes even lay eggs in nests of rejecter hosts (Rothstein 1976, Friedmann et al. 1977, Scott 1977, Strausberger and Ashley 1997, Haas and Haas 1998). Although parasitism of rejecters will not contribute to cowbird population growth, cowbirds could perceive such species as part of the overall avian community when determining where to breed. Although numerous grassland and shrubland hosts possess defenses against parasitism (Hosoi and Rothstein 2000, Peer et al. 2000), cowbird abundance does not seem to respond to changes in proportions of rejecter or mobbing species (Robinson et al. 1999).

Most studies of avian influences on cowbird distribution patterns use either host richness or abundance (Table 1), but each researcher tends to use a different measure: for example, all small to medium, open-cup-nesting passerines (Young and Hutto 1999); all species known to be parasitized (Purcell and Verner 1999); medium passerines that do not reject or abandon nests (Robinson et al. 1999); species that successfully fledge cowbirds (Ward and Smith 2000, Chace 2004); species with >10% of nests parasitized at the study site (Donovan et al. 2000, Thompson et al. 2000); or species with >15% of nests parasitized at the study site (Tewksbury et al. 1999); in some cases, hosts are not explicitly defined (Evans and Gates 1997). Although those subtle distinctions likely change the status of only a few species in any area, it could explain some of the disparities in the following results.

Host species richness and abundance are the most frequent measurements examined, but the relationship is not as obvious or consistent as previously assumed (Table 1; McGeen 1972; Rothstein et al. 1984, 1986; Thompson 1994; Robinson et al. 1995a). For example, Lowther and Johnston (1977) found that cowbirds were most abundant in shrub habitat, where host abundance was highest, even though host richness was highest in forest habitat; whereas Hahn and Hatfield (1995) found that cowbirds were most abundant in forest, where host richness

was high but abundance was low. Those studies highlight the strong habitat–host confound and demonstrate that only very carefully designed studies can separate the relative importance of those two local factors.

Individual host species.—Warbling Vireo and cowbird abundances showed a negative correlation in the Sierra Nevada, but it is unclear whether (1) cowbirds avoid sites with Warbling Vireos, (2) cowbirds cause declines in local Warbling Vireo populations, or (3) both Warbling Vireo and cowbird numbers are correlated to some other confounding variable (Rothstein et al. 1980, Verner and Ritter 1983). Farmer (1999a) examined the relationship between cowbird distribution and the abundance of the four commonly used host species in coastal southern California: Yellow Warbler (*Dendroica petechia*), Wilson's Warbler (*Wilsonia pusilla*), Common Yellowthroat (*Geothlypis trichas*), and Song Sparrow (*Melospiza melodia*). Cowbirds were positively associated with Yellow Warbler abundance in two different data sets, but not in the second year of the study, while there was a positive association with passerine abundance in both years.

Some studies focus on how changes in the local host community affects parasitism frequency. Barber and Martin (1997) discovered that Black-capped Vireo (*V. atricapilla*) parasitism frequency was most strongly correlated with Northern Cardinal (*Cardinalis cardinalis*) abundance. However, unparasitized nests of Northern Cardinals and Yellow-breasted Chats (*Icteria virens*) were within ~2 m, which suggests that actual local cowbird distribution did not change in response to Northern Cardinal density. Many species are aggressive toward cowbirds near their nests (e.g. Robertson and Norman 1976, Neudorf and Sealy 1992, Burhans 2000), but only Red-winged Blackbirds are reported to reduce parasitism by mobbing (Clark and Robertson 1979, Freeman et al. 1990, Strausberger 2001). However, cowbirds are not less abundant in habitats with high proportions of aggressive, mobbing species (Robinson et al. 1999). Those studies provide invaluable information on cowbird–host dynamics, but without a more explicit study design, parasitism studies cannot furnish data on whether cowbird distribution is influenced by local avian factors.

Vegetation strata.—Numerous studies have examined parasitism across host-nest strata

(i.e. ground, shrub, or canopy; Robinson 1992, Martin 1993, Hahn and Hatfield 1995, Robinson et al. 1995a, Farmer 1999a, Hahn and Hatfield 2000, Robinson et al. 2000). In Illinois (Robinson 1992; Robinson et al. 1995a, b, 2000) and southern coastal California (Farmer 1999a), parasitism did not differ among strata. However, cowbirds demonstrate a strong, consistent preference for ground-nesting birds in New York (Hahn and Hatfield 1995, 2000), low-nesting species (<3 m) in Arizona (Staab and Morrison 1999), and low-nesting Yellow Warblers rather than canopy-nesting Least Flycatchers (*E. minimus*) in Manitoba (Briskie et al. 1990). Those studies suggest that cowbirds may prefer to breed in areas with a high abundance of low-nesting species, though they certainly do not avoid canopy-nesting birds (Robinson et al. 1995a, 2000). We know of no study that analyzes the pattern of cowbird distribution on the basis of host, passerine, or total species nesting strata, an aspect that warrants further attention.

Overview of avian influences.—The relationship between cowbirds and host abundance or richness is neither as obvious nor as straightforward as is commonly assumed. A simplistic analysis of Table 1 shows that 58% of studies found a positive relationship between cowbirds and measures of host richness and abundance (richness: 6 of 9 studies; abundance: 8 of 15), and 83% of studies found a positive relationship between cowbirds and overall avian species measures (richness: 2 of 3; abundance: 3 of 3). In all studies, there was a positive relationship between cowbirds and passerine measures (richness: 5 of 5; abundance: 4 of 4). Those results strongly suggest that cowbird distribution is not finely tuned to the composition of the host community; rather, cowbirds may use passerines as indicators of breeding sites. Future studies clearly need to incorporate different community levels and both abundance and richness measures to test that hypothesis.

Donovan et al. (1997) established that local-scale effects depend on landscape context, and Farmer (1999a) showed that host cues used by cowbirds vary temporally. Although elaborate multiscale studies may not be logistically feasible, enough descriptive detail and actual numerical results (i.e. cowbird abundance measures) need to be provided for other researchers to qualitatively evaluate the results considering all the factors discussed above.

Density-dependent habitat selection.—Spatial patterns of cowbird parasitism exist within and among host communities but may vary regionally. Although cowbird habitat-use patterns depend on locally available habitats, those patterns may also be affected by geographic—and perhaps temporal—variation in cowbird density (Robinson et al. 1999, Jensen and Cully 2005a). As cowbird density increases, we can expect cowbirds to spatially broaden their host use within or among host communities (Robinson 1999). Density-dependent habitat selection in cowbirds is evident from Midwestern forests (Donovan et al. 1997, 2000; Thompson et al. 2000), where cowbirds expand their distribution from forest edges to forest interior as cowbird density increases with the degree of forest fragmentation by agriculture. Similarly, in prairie landscapes, as cowbird density and parasitism increase, cowbirds move farther from the prairie-woodland edges and parasitize more hosts in the prairie interior (Jensen and Cully 2005a).

The competitive mechanism driving density-dependent habitat selection in cowbirds is not clearly known, but cowbirds may distribute themselves in an ideal free manner (Fretwell and Lucas 1970, Fretwell 1972) in response to variation in their own conspecific density and resulting effects on their fitness (Winslow 1999, Jensen and Cully 2005a). Several lines of evidence suggest that cowbirds exhibit a free settlement pattern, in which cowbird laying ranges overlap rather than displace one another (despotic distribution) as cowbird density increases: (1) multiple parasitism of single host nests by different female cowbirds (Fleischer 1985, Hahn et al. 1999, McLaren et al. 2003, Strausberger and Ashley 2003) where local cowbird densities are high (Robinson et al. 2000), (2) cowbird territory dissolution (Elliott 1980), (3) cowbird eggs apparently laid randomly with respect to previous parasitism (Johnsgard 1997), and (4) cowbird abundance within host habitats negatively and linearly correlated with distance from cowbird foraging areas (Goguen and Mathews 2000). As the incidence of multiple parasitism within primary host habitats (e.g. habitat edges) increases with increasing cowbird density, cowbird egg and nestling survival decrease (McGeen 1972, Hatch 1983, Trine 2000, Jensen and Cully 2005a). Density-dependent responses by cowbirds in selecting

host habitats may be reinforced by negative effects of multiple parasitism on cowbird fitness (i.e. incentive to exploit secondary-host habitats). It follows that variation in cowbird: host ratios among habitats should not be used to reject ideal free distribution in cowbirds if cowbird fitness is density-dependent or if habitat suitability varies (e.g. variation in host life histories [Martin 1995], availability of perches or cowbird feeding habitat, etc.).

MANAGEMENT APPLICATIONS

In conclusion, we offer a synthesis showing how knowledge of factors affecting distribution and abundance of cowbirds at different spatial scales might be used in reducing parasitism levels on hosts of conservation concern (Fig. 2). However, before management is initiated—or continued—at any scale, two initial considerations must be addressed. First, will reduction or elimination of cowbird parasitism significantly affect population growth rates of the species of interest? Before time and financial resources are devoted to cowbird management, possibly at the expense of alternative management strategies, it should be demonstrated that such management can have a measurable effect on projected population growth (Rothstein and Cook 2000). Also, there needs to be some structure or mechanism for measuring success, so that management actions are scientifically evaluated. Second, management may be more effective for reducing parasitism at some spatial scales than at others; thus, managers need to concentrate management activities at a variety of spatial scales to achieve their goals.

MANAGEMENT CONSIDERATIONS AT THE CONTINENTAL SCALE

Establishment of preserves for hosts in regions where parasitism levels are low could protect possible host source populations, especially if populations that are determined to be parasitism-driven sinks occur in less manageable regions or landscapes. For example, although grassland songbird populations of concern (Vickery et al. 1999) in much of the Midwest are limited to small patches of highly fragmented grassland, cowbird parasitism of those populations is rare (Strausberger and Ashley 1997; Kershner and Bollinger 1998; Robinson et al. 1999, 2000; Peer

et al. 2000). Toward the center of the cowbird's distribution in the Great Plains, the same species are heavily parasitized (Elliott 1978, Hatch 1983, Zimmerman 1983, Koford et al. 2000, Jensen 2003). If regional variation in cowbird parasitism has significant effects on population persistence of grassland bird species, the more fragmented eastern populations may be globally valuable if grassland fragments are large enough to minimize nest depredation (Herkert et al. 2003). Managers must also realize that geographic patterns of cowbird parasitism of a species may be highly variable within states or provinces, independent of variation in habitat structure at local or landscape scales (Jensen and Cully 2005b).

There has been speculation that cowbird control at large winter congregations could reduce parasitism pressure at the continental scale (Griffith and Griffith 2000, Ortego 2000). There is no clear evidence that cowbirds are limiting any host population, and no need for cowbird control at this scale has been demonstrated (Rothstein and Cook 2000, Ortega et al. 2005). Cowbirds congregating in dense winter flocks disperse widely to breeding habitats (Dolbeer et al. 1982); therefore, large winter kills of cowbirds may not have the intended effect of reducing pressure on the few hosts cowbirds actually limit.

MANAGEMENT AT THE REGIONAL AND LANDSCAPE SCALES

Management of cowbird abundance and parasitism becomes somewhat feasible at regional and landscape scales, at which cowbird occupation of host habitats is ultimately limited by availability of cowbird foraging habitat. At the largest scales studied in fragmented Midwestern forests (<10-km radii around forest fragments), cowbird abundance and parasitism declined with increasing forest cover (Donovan et al. 1995, 2000; Robinson et al. 1995b; Thompson et al. 2000). Because cowbirds can commute great distances (≤ 15 km) from their foraging habitats in pasture and agricultural areas to a diversity of host habitats, management to completely omit parasitism from host communities would require landscapes within 15 km to be free of cowbird foraging areas. However, most cowbirds commute shorter distances from foraging areas into host habitat, and relatively few cowbirds penetrate

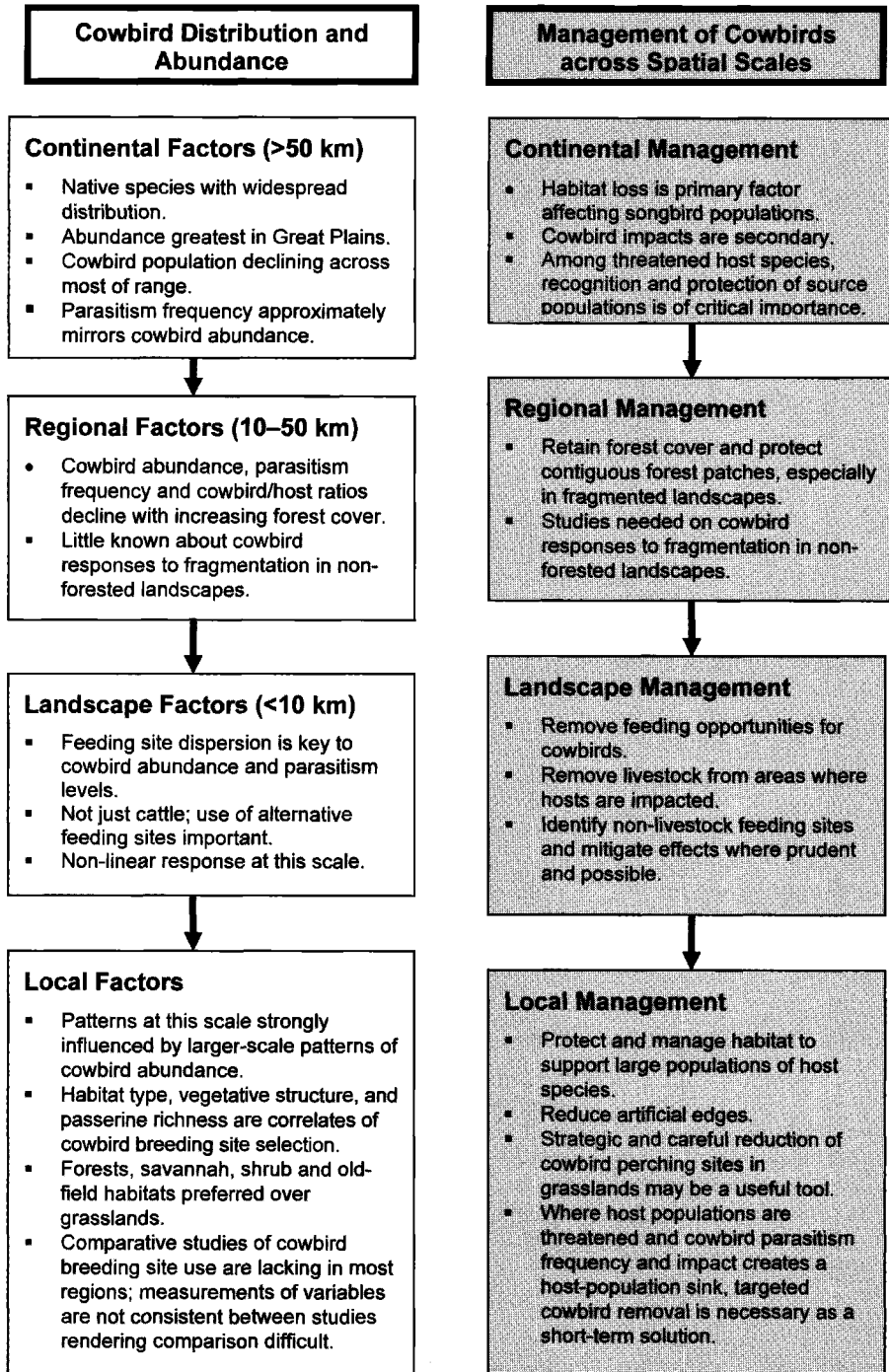


FIG. 2. Adaptive management to match cowbird ecology across spatial scales. Management should be scale-appropriate and cognizant of implications at broader and finer scales.

deep into host habitat (Goguen and Mathews 2000). Also, cowbirds that travel considerable distances into host habitats from feeding areas produce fewer eggs than cowbirds commuting relatively short distances and may not pose a serious threat to habitat interior birds (Curson and Mathews 2003). Therefore, cattle removals or reforestation at landscape scales have the potential to reduce parasitism, but they would be most effective at large spatial scales. Cowbird foraging areas should be displaced as far as possible from critical host habitats.

Reducing the number or spatial extent (or both) of cowbird foraging sites becomes especially problematic when suburban backyards, school playing fields, and golf courses are the foraging locations (Farmer 1999a, Chace et al. 2003). Urban planning may assist in reducing future cowbird foraging opportunities at the suburban edge. Maintaining large open spaces and promoting clustered homes on smaller lot sizes in new developments would reduce cowbird foraging area, creating buffers between residential areas and nature reserves that increase the distance cowbirds need to travel (J. J. Walsh and J. F. Chace unpubl. data). Educational efforts can encourage voluntary compliance—through curtailing of bird feeding during the breeding season and increasing of native vegetation at the expense of short, shaded, and well-watered lawns—with the goal of reducing cowbird feeding opportunities (Chace et al. 2003).

The regional and landscape scales of management require the longest-term investment and greatest incentives to private landholders. Removal of cattle grazing at large scales could entail considerable expense. Purchasing land at such scales is also expensive, and land acquired by donation—though economical—is not likely targeted specifically for cowbird-free, high-quality habitats for threatened cowbird hosts. Reforestation of agricultural areas on a regional scale relies on economic changes outside the scope of cowbird management.

MANAGEMENT AT THE LOCAL SCALE

Options for reducing cowbird parasitism at local scales are limited to (1) manipulations of habitat structure and (2) reducing local cowbird abundance as compared with host abundance, though those options are not mutually exclusive. Diversity of hosts, host communities, and

vegetative habitats throughout the range of the cowbird limit our ability to generalize about habitat manipulations that might reduce parasitism across regions. Reductions in the amount of “edge” habitat in forests and prairies might reduce local parasitism levels, but that may not be effective where cowbird density is particularly high (e.g. in much of the Great Plains). Cowbird preference for certain vegetative and associated host communities vary regionally.

Manipulation of the vegetation structure of important host habitats might reduce parasitism levels by physically reducing host-nest detectability. It is possible that habitat enhancement of cowbird-preferred avian communities that have large proportions of rejecter species (e.g. eastern shrublands) might create local cowbird population sinks (Grzybowski and Pease 1999, Robinson et al. 1999), but those models need to be tested. Managed vegetation structure may allow hosts to build nests at heights that allow for reduced parasitism. Elevated perches (e.g. trees, shrubs, or snags) can facilitate cowbird parasitism in open habitats, and could thus be reduced or eliminated from targeted areas. However, alteration of vegetative habitats may adversely affect habitat quality for other species (Staab and Morrison 1999). Habitat manipulations that increase the amount of host habitat, and thus host abundance, may indirectly reduce parasitism by decreasing local cowbird: host ratios, if cowbird populations remain stable or are reduced (Rothstein et al. 2003). In the latter case, reductions in local cowbird population size may occur if host habitat enhancement also reduces cowbird feeding areas. That would be preferred, because increases in local host abundance or diversity might promote a functional or numerical response in cowbird parasitism and density (Table 1) if foraging habitat remains accessible to cowbirds.

Cowbird trapping programs are frequently employed to reduce cowbird abundance and parasitism of hosts (Hayden et al. 2000). However, cowbird trapping presents only a temporary solution—if it affects host population persistence at all—and may divert financial resources from more efficacious management strategies (Rothstein and Cook 2000, Wiedenfeld 2000, Rothstein et al. 2003). Continuous trapping effort would be required to counter cowbird dispersion from

outside designated cowbird trapping areas. Conversely, if host populations are restored through cowbird trapping efforts, further trapping might not be needed if cowbird:host ratios are lowered to the point where parasitism no longer has an effect on host population growth (Rothstein et al. 2003). Therefore, host habitat restoration is preferred over cowbird trapping, but trapping programs may be a necessary first step in recovery of very small, highly parasitized populations (Rothstein and Cook 2000).

Management to thwart cowbird parasitism of hosts at a fine-grain, local scale is less straightforward than recommendations at larger landscape scales. Management recommendations are further complicated by inconclusive results from research conducted at local scales. That does not mean that local vegetative habitats cannot be managed for improved nesting success by reducing nest depredation. However, cowbird distribution and parasitism at local scales seem more dependent on geographic and landscape patterns in cowbird abundance.

INTERACTIONS AMONG SCALES

Patterns of cowbird abundance at larger spatial scales (continental, regional, landscapes) may affect spatial patterns of parasitism at finer scales. Those complicated interactions must be appreciated when considering cowbird management options. Cowbird host-use patterns among habitats—and host species (Woolfenden et al. 2003)—may change with variation in cowbird density. Thus, management activities to reduce cowbird abundance at landscape scales may only reduce parasitism at local scales in secondary cowbird habitats, or on secondary hosts, because the residual cowbird population still uses primary cowbird habitats and hosts (Robinson et al. 1999, Jensen and Cully 2005a). A similar concentration of parasitism on primary hosts could result from management to reduce cowbird abundance at local scales (e.g. trapping). Similarly, if cowbird density increases (naturally or anthropogenically), cowbirds may use secondary hosts in habitats they otherwise appear to avoid (e.g. grassland or forest interior). Those patterns of density-dependent habitat selection at the local scale are also expected across regional and continental gradients in cowbird abundance.

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For information on BBIRD and access to the database, see pica.wru.umt.edu/BBIRD/.

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CHAPTER 6

BEHAVIORAL ECOLOGY OF THE BROWN-HEADED COWBIRD (*MOLOTHRUS ATER*) IN A BISON-GRAZED LANDSCAPE IN NEW MEXICO

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ABSTRACT.—Brown-headed cowbirds (*Molothrus ater*; hereafter “cowbirds”) often forage with grazing ungulates. Although domestic livestock have largely replaced American bison (*Bos bison*) as the cowbird’s foraging associate, recent restoration of bison to their former territories has increased opportunities for cowbirds to interact with this native grazer. During summer 2002, we studied the behavior of cowbirds and bison in a 27,000-ha shortgrass prairie pasture in northeastern New Mexico. We monitored afternoon distribution of bison and native ungulates within the pasture. We used radiotelemetry to monitor daily movements and behavior of female cowbirds breeding in adjacent pinyon and juniper woodlands; we located and monitored host nests to measure parasitism rates. Our objectives were to (1) measure the spatial and temporal distribution of bison, (2) examine effects of daily changes in bison distribution on breeding and foraging strategies of female cowbirds, and (3) compare the behavior of cowbirds in a bison-grazed landscape with that in a cattle-grazed one. The number of bison within 10 km of the radiotagged cowbirds’ breeding grounds varied daily, ranging from 6 to 1,161 individuals. Radiotagged female cowbirds ($n = 10$) were typically involved in breeding activities in pinyon–juniper woodlands in the mornings and commuted an average of 7.24 km to prairie sites to feed during afternoons. Radiotagged cowbirds fed primarily with bison (77.0% of feeding relocations), but they also fed with elk (*Cervus elaphus*; 9.9%), without ungulates at a dry lakebed (10.6%), and in a bison-handling corral (1.9%). When few bison were within 10 km of the cowbird breeding ranges, cowbirds foraged with elk or without ungulates. Mean commuting distance was related to distance of the nearest bison from the breeding grounds. Females in the bison-grazed landscape commuted farther and had larger feeding areas and overall home ranges than those in the cattle-grazed landscape. Differences in commuting behavior resulted from bison mobility and differences in management strategies. Increased commuting distances caused by bison mobility may result in reduced egg-laying rates for cowbirds, potentially benefiting breeding songbirds.

RESUMEN.—*Molothrus ater* suele alimentarse junto a ungulados herbívoros. Aunque el ganado doméstico ha reemplazado al bisonte americano (*Bos bison*) como especie asociada durante la alimentación de *M. ater*, la restauración reciente de los bisontes a sus territorios habituales ha incrementado las oportunidades que tiene *M. ater* de interactuar con este herbívoro nativo. Durante el verano de 2002 estudiamos el comportamiento de los *M. ater* y bisontes en una pradera de pastos cortos de 27,000 ha en el nordeste de Nuevo México. Monitoreamos la distribución de bisontes y ungulados nativos durante la tarde dentro de la pastura. Utilizamos radiotelemedría para monitorear los movimientos y el comportamiento diario de las hembras de *M. ater* reproduciéndose en zonas adyacentes a bosques de piñones y enebros, y localizamos y monitoreamos nidos de los hospederos para medir las tasas de parasitismo. Nuestros objetivos fueron: (1) medir la distribución espacial y temporal de los bisontes, (2) examinar el efecto del cambio diario en la distribución del bisonte en la reproducción y estrategias de alimentación de las hembras de *M. ater*, y (3) comparar el comportamiento de los *M. ater* en un ambiente que es mantenido por el pastoreo de bisontes contra otro mantenido por el pastoreo de ganado

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doméstico. El número de bisontes dentro de los 10 km de las áreas reproductivas de *M. ater* con radiotransmisores variaron diariamente, en un rango de 6 hasta 6,161 individuos. Las hembras de *M. ater* con radiotransmisores ($n = 10$) típicamente se involucraron en actividades reproductivas en los bosques de piñón-enebro durante la mañana, mudándose en promedio a 7.24 km de distancia a alimentarse a zonas de praderas durante la tarde. Los *M. ater* con radiotransmisores se alimentaron principalmente con los bisontes (77% de las relocalizaciones de alimentación), pero se alimentaron también con alces (*Cervus elaphus*; 9.9%), sin ungulados en un fondo seco de lago (10.6%), y en un corral para la manipulación de bisontes (1.9%). Cuando había pocos bisontes dentro de los 10 km de las áreas reproductivas de los *M. ater*, éstos se alimentaron con alces o sin ungulados. La distancia media de movimiento de los *M. ater* estuvo relacionada con la distancia al bisonte más cercano de su área de reproducción. Las hembras de *M. ater* de ambientes mantenidos por el pastoreo de bisontes se mudaron más lejos y poseían áreas de alimentación y áreas de acción totales mayores que aquellas pertenecientes a ambientes mantenidos por el pastoreo de ganado. Las diferencias en los movimientos fueron causadas por la movilidad de los bisontes y diferencias en estrategias de manejo. El aumento en la movilidad de las hembras de *M. ater* causado por la movilidad de los bisontes podrían implicar una disminución en su tasa de puesta de huevos, potencialmente beneficiando a las aves canoras.

As ITS NAME implies, the brood-parasitic Brown-headed Cowbird (*Molothrus ater*; hereafter "cowbird") often associates with cattle (*Bos taurus*) and other domestic livestock (Mayfield 1965, Goguen and Mathews 2001). Cowbirds forage beside those grazing ungulates or perch upon them, presumably because of increased feeding efficiency (Goguen and Mathews 1999). Prior to introduction of domestic cattle to North America, cowbirds associated with native grazers, particularly bison (*Bos bison*; Freidmann 1929). Although bison were nearly eliminated from the wild during the late 19th century (Roe 1970), recent bison restoration and ranching throughout the United States has substantially increased the distribution and abundance of bison (MacDonald 2001), resulting in increased opportunities for cowbirds to associate with them.

Although cattle and bison are similar, managers have often justified bison restoration efforts on the basis of perceived ecological benefits (Truett et al. 2001). The bison is considered a keystone species, because of its critical role in maintaining grassland biodiversity (Knapp et al. 1999). For example, although both cattle and bison feed primarily on graminoids, bison incorporate fewer forbs and shrubs in their diets (<10% for bison vs. 10–25% for cattle; Peden et al. 1974, Van Vuren and Bray 1983, Hartnett et al. 1997), which enhances forb abundance and increases plant species diversity (Fahnestock and Knapp 1994, Steuter and Hidinger 1999). Compared with cattle, bison have a more efficient digestive system; therefore, they spend less time grazing (Plumb and Dodd 1993).

They also spend less time than cattle in riparian zones or at other water sources; instead, they move longer distances to sites where forage is more abundant (Hartnett et al. 1997, Steuter and Hidinger 1999, Van Vuren 2001). Bison are nomadic at both large and small spatial scales, wandering broadly and irregularly in large herds, apparently seeking high-quality grazing sites, such as recently burned areas (Coppedge and Shaw 1998), or moving in response to an exhausted grass supply (England and DeVos 1969, Roe 1970). Domestic cattle, in contrast, are sedentary (Van Vuren 1983) and are usually managed intensively to promote uniform forage, resulting in highly controlled spatial distribution (Truett et al. 2001).

For cowbirds, behavioral differences between bison and cattle may influence the costs and benefits of foraging associations. For example, cowbirds tend to associate with actively foraging ungulates, probably because moving individuals flush more insects than sedentary ones (Goguen and Mathews 2001). The reduced feeding time of bison may result in lower availability of bison engaged in activities that benefit foraging cowbirds. Additionally, the frequent and irregular movements of bison and their tendency not to congregate at predictable locations, such as water sources, may increase the search time and commuting distances of cowbirds that associate with them. For example, in a cattle-grazed landscape in northeastern New Mexico, female cowbirds maintained morning breeding ranges in forested habitats with high host densities and commuted only 1–2 km in the

early afternoon to prairie pastures where they could easily locate cattle (Goguen and Mathews 2001). Although it is unknown how cowbirds locate their afternoon feeding sites, the frequent and erratic movements of bison in comparison with cattle may make the search more difficult and energetically costly for cowbirds in large, bison-grazed landscapes.

We studied the behavior of cowbirds and bison in a 27,000-ha pasture in northeastern New Mexico. During our study, all bison had unrestricted access to the entire pasture. We evaluated three main questions: (1) How does the spatial distribution of bison vary across time within a large pasture? (2) How do daily changes in the spatial distribution of bison influence the breeding or foraging strategy of cowbirds? (3) How does the behavior of cowbirds in this bison-grazed landscape differ from that of cowbirds breeding in an adjacent cattle-grazed landscape? Interest in bison restoration on western

rangelands is growing; so is interest in the effects of cowbird parasitism on songbirds. Knowledge of cowbird behavior within bison-grazed landscapes is essential for fully evaluating the potential benefits and costs of bison restoration to songbird communities, and the results may be useful for developing management plans for bison reserves. In addition, the present study may provide some insight into the benefits and challenges historically experienced by cowbirds when bison freely roamed the West.

METHODS

Study area.—We conducted our study from May through July 2002, on a portion of the 159,000-ha Vermejo Park Ranch (VPR) in northeastern New Mexico. The VPR is a privately owned property that extends across the Sangre de Cristo Mountains of western Colfax and eastern Taos Counties, New Mexico, with a small portion extending into Costilla County, Colorado (Fig. 1). Current management efforts on the

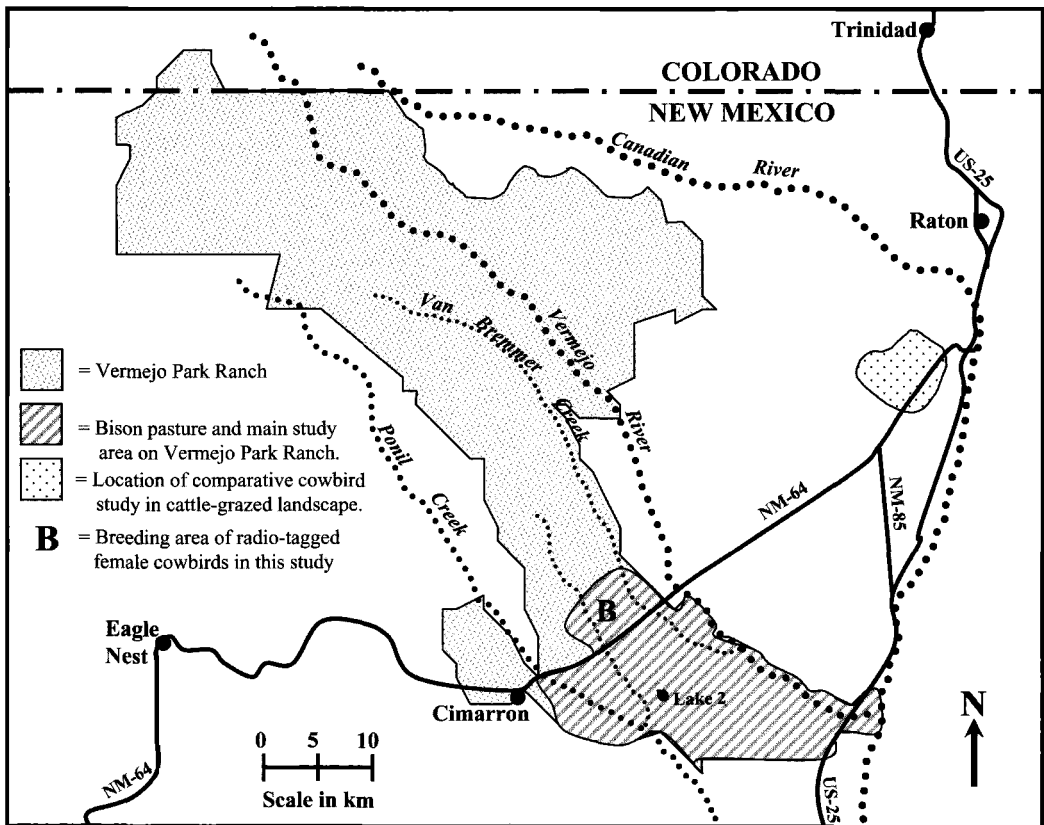


FIG. 1. Map of the study region in northeastern New Mexico, USA.

ranch have focused on ecosystem restoration, with the goal of restoring as much natural biodiversity as possible. Domestic livestock have been absent from the ranch since 1996, and efforts to restore habitats and reintroduce extirpated native vertebrates are ongoing.

Although most of the VPR consists of mixed conifer forests or mountain meadows typical of elevations >2,200 m in the region, our research was conducted primarily within a 27,000-ha pasture located at elevations of 1,800–2,100 m on the southeastern portion of the ranch, within Colfax County, New Mexico (Fig. 1). The pasture is at the interface between the Great Plains and the forested foothills of the Sangre de Cristo Mountains, ~15 km northeast of Cimarron, New Mexico. It consists primarily of shortgrass prairie dominated by blue grama (*Bouteloua gracilis*) but also supports a narrow woodland of pinyon pines (*Pinus edulis*) and one-seed junipers (*Juniperus monosperma*) along the lower mountain slopes at its westernmost edge. The western half of the pasture, where most of our work was conducted, is traversed by three small river systems, each of which supports narrow riparian habitat dominated by willows (*Salix* spp.), cottonwoods (*Populus* spp.), or both. A large reservoir in the pasture (Lake 2) was mostly dry during 2002 because of a severe drought.

Bison were reintroduced to the site starting in 1996; by 2002, ~2,300 adult bison, plus calves, were present. Bison were confined to the pasture by electric fencing, but they had access to the entire pasture throughout the study period. Elk (*Cervus elaphus*) and pronghorn (*Antilocapra americana*) were also abundant within the prairie and riparian habitats, and mule deer (*Odocoileus hemionus*) were present primarily along the pinyon–juniper edge.

Bison distribution surveys.—During most afternoons from 5 June to 6 July, we drove a route through the western half of the pasture and recorded locations of all adult bison within 10 km of the pinyon–juniper breeding habitats used by radiotagged female cowbirds (see below). The route followed dirt roads throughout the pasture, so it is unlikely that any bison were missed. When bison were detected, we recorded number of adults and habitat. We determined their location with a global positioning system (GPS) unit. We also recorded the same data for other ungulate herds (primarily elk); for all herds that were close enough, we looked for feeding cowbirds.

Cowbird movements and behavior.—From late May through early June, we captured female cowbirds during mornings in pinyon–juniper habitats along the western edge of the pasture (Fig. 1), using portable box traps baited with birdseed and live cowbirds as decoys (Robinson et al. 1993). Upon capture, we marked all cowbirds with metal federal bands. We fitted females with a 1.3-g radiotransmitter with a 30-day battery life (Advanced Telemetry Systems, Isanti, Minnesota). We attached the transmitter to the

female's lower back using a figure-eight leg harness of elastic cord (Rappole and Tipton 1991). After their release, females were allowed a 2- to 3-day period to acclimate to the transmitter prior to data collection.

We tracked radiotagged cowbirds almost daily in the morning and afternoon from late May through early July. We relocated each radiotagged female at least once in the morning by walking toward their signals until visual contact was made. At each relocation, we recorded universal transverse mercator (UTM) coordinates, time, habitat, behavior, and number and sex of associated cowbirds. When females were located more than once during the morning, successive relocations were ≥ 2 h apart. We typically relocated females only once during each afternoon. During afternoon searches, we scanned for females on both the breeding grounds and throughout the western half of the pasture (within 10 km of the breeding grounds) while we surveyed the distribution of bison. We recorded location, time, habitat, behavior, associated cowbirds, and associated ungulates.

We used afternoon feeding locations of radiotagged birds to describe patterns of feeding-site selection. Feeding locations were summarized on the basis of associated ungulate type, or, in cases where cowbirds fed without ungulates, the specific habitat type that was used. To estimate daily commuting distance between breeding range and feeding grounds, we calculated the straight-line distance between the midpoint of a female's breeding range and afternoon feeding location for each afternoon she was detected. For each individual female, we calculated an average of all daily commuting distances. We used a simple linear-regression analysis to evaluate the importance of the following variables in predicting mean daily commuting distances of radiotagged cowbirds: number of bison within 10 km of the center of the cowbird breeding grounds, distance of the nearest bison from the center of the cowbird breeding grounds, and distance of the nearest group of ≥ 5 bison from the center of the cowbird breeding grounds.

We calculated breeding, feeding, and overall home-range sizes using the minimum convex polygon (MCP) estimation technique (Mohr 1947) as calculated in SEAS (J. R. Cary, University of Wisconsin, unpublished program). We calculated a 95% MCP estimate of the overall home range (breeding plus feeding locations) for all females with ≥ 29 locations. We calculated separate 95% MCP estimates for breeding and feeding ranges (or both) for females with ≥ 14 locations in a given range type.

Cowbird parasitism rates.—To determine cowbird host selection and parasitism rates, we located and monitored nests within pinyon–juniper habitat along the western edge of the pasture, where radiotagged female cowbirds had their breeding ranges. From early May through early July, we searched for nests of all possible cowbird host species within four

35-ha study plots. All plots were within 5 km of each other, and two plots were within the breeding areas of several radiotagged female cowbirds. We used adult behavior and, in some cases (e.g. Spotted Towhees), systematic searching to locate nests. After discovery, nest contents were checked using an extendable mirror pole. Nests were subsequently revisited every 2–3 days to determine parasitism status and to monitor nest fate. For all host species, we calculated percentage of total nests parasitized. Because we could not confirm parasitism status of nests found with only host nestlings, we used only nests monitored through at least part of incubation.

Comparison with cattle-grazed landscape.—To compare behavior of cowbirds in bison-grazed with that in cattle-grazed landscapes, we used data from research conducted on the nearby National Rifle Association Whittington Center, V-7 ranch, and adjacent lands during the summers of 1992–1997. The study area was located 30 km northeast of our VPR bison pasture (Fig. 1) and occupied a similar topographical position along the prairie–mountain interface. At those sites, cattle were the primary grazing ungulates (Goguen and Mathews 1998, 2001).

Within the cattle-grazed study area, we conducted intensive studies of cowbird behavior and host nesting success in relation to livestock grazing. From 1992 to 1995, we located and monitored host nests on eight 35-ha plots located within pinyon–juniper habitat (Goguen and Mathews 1998). From 1995 to 1997, we studied the behavior and movements of female cowbirds breeding in the pinyon–juniper woodlands and feeding in the cattle-grazed landscape (Goguen and Mathews 2001). We used similar nest-monitoring protocols and calculated parasitism rates as for VPR above. We radiotagged female cowbirds that bred in pinyon–juniper habitats bordering the grasslands; the few females that did not have breeding ranges close to the grassland border were omitted from the comparison. We tracked those females nearly daily, in both morning and afternoon, and recorded information about foraging microhabitat and ungulate use for each feeding relocation. Because cattle were held in smaller pastures (mostly <2,000 ha) and managed more intensively (i.e. rotated occasionally), we did not conduct cattle distribution surveys in a manner comparable to the bison surveys described previously. Instead, we recorded stocking densities and dates when cattle were rotated from one pasture to another (Goguen and Mathews 2001).

We used a combination of published (Goguen and Mathews 1998, 2001) and unpublished data to compare cowbird behavior in the cattle-grazed landscape with that in the VPR bison-grazed landscape. Specifically, we used radiotelemetry data to compare daily behavior pattern, feeding-site selection, breeding- to feeding-range commuting distances, and home-range sizes of female cowbirds. Additionally, we used host-nest

data to compare host species selection and parasitism intensities within pinyon–juniper habitats of the two landscapes. Because data fit statistical assumptions, we used *t*-tests for statistical comparisons.

RESULTS

Bison distribution surveys.—We surveyed the abundance and distribution of bison for 32 afternoons from 5 June to 6 July. Number of bison within 10 km of the radiotagged cowbirds' breeding grounds varied greatly on a daily basis, ranging from 6 to 1,161 individuals (Fig. 2). The spatial distribution of bison also varied greatly over the study period (Fig. 3), as did the distance of the nearest bison from the cowbird breeding grounds (range: 2.67–9.49 km). Cowbirds foraged daily with bison during surveys.

We detected elk during 56% of the afternoon surveys; however, because elk commonly concealed themselves within dense riparian thickets, detections probably underestimated their actual numbers. During afternoon surveys, detections ranged from 0 to 260 individuals. During most afternoons (75%), <50 elk were observed. However, from 27 June to 3 July, we detected an average of 169 adult elk daily; most were clustered in a large cow–calf herd along Ponil Creek. We commonly observed cowbirds feeding in association with elk herds. We also detected pronghorn daily, but we did not count them, because we observed cowbirds with pronghorn in only one instance.

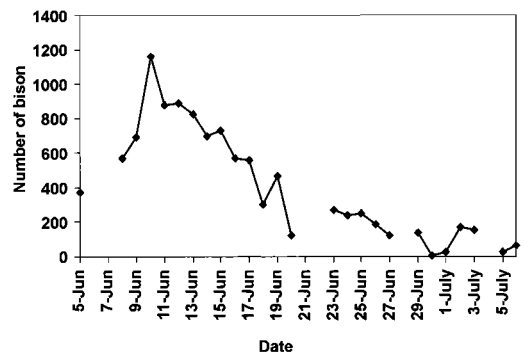


FIG. 2. Daily abundance of bison within the western portion of the Vermejo Park Ranch study pasture during June and July 2002. Number of bison is the total number of bison detected within 10 km of the overall center of the breeding areas of the 10 radiotagged cowbirds in the study.

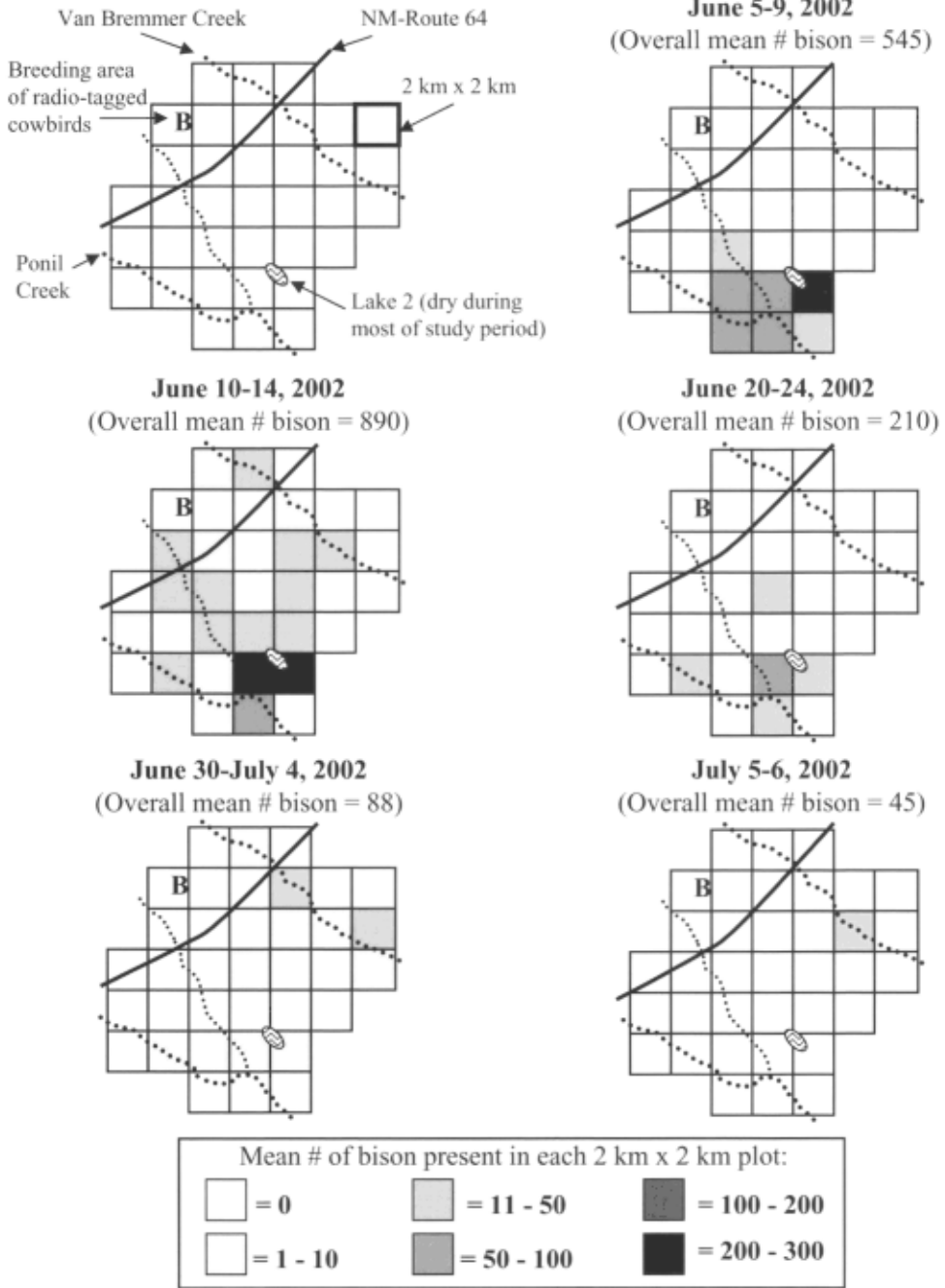


FIG. 3. Distribution of bison within the western portion of the Vermejo Park Ranch study pasture during June and July 2002. The contiguous bison pasture continues ~10 km to the east beyond the gridded portion shown. Mean number of bison present within each 2 x 2 km grid square was calculated by averaging the daily counts for that grid square across all afternoon bison surveys during the interval. The "overall mean # bison" for each period was calculated by averaging the daily total number of bison detected within the entire gridded landscape across all days in the interval.

Cowbird movements and behavior.—We radiotagged and tracked 10 female cowbirds from late May to 6 July. We stopped on 6 July because cowbird breeding ends by early to mid-July in the region (Goguen and Mathews 2001), and few transmitters were still active by then. Overall, we were successful at relocating females during both mornings (92% success across all birds and all mornings) and afternoons (86% success across all birds and all afternoons). On average, we located each female 45.8 times (range: 29–64 locations), with an average of 29.5 locations on their pinyon–juniper breeding grounds and 16.3 locations on their feeding grounds.

All females exhibited the typical cowbird commuting pattern that has been documented in most other telemetry studies (e.g. Rothstein et al. 1984, Thompson 1994, Gates and Evans 1998); in the mornings, females were primarily engaged in breeding activities (e.g. nest-searching, social interactions) within territories in pinyon–juniper habitat; whereas in the afternoons, females were found primarily away from those areas at distant prairie or riparian sites, engaged in feeding.

On the basis of afternoon telemetry relocations, females fed with bison (77.0%, $n = 161$ feeding relocations), elk (9.9%), without ungulates on the dry lakebed (10.6%), without ungulates at a bison-handling corral (1.9%), and without ungulates on the open prairie (0.6%). Although 23% of the feeding locations were without bison, most were used on days when few bison were within 10 km of the cowbird breeding ranges (during late June and early July). Specifically, all locations where cowbirds

fed without ungulates, and most (63% of 16) where they fed with elk, were used between 29 June and 5 July, a period during which <200 bison, and on many days <100 bison, were within 10 km of the cowbird breeding ranges (Fig. 2). When radiotagged birds fed without ungulates on the dry lakebed or at the bison-handling corral, they were typically present with numerous other cowbirds, which suggests that other cowbirds also chose those sites when ungulates were not widely available (dry lakebed: mean = 26.25 additional cowbirds, $n = 17$ observations; bison corral: mean = 33.3 additional cowbirds, $n = 3$ observations).

Radiotagged cowbirds commuted an average of 7.24 km (SE = 0.43, $n = 10$ females) between their morning breeding areas and afternoon feeding sites, though average commuting distances varied substantially among the 10 females, and the daily commuting distance traveled by individuals varied substantially during the study period (Table 1). Mean daily commuting distance was not related to the number of bison within 10 km of the cowbird breeding grounds ($r^2 = 0.0001$, $n = 26$, $P = 0.95$), but was related to the distance of the nearest bison from the breeding grounds ($r^2 = 0.24$, $n = 26$, $P = 0.011$) and distance of the nearest group of ≥ 5 bison from the breeding grounds ($r^2 = 0.29$, $n = 26$, $P = 0.0049$). Although commuting distances were long and variable, females did not appear to alter their basic daily behavior in response to bison distribution, nor did any female alter the location of her morning breeding area. Long, variable commutes, however, resulted in large feeding-area and overall home-range sizes (Table 2).

TABLE 1. Commuting distances from breeding to feeding grounds for radiotagged female Brown-headed Cowbirds breeding in a bison-grazed landscape in northeastern New Mexico, 2002.

Female number	n^a	Mean \pm SD (km)	Minimum (km)	Maximum (km)
072	11	7.27 \pm 0.65	6.27	8.46
101	25	8.74 \pm 2.10	4.04	11.12
134	12	6.42 \pm 2.07	3.00	9.00
191	10	5.28 \pm 2.21	2.38	9.13
221	18	7.11 \pm 2.46	3.43	10.37
281	20	8.63 \pm 1.78	4.66	10.76
312	18	9.51 \pm 2.47	4.66	11.81
343	14	7.97 \pm 1.85	4.32	9.96
373	17	6.45 \pm 2.33	0.16	9.05
851	13	4.98 \pm 1.88	2.37	7.76

^a Number of daily commuting distances measured for each individual bird. For each day available, commuting distance was calculated as the distance from the center of a female's morning breeding area to the position where she was first located feeding later in the day.

TABLE 2. Home-range estimates of radiotagged female Brown-headed Cowbirds in a bison-grazed landscape on the Vermejo Park Ranch, 2002, and in an adjacent cattle-grazed landscape, 1995–1997.

	95% Minimum convex polygon estimate			
	Female cowbirds ^b (<i>n</i>)	Mean ± SE (ha)	Minimum	Maximum
Bison-grazed landscape (2002)				
Overall home range ^a	10	3,238.3 ± 460.7	1,294.8	5,843.1
Breeding only ^a	9	38.5 ± 6.4	8.1	71.9
Feeding only ^a	7	1,937.9 ± 450.8	889.5	4,283.6
Cattle-grazed landscape (1995–1997)				
Overall home range ^a	20	699.7 ± 109.3	125.8	1,632.3
Breeding only ^a	13	53.8 ± 7.5	19.0	117.3
Feeding only ^a	16	740.3 ± 137.1	66.9	1,792.8

^a“Overall home range” is an estimate of the entire area used by a female and was calculated using all telemetry locations acquired. “Breeding only” is an estimate of a female’s breeding-area size and was calculated using only telemetry locations acquired within the morning breeding area. “Feeding only” is an estimate of the area used by a female for feeding and was calculated using only locations in which the female was located while engaged in feeding activities.

^b*n* = number of different female cowbirds used in estimates. Overall home-range size was calculated using only females for which we had ≥29 total telemetry locations. Breeding- and feeding-area sizes were calculated using only females for which we had ≥14 breeding or 14 feeding locations, respectively.

Cowbird parasitism rates.—We determined parasitism status for 96 nests of 11 potential cowbird hosts. Parasitism rates varied substantial among species but were highest for Western Tanager, Plumbeous Vireo, Black-throated Gray Warbler, and Blue-gray Gnatcatcher (Table 3).

Comparison with cattle-grazed landscape.—Radiotagged female cowbirds in the bison-grazed (*n* = 10) and cattle-grazed landscapes (*n* = 24) exhibited the same basic daily behavioral pattern and host preferences. In both landscapes, radiotagged females spent their mornings in pinyon–juniper woodlands engaged in breeding activities and, in late morning or early afternoon, commuted to grassland sites to feed, primarily with large ungulates. In both landscapes, female breeding

areas were stable throughout the season, and average breeding area size did not differ between landscapes (*t* = 1.54, *df* = 20, *P* = 0.14; Table 2). Although sample sizes are small and represent only one year for the bison-grazed landscape, parasitism was similar for the bison-grazed and cattle-grazed landscapes. The three most heavily parasitized hosts in the cattle-grazed landscape (Western Tanager, Plumbeous Vireo, and Blue-gray Gnatcatcher; Goguen and Mathews 1998) were also heavily parasitized in the bison-grazed landscape (Table 3).

The primary behavioral differences between cowbirds in the bison-grazed and cattle-grazed landscapes were related to feeding-habitat selection. In the cattle-grazed landscape, cowbirds fed almost exclusively (98% of feeding

TABLE 3. Cowbird parasitism rates of potential host species nesting in pinyon–juniper woodland habitats of the Vermejo Park Ranch bison pasture in northeastern New Mexico, 2002.

Species	Number of nests	Number of nests parasitized	Percentage of nests parasitized
Western Tanager (<i>Piranga ludoviciana</i>)	16	16	100
Plumbeous Vireo (<i>Vireo plumbeus</i>)	12	11	91.7
Black-throated Gray Warbler (<i>Dendroica nigrescens</i>)	3	2	66.7
Blue-gray Gnatcatcher (<i>Poliophtila caerulea</i>)	14	6	42.9
Western Wood-Pewee (<i>Contopus sordidulus</i>)	19	1	5.3
Spotted Towhee (<i>Pipilo maculatus</i>)	10	0	0.0
Chipping Sparrow (<i>Spizella passerina</i>)	3	0	0.0
Gray Flycatcher (<i>Empidonax wrightii</i>)	8	0	0.0
Virginia’s Warbler (<i>Vermivora virginiae</i>)	1	0	0.0
Black-headed Grosbeak (<i>Pheucticus melanocephalus</i>)	4	0	0.0
Lark Sparrow (<i>Chondestes grammacus</i>)	6	0	0.0

observations) with cattle or horses or at active livestock corrals. On average, radiotagged females commuted only 1.78 km (SE = 0.12, $n = 24$ females) from their morning breeding grounds to feeding sites, significantly less than the 7.24 km average of females in the bison-grazed landscape ($t = -12.27$, $df = 12$, $P < 0.001$). Feeding ranges and overall home ranges were larger in the bison-grazed landscape (Table 2; feeding range: $t = -2.54$, $df = 7$, $P = 0.038$; overall home range: $t = -5.36$, $df = 10$, $P = 0.0003$).

DISCUSSION

Bison distribution and movements.—Within the large VPR pasture, bison distribution and abundance varied considerably and strongly influenced cowbird behavior. Unlike domestic cattle, which tend to concentrate around water sources, riparian zones, or shade trees even when forage quality is higher at more distant sites (Roath and Kruger 1982, Andrew 1988), bison move regularly and across considerable distances to get to richer foraging sites, regardless of water or topographic constraints (Van Vuren 2001). For example, in a montane region of Utah, compared with cattle, the distribution of free-ranging bison was not influenced by topography (e.g. slope, elevation) or distance to water sources (Van Vuren 2001), and bison summer home ranges averaged >5,200 ha (Van Vuren 1983). Similarly, in a grassland pasture in Kansas, bison moved regularly to get to high-quality feeding sites, such as recently burned areas or lowland sites that maintained soil moisture during drier periods (Knapp et al. 1999).

A potential limitation of our study is that we monitored bison movements for only one summer in a landscape that was affected by an extended drought. During that period, new grass was concentrated along river floodplains and prairie depressions, which may have caused bison to spend more time than usual in areas near water. Even under those conditions, however, bison moved extensively across the landscape and similarly to those in other studies (e.g. Van Vuren 1983, Knapp et al. 1999). Thus, we assume that the bison behavior we observed was representative, though we acknowledge that additional study of bison movement patterns under nondrought conditions are needed to confirm that.

How did bison movements influence cowbird behavior?—The primary effect of bison movements on cowbird behavior is on afternoon feeding-site selection and commuting behavior. Cowbirds almost always foraged with bison when bison were abundant close to the breeding grounds, and all relocations where radiotagged cowbirds foraged with elk or without ungulates occurred when few bison were within 10 km of the breeding grounds. Although cowbirds are relatively flexible in their feeding habitats, cowbirds in many regions prefer feeding with large ungulates, perhaps because grazing animals stir up insects or because they represent large, easily visible congregation points where birds can assemble in afternoon feeding flocks (Goguen and Mathews 1999, 2001). Elk often grazed in open grasslands in large groups and presumably offered the same foraging benefits to cowbirds as bison. However, compared with bison, elk are more strongly associated with wooded habitats (Wisdom and Cook 2000) and were far less abundant at our study site; thus, they were not as available to cowbirds.

It is not currently known how cowbirds select and locate afternoon feeding sites, especially when they depend on grazing ungulates whose positions vary daily. Harper et al. (2002) used modeling to address that problem in a large landscape grazed by free-ranging cattle. Temporal movements of cattle herds were simulated using rules involving habitat type, forage quality, proximity to water or supplemental feeding sites, and published reports of typical distances that cattle move daily. Harper et al. (2002) found that a search strategy in which cowbirds used memory to revisit sites where they had recently found cattle, but also were allowed to assess sites for feeding en route, best approximated actual cowbird movements observed in the study landscape. Our findings support that result. In our landscape, commuting distance was correlated with distance to the nearest bison, which suggests that cowbirds assessed the foraging potential of habitats they flew over while commuting. However, the relatively weak relationship ($r^2 = 0.29$) may also illustrate the challenge faced by commuting cowbirds. A commuting cowbird can search only a limited corridor of habitat for ungulates while commuting to the prairie. Depending on the current distribution of bison, that corridor may or may not contain the nearest bison. That could result in longer commutes

and perhaps considerable energy expenditure in broad searches. Estimated commuting distances represent straight-line distances between breeding and feeding sites but did not incorporate any additional search efforts that may have been necessary to locate a feeding site.

Average overall home-range size for female cowbirds in the bison-grazed landscape was exceptionally large, greatly exceeding all previous estimates reported from other populations, though overall home-range sizes of some individual birds in other studies have been comparable (i.e. >3,000 ha; Gates and Evans 1998, Thompson and Dijak 2000, Goguen and Mathews 2001). Consistently large home-range sizes in our study were not attributable to large or variable breeding ranges; breeding areas were fixed throughout the summer, and average breeding-range size was similar to estimates from other western habitats (Rothstein et al. 1984, Goguen and Mathews 2001). Instead, large overall home-range sizes were attributable to the variable and often long distances that females traveled to locate afternoon feeding sites with bison.

Although cowbirds have been recorded commuting >12 km from breeding to feeding areas (Curson et al. 2000), radiotagged females in our study generally did not extend their commuting flights beyond 10 km. When few bison were within 10 km of the cowbirds' breeding grounds, females often foraged without ungulates at closer sites and did not commute from their breeding grounds to locate more distant bison. All but one of the cowbird feeding relocations that did not involve ungulates occurred on either the dry lakebed or at the main bison-handling corral. Both of those sites are similar; they are highly visible from a distance and provided foraging habitats for cowbirds, even in the absence of bison. The dry lakebed, for example, contained little vegetation to hinder cowbird foraging and had a large seedbank that cowbirds could exploit (C. B. Goguen pers. obs.). The bison-handling corral was also sparsely vegetated and may have contained waste grain provided for bison in the past. Those sites may have represented predictable, alternative feeding and congregation points for cowbirds when bison could not be detected within a bird's typical search area. The large numbers of cowbirds congregating and feeding at those sites at those times supports that hypothesis.

Cowbird behavior in the cattle-grazed versus bison-grazed landscapes.—Aspects of cowbird behavior differed between the bison-grazed and cattle-grazed landscapes, even though both sites were in proximity and both cowbird populations occupied a similar landscape context (i.e. both bred in pinyon–juniper habitats at the prairie–forest interface). Although cowbirds in both landscapes exhibited similar basic breeding and commuting patterns and fed primarily in association with grazing ungulates, cowbirds in the cattle-grazed landscape had shorter commuting distances and smaller feeding-areas and overall home-range sizes. The primary differences between the landscapes that presumably caused differences in cowbird behavior were the type of dominant grazing ungulate present and, perhaps more importantly, management activities.

Differences in ungulate behavior probably contributed to the contrasting cowbird commuting patterns. Cattle are more constrained by availability of water and shade trees, and by steep topography (Steuter and Hiding 1999, Van Vuren 2001). Cattle are also more sedentary. In Utah, where estimated bison summer home-range size was >5,200 ha, sympatric free-ranging cattle limited their summer movements to a 375-ha open basin (Van Vuren 2001). In another study of free-ranging cattle, when herds switched foraging areas, they typically moved to adjacent sites rather than to more distant sites (Bailey et al. 1990).

Even more important than the behavioral differences between the ungulate species was the manner in which the animals were pastured and managed. Although pastured bison and cattle differ in behavior, they are more similar than pastured bison and historical wild bison (Plumb and Dodd 1993), and the way ungulates are managed can strongly influence behaviors that may be important to cowbirds. Bison on our study site had access to a huge pasture; they were kept at low stocking rates, and their distribution and movement patterns were rarely influenced by managers. In contrast, domestic livestock managers on western rangelands often control the distribution of cattle through use of water and salt placement, fencing, and sometimes herding or specialized grazing systems (Holechek et al. 1989, Coughenour 1991). Those actions are used to achieve a more uniform use of available forage but can also result in a higher

density and a more predictable distribution of animals. For example, in the cattle-grazed landscape that we studied, ranchers commonly divided their land into multiple pastures and used a seasonal grazing system in which cattle were held in smaller pastures at higher stocking rates and were rotated as forage was depleted (Goguen and Mathews 2001). Therefore, cattle were located in smaller pastures close to cowbird breeding habitats during most of the summer. Given different management approaches, mobility of bison, and preference of cowbirds to feed with ungulates, it is not surprising that cowbirds in the bison-grazed landscape moved over much larger areas in search of afternoon feeding sites.

Conservation implications and conclusions.—Current efforts to restore bison to natural areas have often been justified by the potential ecological benefits that bison can bring to grassland ecosystems. Bison enhance plant structural and species diversity through grazing, trampling, and wallowing; and those changes appear to benefit many wildlife species, including songbirds (Truett et al. 2001). Bison grazing, however, also provides conditions suitable for cowbirds. Given the major negative effects that cowbird parasitism can have on songbird populations (Mayfield 1965, May and Robinson 1985), it is essential to consider that relationship closely to fully evaluate the benefits and costs of bison restoration to songbird communities.

Cowbirds in our study area typically fed with bison and were willing to commute long distances to feed with them. Thus, like domestic livestock, bison apparently provide high-quality feeding opportunities for cowbirds, and the distribution of bison may influence abundance and distribution of cowbirds within a landscape (Goguen and Mathews 2000). Because of those similarities, it may become necessary to keep bison away from sensitive host-nesting habitats, as has been proposed with livestock removals from areas near sensitive host habitat to reduce cowbird feeding opportunities and protect the host species from parasitism (Goguen and Mathews 1999).

Our comparison of cowbird behavior in bison-grazed and cattle-grazed landscapes, however, suggests that, in terms of cowbird energetics, bison may actually be a less desirable associate than cattle; therefore, bison grazing could potentially result in lower frequencies

of cowbird parasitism. Female cowbirds are capable of producing ≥ 40 eggs per breeding season (Scott and Ankney 1980), and they meet the prolonged energetic costs of egg production through their daily dietary intake (Ankney and Scott 1980). Curson and Mathews (2003) recently demonstrated that commuting flights and egg production compete for that limited energy intake, and female cowbirds that commute longer distances produce fewer eggs. In the bison-grazed landscape, cowbirds had to commute long distances to find bison. On several days, when bison nearly vacated the western half of the pasture, cowbirds spent their afternoons feeding without ungulates and may have had to focus on seeds rather than high-protein insects. Both of those factors could affect egg production. In the cattle-grazed landscape, cowbird commutes were shorter, livestock were closer to cowbird breeding habitats throughout the breeding season, and those cowbirds exhibited a high rate of egg production (Curson and Mathews 2003).

High parasitism rates in both the bison-grazed and cattle-grazed landscapes do not seem to support our previous argument. However, seasonal parasitism rates are determined not only by laying rate, but also by cowbird density. Results of point-count surveys suggest that cowbird abundance in the pinyon-juniper breeding habitats of the bison-grazed landscape was nearly twice as high as in the cattle-grazed landscape (bison-grazed: mean = 4.92 cowbirds per 35-ha plot; cattle-grazed: mean = 2.59 cowbirds per 35-ha plot; C. B. Goguen and D. R. Curson unpubl. data). Thus, it is possible that increased movements reduced egg-laying rates. In any case, for cowbirds to be affected, bison need to be managed in pastures large enough to allow them to express their mobile behavior. From a commuting cowbird's point of view, bison in intensively managed small pastures would probably not differ significantly from cattle.

Historically, wild bison moved in an irregular, unpredictable manner, such that particular locations were occupied in some months or years and unoccupied in others (Roe 1970, Shaw and Meagher 2000). Although that scenario is unlikely in the near future, it does raise the question of how cowbirds behaved in the past, when bison were free to roam. For example, what did cowbirds do when bison left a particular area and did not return during that breeding season?

In our study, cowbirds dealt with that situation in the short term by maintaining their breeding areas and switching to alternative feeding areas, though that switch may have resulted in reduced productivity. Historically, cowbirds faced with the lack of bison in the long term may have also responded in that manner. However, it is also possible that poor foraging success because of habitat recovery (e.g. grass regrowth) or lack of ungulates for use as insect beaters could have lead to the temporary desertion of those sites.

The question has important implications for current cowbird-management issues—in particular, the effectiveness of removing grazing ungulates to protect endangered hosts from cowbird parasitism.

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CHAPTER 7

HOST DEFENSES AGAINST COWBIRD (*MOLOTHRUS* SPP.) PARASITISM: IMPLICATIONS FOR COWBIRD MANAGEMENT

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ABSTRACT.—Brown-headed Cowbird (*Molothrus ater*; hereafter “cowbird”) parasitism is costly to host fitness, especially for smaller hosts whose nestlings have to compete with larger cowbird nestlings that often hatch earlier. Those fitness costs select for a variety of host defenses, including inconspicuous nests, aggression toward cowbirds, deserting parasitized nests, burying cowbird eggs, and ejecting cowbird eggs from nests. Egg ejection is the most effective defense against parasitism, but there are only 30 hosts known to regularly eject cowbird eggs. Evolutionary lag is the most likely reason that relatively few hosts demonstrate ejection. However, once ejection evolves in a host, some evidence indicates that it is maintained for long periods of time, even in the absence of brood parasitism—which suggests that host communities are becoming increasingly resistant to parasitism over time. With progressively fewer naive hosts to exploit, cowbirds may specialize on just a few host species. Retention of host defenses is also important because cowbirds were probably more common in the past, when mammalian megafauna were present. As a result, not every newly exposed host population requires cowbird control programs, because many have maintained defenses after inheriting them from ancestors that were exposed to parasitism, making them well defended against new bouts of parasitism. Several hosts that are currently the focus of control programs demonstrate defenses against parasitism, and their populations have increased. We suggest that the time has come to relax control of some of those species, to determine whether they can sustain their populations in the presence of parasitism and to allow their natural defenses to increase, so that they will not be perpetually dependent on human intervention.

RESUMEN.—El parasitismo de *Molothrus ater* es costoso en términos de la adecuación de sus hospederos, en especial de aquellos de pequeño tamaño cuyos pichones deben competir con los pichones de *Molothrus* más grandes que en general eclosionan más temprano. Estos costos en adecuación seleccionan en favor de varias defensas por parte de los hospederos, que incluyen: nidos inconspicuos, agredir a los *Molothrus*, abandonar los nidos parasitados, y enterrar o rechazar los huevos de *M. ater* del nido. El rechazo del huevo es la defensa más efectiva contra el parasitismo, pero se sabe que sólo 30 especies de hospederos rechazan regularmente los huevos de *M. ater*. El retraso evolutivo es la causa más probable para explicar porqué tan bajo número de hospederos demuestran rechazo. Sin embargo, una vez que el rechazo evoluciona en un hospedero, existe evidencia indicando que es mantenido por largo tiempo, aún en ausencia de parasitismo de cría. Este último fenómeno sugeriría que las comunidades de hospederos se estarían volviendo cada vez más resistentes al parasitismo. Con una progresión hacia un menor número de hospederos “inocentes” para explotar, los *Molothrus* pueden especializarse en unas pocas especies hospederas. La retención de las defensas en los hospederos es también importante porque los *Molothrus* fueron probablemente más abundantes en el pasado, cuando la megafauna de mamíferos estaba presente. En consecuencia, no todas las especies de hospederos recientemente expuestas al parasitismo por *Molothrus* requerirían de programas de manejo de

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Molothrus. Muchas de ellas podrían mantener defensas que habrían heredado de ancestros que si estuvieron expuestos al parasitismo, haciendo que estuvieran bien defendidas contra nuevos eventos de parasitismo. Varios hospederos que actualmente son centro de programas de control demostraron defensas contra el parasitismo, y sus poblaciones se han incrementado. Nosotros sugerimos que ha llegado el tiempo de relajar el control sobre algunas de dichas especies, y de esta manera determinar si pueden mantener sus poblaciones en presencia del parasitismo. Al mismo tiempo, se estaría permitiendo que sus defensas naturales se incrementaran, y de este modo, que no dependieran perpetuamente de la intervención humana.

WHEN SELECTION PRESSURES for an adaptation are relaxed, the adaptation may be lost because of fitness costs. However, conditional behavioral traits that are elicited only in response to specific stimuli may become neutral in the absence of selection pressures and will then be lost only through genetic drift. As a result, such traits may be retained for long periods and may be in place if selection pressures are renewed. For example, a number of prey species demonstrate antipredator behaviors in areas where the predators are absent, which suggests that the costs of maintaining those behaviors are minimal (Byers 1997, Coss 1999, Rydell et al. 2000).

Interactions between avian brood parasites and their hosts, because of their dynamic nature, are excellent models for studying retention of behaviors in the absence of selection pressures. Parasites may switch to new hosts once the old hosts evolve defenses, and parasitism pressures change as the ranges of hosts and parasites change. Whether host defenses are lost or retained has important implications for management of brood parasites, such as the Brown-headed Cowbird (*Molothrus ater*; hereafter "cowbird"; see also Berger et al. 2003). If some hosts retain defenses, not every newly exposed host population needs to be the focus of cowbird control programs. As we will demonstrate, many "new" hosts may have suffered cowbird parasitism as recently as the late Pleistocene (i.e. ~10,000 years ago) or are descended from ancestors that were exposed to parasitism, and possess defenses retained from those past bouts. Here, we review the costs of cowbird parasitism to hosts and the nature and effectiveness of host defenses. We also review our studies on retention of host defenses when hosts are no longer parasitized and the implications of those studies for cowbird management programs. We suggest that, in some situations, cowbird controls programs should be relaxed to allow host defenses that are already present to increase. Relaxing control would allow us

to determine whether recovered host species can, without human intervention, sustain their populations in the presence of parasitism.

COSTS OF PARASITISM TO HOSTS

Cowbird parasitism is almost always costly to hosts. Hosts that accept parasitic eggs ("accepters") typically raise fewer of their own offspring when parasitized. Many smaller hosts raise only cowbirds when parasitized, and none of their own offspring. Such species include the Bell's Vireo (*Vireo bellii*), Blue-gray Gnatcatcher (*Poliophtila caerulea*), Warbling Vireo (*V. gilvus*), Empidonax flycatchers, and Eastern Phoebe (*Sayornis phoebe*) (Rothstein 1975b, Rothstein et al. 1980, Goguen and Mathews 1996, Whitfield and Sogge 1999, Budnik et al. 2001). The phenomenon is attributable, in part, to cowbirds' short incubation period, which allows them to hatch sooner than most hosts (Briskie and Sealy 1990, Peer and Bollinger 2000). Hatching earlier than host nestlings allows cowbirds to gain a developmental "head start," which is critical in nests with larger hosts (Peer and Bollinger 1997a, Peer and Sealy 2004b). In nests of smaller hosts, the size disparity between cowbirds and hosts further reduces chances of host nestling survival (Marvil and Cruz 1989). When cowbird eggs hatch earlier, hosts may also spend less time incubating their own eggs, which results in delayed hatching or in no hatching at all (Hauber 2003; but see McMaster and Sealy 1999).

Although the costs of parasitism to larger hosts are usually not as great, they can be significant. Wood Thrush (*Hylocichla mustelina*) raise 0.9–2.5 fewer offspring in successful parasitized nests, Red-winged Blackbirds (*Agelaius phoeniceus*) 0.2 to 1.5 fewer, and Western Meadowlarks (*Sturnella neglecta*) 1.7 fewer (Lorenzana and Sealy 1999). Cowbirds usually avoid parasitizing hosts with diets of seeds or fruit, because their young require protein diets consisting primarily of insects. Nonetheless, when those

unsuitable hosts are parasitized, they are affected, because food is diverted to the cowbird young instead of their own. Frugivores, such as the Cedar Waxwing (*Bombycilla cedrorum*), and granivores, such as the American Goldfinch (*Carduelis tristis*) and House Finch (*Carpodacus mexicanus*), fledge fewer young in parasitized nests (Rothstein 1976a, Lorenzana and Sealy 1999).

Even species that reject cowbird eggs ("rejecters") incur costs from parasitism. Smaller hosts, such as Blue-gray Gnatcatchers and Bell's Vireos, sometimes desert parasitized nests, but they must expend energy in building a new nest, and subsequent broods may be parasitized as well (Goguen and Mathews 1996, Kershner et al. 2001, Kus 2002). Likewise, Yellow Warblers (*Dendroica petechia*) that bury cowbird eggs with a new nest lining are sometimes parasitized again (Clark and Robertson 1981, Peck and James 1987). Species that eject cowbird eggs from their nests are freed from parasitism and do not suffer the costs of renesting; however, they sometimes have eggs removed by Brown-headed Cowbirds or punctured by Shiny (*M. bonariensis*) and Bronzed (*M. aeneus*) cowbirds (Scott 1977, Carter 1986, Peer and Sealy 1999b, Nakamura and Cruz 2000). Cowbirds also depredate nests, which may force renesting, thereby providing the cowbird with another attempt at parasitism (Arcese et al. 1996, Elliott 1999, Pietz and Granfors 2000); but how often that behavior occurs is unclear (e.g. McLaren and Sealy 2000). Because costs of parasitism are intense, selective pressure for antiparasite behaviors is high.

ANTIPARASITE BEHAVIORS

NEST LOCATION AND DEFENSE

Hosts may be able to avoid parasitism by constructing well-concealed nests and behaving surreptitiously so that they will not be observed by cowbirds. Female cowbirds locate nests by watching hosts, often from unobstructed perches (Hann 1941, B. D. Peer pers. obs.). Not surprisingly, nests that are placed near perch sites are parasitized more frequently (Freeman et al. 1990, Larison et al. 1998, Hauber and Russo 2000). In the Midwest, cowbirds also appear to prefer hosts that nest in shrublands and forests over those in grasslands, partly because grassland host nests may be more inconspicuous (Robinson

et al. 1999, 2000; Peer et al. 2000). In some cases, inconspicuous hosts with well-concealed nests are parasitized less frequently, but the evidence is mixed and requires further study (Robinson et al. 1995, Peer and Sealy 2004a). Host community composition may also influence patterns of parasitism; cowbirds appear to be attracted to conspicuous hosts, such as Northern Cardinals (*Cardinalis cardinalis*), and species nesting near conspicuous hosts may be at higher risk of parasitism (Barber and Martin 1997).

Once a cowbird approaches a nest, hosts may respond aggressively in an attempt to thwart parasitism or egg removal. A number of hosts respond more aggressively to cowbird mounts than to control mounts (e.g. Robertson and Norman 1976, Ortega and Cruz 1991, Peer and Bollinger 1997a); Yellow Warblers respond with cowbird-specific alarm calls (Hobson and Sealy 1989, Gill and Sealy 2003). Robertson and Norman (1976) suggested that accepter species should respond to cowbirds more aggressively than rejecter species because of the higher costs of parasitism. Sealy et al. (1998) studied 11 hosts and concluded that, in general, accepters respond more aggressively to cowbirds than to control mounts. Rejecters were equally aggressive toward cowbirds and controls, but such generalized defense given by rejecters may be adequate to deter cowbirds.

Although many of those studies have demonstrated that hosts sometimes recognize cowbirds for the unique threat they represent, use of control mounts to assess aggressiveness is problematic, because the mounts may not be realistic enough to elicit host behavior toward live cowbirds, and other cues may be used for recognition (Ortega and Cruz 1991, Gill et al. 1997b, Sealy et al. 1998). Moreover, relatively few studies have addressed whether hosts are actually present at their nests when cowbirds come to lay eggs just before sunrise (Scott 1991, Peer and Sealy 1999a). Aggression may help later in the day by preventing cowbirds from monitoring the status of host nests and removing eggs (Sealy 1992, Tewksbury et al. 2002). However, unless the hosts are present when cowbirds come to lay eggs, aggression is of little benefit in preventing parasitism.

When hosts are present, they are sometimes successful in preventing parasitism, but not always. Budnik et al. (2001) observed that Bell's Vireos are usually present when cowbirds lay

eggs; in one instance, a female remained on the nest when a female cowbird attempted to lay an egg, and a cowbird egg was found on the ground below the nest. Budnik et al. (2001) found eight cowbird eggs under nests, which suggested that Bell's Vireos may sometimes be successful in preventing parasitism (also see Kus 2002). However, Burhans (2000) found that, though Field Sparrows (*Spizella pusilla*) are usually present when cowbirds lay eggs, their aggression does not stop parasitism. Instead, the sparrows use presence of a cowbird as a cue to desert parasitized nests (Burhans 2000). Neudorf and Sealy (1994) monitored early-morning attentiveness for 10 host species and found no correlation between parasitism and nest attentiveness. They even observed a cowbird entering and laying an egg in the nest of a Baltimore Oriole (*Icterus galbula*) despite the presence of the female oriole. Some have suggested that aggressive behavior may help cowbirds to locate nests (Robertson and Norman 1976, 1977; Smith 1981), but a test of that hypothesis failed to demonstrate a connection between nest defense and the likelihood of parasitism (Gill et al. 1997a).

Although it may not be an adaptation against parasitism, nesting in a colony may also be beneficial because there are more individuals to repel parasites. Denser colonies of Red-winged Blackbirds and Greater Antillean Grackles (*Quiscalus niger*) experience decreased levels of Brown-headed Cowbird and Shiny Cowbird parasitism, respectively (Wiley 1982, Freeman et al. 1990). However, other colonial species such as the Common Grackle (*Q. quiscula*), Great-tailed Grackle (*Q. mexicanus*), and Yellow-headed Blackbird (*Xanthocephalus xanthocephalus*) experience little or no parasitism in both small and large colonies (Ortega and Cruz 1991, Peer and Bollinger 1997a, Peer and Sealy 2004b). Overall, the effectiveness of aggressive nest defense may be limited in preventing parasitism. If a cowbird attempts to parasitize a nest, it is generally successful, despite the potential risk of injury (e.g. Leathers 1956, Tewksbury et al. 2002).

NEST DESERTION AND EGG BURIAL

Hosts that desert parasitized nests or bury cowbird eggs are relatively small and have bills that may be too small to allow them to eject cowbird eggs. Hosoi and Rothstein (2000)

analyzed desertion frequencies of 35 species and found that desertion rates were higher in nonforest than in forest-nesting species, which indicates a probable evolutionary lag because forest species have had less time to evolve defenses against parasitism. However, birds desert nests for a variety of reasons, and few studies have been performed with adequate controls to determine the proximate stimulus that triggers nest desertion in response to parasitism or to other disturbances. Graham (1988) presented evidence showing that naturally parasitized nests are deserted much more frequently than unparasitized nests and experimentally parasitized ones, which indicates that presence of a cowbird egg is not the proximate stimulus for desertion. For example, hosts such as the Eastern Phoebe and Clay-colored Sparrow (*S. pallida*) desert parasitized nests in response to reductions in clutch volume by cowbird egg removal, not in response to cowbird eggs (Rothstein 1986, Hill and Sealy 1994).

Of the few hosts tested in depth, Field Sparrows desert parasitized nests (Strausberger and Burhans 2001), and Yellow Warblers respond to cowbird eggs by deserting the nest or burying the cowbird egg under a new nest lining (Sealy 1995). Blue-gray Gnatcatchers, Bell's Vireos, White-crowned Sparrows (*Zonotrichia leucophrys*), and Northern Cardinals desert parasitized nests at high frequencies (Trail and Baptista 1993, Goguen and Mathews 1996, Budnik et al. 2001, Kershner et al. 2001, Kus 2002, Whitehead et al. 2002), but the proximate stimulus for desertion is unclear in most cases. Field Sparrows desert parasitized nests only after they have witnessed a cowbird at their nest (Burhans 2000). Despite extensive research, the cues that stimulate Yellow Warblers to bury eggs are unknown (Sealy 1995, Sealy and Lorenzana 1998). Experiments show that the Cedar Waxwing is the only species that often deserts in response to cowbird eggs *per se*, but that species also ejects cowbird eggs, and desertions may occur primarily after failed attempts at ejection (Rothstein 1976b).

Hosts that desert parasitized nests may require cues in addition to cowbird eggs, whereas species that eject cowbird eggs require only the appearance of the egg in their nest. Hosoi and Rothstein (2000) pointed out that the former hosts do not seem to show egg recognition, whereas ejecting species clearly

demonstrate egg recognition. They suggested that once a parasitized species evolves egg recognition, selection quickly results in ejection behavior because ejection is more adaptive than nest desertion, even if ejection incurs some costs (i.e. a "deserter" species that evolves egg recognition will quickly become an "ejecter"). Nest desertion is in need of further study with carefully controlled experiments.

EGG EJECTION

Egg ejection is probably the most effective defense against parasitism, other than avoiding parasitism altogether. Rather than simply ejecting the odd egg from their clutch, at least some birds apparently learn the appearance of their own eggs and recognize any eggs that are sufficiently different from their own (Rothstein 1975a, Peer and Sealy 2001). Recognition can be based on differences in at least three parameters: egg size, background color, and maculations (Rothstein 1982). Once a bird recognizes the egg as foreign, it grasps the egg between its mandibles and removes it from the nest; smaller hosts that cannot grasp-eject instead puncture-eject by pecking a hole in the egg and removing it whole or piecemeal (Rothstein 1975a, Sealy 1996, Peer and Sealy 2004b).

Relatively few Brown-headed Cowbird hosts have evolved ejection behavior, especially as compared with Common Cuckoo (*Cuculus canorus*) hosts (Rothstein 1992). Of 62 cowbird hosts tested for egg ejection behavior, only 30 demonstrate intermediate or higher levels of ejection (Peer and Sealy 2004a). Three more, including the Yellow-breasted Chat (*Icteria virens*), Northern Cardinal, and Chestnut-collared Longspur (*Calcarius ornatus*), eject non-mimetic eggs at intermediate frequencies, and one species, the Common Grackle may have lost most of its ejection behavior (Peer and Bollinger 1997a, Peer and Sealy 2004b).

Why do relatively few hosts eject cowbird eggs, given the associated fitness costs? Some researchers have suggested that an evolutionary equilibrium exists, in which the costs of egg ejection outweigh the benefits. For example, small hosts may accept parasitism because their bills are too small to grasp-eject cowbird eggs between their mandibles, making it necessary for them to puncture-eject cowbird eggs, which may cause damage to their own eggs when their

bill deflects off the cowbird eggs (Rohwer and Spaw 1988). In support of that hypothesis, Spaw and Rohwer (1987) pointed out that cowbird eggshells are exceptionally strong. However, it is unlikely that such ejection costs make it more beneficial for smaller hosts to accept cowbird eggs rather than risk damage to their own eggs, because many of those small hosts raise only cowbirds and none of their own young when parasitized. Therefore, they should attempt to eject the cowbird egg even if ejection results in a high likelihood of losing their entire clutch. The eastern Warbling Vireo (*V. g. gilvus*) is a small ejecting host, and when parasitized, it does not raise any of its own young (Rothstein et al. 1980). Sealy (1996) found that it lost only 0.3 eggs for each ejection of a cowbird egg. Clearly, the costs of egg ejection to Warbling Vireos are negligible in comparison with the costs of parasitism; consequently, they eject cowbird eggs. If Warbling Vireos can eject cowbird eggs with little cost, other small hosts probably can too.

Hosts may incur "recognition costs" when, in attempting to eject cowbird eggs, they accidentally eject one of their own eggs. That may be especially likely for species with eggs that resemble cowbird eggs. Experiments with hosts whose eggs resemble cowbird eggs have demonstrated that they are more likely to eject immaculate eggs than spotted eggs; those species include Yellow-breasted Chats, Northern Cardinals, Northern Mockingbirds (*Mimus polyglottos*), Chestnut-collared Longspurs, and Western Meadowlarks (reviewed in Peer and Sealy 2004a). Several smaller hosts with spotted eggs rarely eject normal-sized cowbird eggs, but eject undersized unspotted eggs regularly. Those species include Lark Sparrows (*Chondestes grammacus*), Grasshopper Sparrows (*Ammodramus savannarum*), and Vesper Sparrows (*Pooecetes gramineus*; Peer et al. 2000).

Depending on the recognition costs involved, an evolutionary equilibrium resulting in acceptance of cowbird eggs may exist for hosts with eggs that are similar to cowbird eggs. For example, Northern Cardinal eggs are very similar to cowbird eggs, the only noticeable differences being their slightly larger size, larger spots, and less rounded shape. Northern Cardinals can also raise some of their own young when parasitized, and cowbirds do not survive well in Northern Cardinal nests (Scott and Lemon 1996). Therefore, depending on the

costs incurred from diverting food to cowbird nestlings, it may be beneficial for a Northern Cardinal to accept a cowbird egg rather than risk ejecting one of its own eggs by accident (Peer and Sealy 2004a). Indeed, Burhans et al. (unpubl. data) found that Northern Cardinals are much more likely to eject immaculate eggs than spotted eggs.

Dickcissels (*Spiza americana*), which experience ejection costs, ejected only 11% of experimental cowbird eggs (Peer et al. 2000; B. D. Peer unpubl. data). They ejected all undersized spotted eggs without damaging their own ($n = 3$), which suggests that they may refrain from ejecting cowbird eggs because of ejection costs (Peer et al. 2000). Effects of cowbird parasitism on Dickcissels are not as great as effects on some other hosts (Hatch 1983); thus, they may be another example of a host that should accept cowbird parasitism because of an evolutionary equilibrium. Both the Dickcissel and Northern Cardinal host-parasite relationships require further study.

A more likely explanation for widespread acceptance of cowbird parasitism is evolutionary lag (Rothstein 1990, Sealy 1996, Rothstein et al. 2002, Peer and Sealy 2004a). According to that hypothesis, hosts have not had time to evolve ejection behavior, because the necessary mutations and recombinants that code for ejection have not appeared in their populations. For example, unlike eastern Warbling Vireos, western Warbling Vireos (*V. g. swainsonii*) also lose their entire brood when parasitized, yet they do not eject (Sealy 1996, Sealy et al. 2000, Ortega and Ortega 2003). Given that eastern Warbling Vireos eject, and that the two are virtually identical sibling species, it seems that evolutionary lag must be responsible for the lack of ejection in western Warbling Vireos (Sealy 1996, Sealy et al. 2000). The other aforementioned species that usually lose all their young but that do not try to eject may be additional examples of evolutionary lag. Our knowledge of the numbers of hosts that demonstrate ejection is incomplete, and more hosts need to be tested.

RETENTION OF HOST DEFENSES IN THE ABSENCE OF PARASITISM

Once hosts evolve defenses such as egg ejection, they seem to retain those behaviors for long periods. We have found that numerous hosts demonstrate antiparasite behaviors even

though they are not in contact with parasites, which indicates that they may have retained those defenses from past episodes of brood parasitism. Other circumstances that could select for appearance and maintenance of egg ejection behavior are (1) conspecific brood parasitism, (2) dense colonial nesting as seen in ground-nesting seabirds that have evolved the ability to recognize their own eggs, and (3) nest usurpation in Mourning Doves (*Zenaidura macroura*) that take over active nests of other birds and eject their eggs (reviewed in Rothstein 2001, Peer and Sealy 2004b). None of those selection pressures applies to the birds we have studied.

Rothstein (2001) found that Gray Catbirds (*Dumetella carolinensis*) on Bermuda and Loggerhead Shrikes (*Lanius ludovicianus*) in North America, where they are not parasitized, demonstrate high frequencies of egg ejection. Gray Catbirds on the mainland of North America are parasitized by cowbirds and eject 95% of cowbird eggs (Rothstein 1975a). Gray Catbirds on Bermuda, where there are no cowbirds or other brood parasites, eject 83% of experimentally added cowbird eggs, which suggests that they inherited ejection from their common ancestor with mainland North American Gray Catbirds. Only one case of parasitism of the Loggerhead Shrike has been reported (DeGeus and Best 1991), whereas other shrike species in Eurasia, including the Northern Shrike (*L. excubitor*), are parasitized regularly by Common Cuckoos (Nakamura 1990, Moksnes and Røskaft 1995). Some of those species are ejectors, and although the Northern Shrike has not been tested (Nakamura et al. 1998, Moskat and Fuisz 1999), Rothstein (2001) suggested that ejection in the Loggerhead Shrike may be an atavistic trait inherited from its common ancestor with other shrikes, nearly all of which are Old World species exposed to parasitic Common Cuckoos.

Likewise, Yellow-billed (*Pica nuttalli*) and Black-billed (*P. hudsonia*) magpies are ejectors and unsuitable cowbird hosts; therefore, they may have inherited ejection from Eurasian Magpies (*P. pica*) that eject cuckoo eggs in Eurasia (Soler et al. 1999, Bolen et al. 2000). Peer and Sealy (2004b) found that unparasitized populations of Great-tailed and Boat-tailed (*Q. major*) grackles may have retained egg ejection, the latter having retained it for as long as 800,000 years. Other grackles also have high

levels of ejection despite being rarely parasitized (Peer and Sealy 2004b).

Island Scrub-Jays (*Aphelocoma insularis*), Bohemian Waxwings (*B. garrulus*), American Robins (*Turdus migratorius*), and Yellow Warblers all demonstrate high levels of egg rejection in areas where there are no brood parasites (Peer et al. unpubl. data, Kuehn et al. unpubl. data). Island Scrub-Jays are endemic to Santa Cruz Island, which lacks cowbirds and is ~40 km off the coast of southern California, where cowbirds began to breed in the early 1900s (Rothstein 1994). They apparently inherited that behavior from their common ancestor with the Western Scrub-Jay (*A. californica*) and Florida Scrub-Jay (*A. coerulescens*), which are also unparasitized but demonstrate high levels of egg ejection (Fleischer and Woolfenden 2004, B. Peer et al. unpubl. data).

Bohemian Waxwings, American Robins, and Yellow Warblers in Alaska, beyond the range of the cowbird and cuckoos, show antiparasite behaviors at frequencies that are near or only slightly below those shown by conspecific or congeneric populations that are sympatric with cowbirds (Rothstein 1975a, Kuehn et al. unpubl. data, Peer et al. unpubl. data). Ejection in the Bohemian Waxwings is particularly significant, because nearly all of that species' range is allopatric with cowbirds. Its ejection behavior was likely inherited from its common ancestor with the Cedar Waxwing, an ejecter that is sympatric with and parasitized by cowbirds (Rothstein 1976a). By comparing mitochondrial DNA sequences between closely related species pairs (e.g. between the Cedar and Bohemian waxwings), we have been able to determine that ejection has been maintained in those hosts in the absence of brood parasitism at least since the end of the Pleistocene (~10,000 years) and possibly longer (Peer et al. unpubl. data).

In findings similar to ours, others have reported high levels of egg ejection by Shiny Cowbird hosts in the Caribbean despite the recent arrival of that cowbird, which indicates that the behavior may have been retained in those hosts from past interactions with brood parasites (Cruz et al. 1985, Post et al. 1990, Baltz and Burhans 1998). The reason for retention of ejection by those hosts is that the behavior likely becomes neutral in the absence of parasitism, because the only context in which birds have foreign eggs in their nest is brood parasitism.

Thus, in the absence of parasitism, the behavior may not be expressed and could remain neutral until a lineage is exposed to parasitism again (Rothstein 1990, 2001; Peer and Sealy 2004b).

Such results suggest that brood parasites and their hosts follow what has been termed a "single trajectory," whereby the community of actual and potential host species becomes increasingly resistant to parasitism over time because once they evolve those defenses, they tend to maintain them (Rothstein 2001). A parasite will use a host until the host evolves a high level of defense, and then it must switch to new hosts that will accept its eggs. If hosts maintain defenses in the absence of parasitism, as our data suggest, at some point in the coevolutionary "arms race" most available hosts will be well defended, and the parasite will have to evolve very specific adaptations to counter the defenses of a small number of host species. For example, to circumvent egg ejection, a parasite will be forced to evolve mimetic eggs to match those of a specific host or hosts that have similar-looking eggs. That will force the parasite to become more specialized. If progressively more hosts evolve defenses against parasitism and retain them, the pool of available acceptor hosts for the cowbird will decline. That has apparently occurred in the Common Cuckoo-host system, in which most hosts have evolved defenses against parasitism (Rothstein 1992). As a result, individual female Common Cuckoos have evolved specific egg types to match those of specific hosts (Brooke and Davies 1988).

If, on the other hand, hosts lose egg ejection behavior after they are no longer parasitized (e.g. because of host shifts by the parasite or changes in a host's or parasite's geographic range), the parasite could persist indefinitely by alternating from well-defended hosts to those that lack or have lost defenses. In other words, a parasite uses a host species until it ejects, switches to a new host until it ejects, and then switches either to another new host or back to old hosts that lost ejection in the absence of parasitism, in a series of never-ending coevolutionary cycles (Rothstein 2001).

Hosts could lose rejection in the absence of parasitism through genetic drift or through natural selection if they mistakenly eject their own oddly colored eggs. Those potential processes have led to suggestions that hosts often lose defenses in the absence of parasitism (Davies and Brooke 1989, Cruz and Wiley 1989). However, most hosts have

relatively uniform eggs, with little intraclutch egg variation, so natural selection against mistaken ejections is probably not a significant factor. The only host that appears to support the loss of egg recognition is the Common Grackle, which is very unusual in its high degree of intraclutch egg variation (Peer and Bollinger 1997a, b; Peer and Sealy 2004b). In most birds, eggs within a clutch appear similar to one another; but the last laid egg in Common Grackle clutches is sometimes distinctly different in appearance, often being much lighter in color and with less maculations than the other eggs (Peer and Sealy 2004b, S. I. Rothstein unpubl. data). Common Grackles are also unusual in that they are rarely parasitized by cowbirds and eject a low frequency of cowbird eggs (Peer and Bollinger 1997a, Peer et al. 2001, Peer and Sealy 2004b). Thus, it is possible that the Common Grackle was once parasitized more regularly and, in response, evolved a high frequency of ejection, after which the cowbird stopped parasitizing it and the Common Grackle lost most of its ejection behavior in the absence of parasitism because it ejected those oddly colored eggs (see Peer and Bollinger 1997a, Peer and Sealy 2004b for further details).

However, even if ejection declines in the absence of parasitism, evidence suggests that it can increase within a population rapidly, once selection from brood parasitism is renewed. The Village Weaver (*Ploceus cucullatus*) may have lost ejection after it was introduced from Africa to Hispaniola (Cruz and Wiley 1989), but ejection has increased rapidly in that population with the onset of Shiny Cowbird parasitism (Robert and Sorci 1999). Alternatively, it is also possible that Cruz and Wiley's (1989) experimental methods were divergent from those used in studies that showed high rejection in Village Weavers and were therefore not sufficient to demonstrate a loss of ejection in the population on Hispaniola (Rothstein 2001). Presumably, a lineage would eventually lose ejection in the absence of selection through drift alone, but such a loss may take so long that the lineage is likely to again encounter parasitism before the absence of ejection becomes fixed.

MANAGEMENT IMPLICATIONS OF RETENTION OF HOST DEFENSES

Because most hosts appear to retain defenses, host populations newly exposed to parasitism

are not necessarily defenseless and in need of cowbird control. Cowbirds have been in North America for up to 1 million years or longer (Rothstein et al. 2002), and they may have been more abundant and widespread when mammalian megafauna were extant (Rothstein 2004). Therefore, just about all passerine taxa, except forest-nesting species, have likely experienced parasitism in their history and may have retained those defenses after parasitism stopped.

Indeed, most endangered cowbird hosts have habitat preferences that suggest prehistoric contact with cowbirds, or conspecific populations with known overlap with cowbirds during historical time. Those birds nest in relatively open areas and also tend to desert parasitized nests, they include the Black-capped Vireo (*Vireo atricapilla*), Least Bell's Vireo (*V. bellii pusillus*), and Southwestern Willow Flycatcher (*Empidonax traillii extimus*; Graber 1961, Sedgwick and Knopf 1988, Tazik and Cornelius 1993, Budnik et al. 2001, Kus 2002). The one exception is Kirtland's Warbler (*D. kirtlandii*), which is within a lineage of mostly forest-breeding species (the wood warblers or Parulinae) and may have never experienced parasitism until cowbirds colonized its range during the late 1800s (Mayfield 1965). That species may be unique among those hosts in showing no defenses whatsoever toward cowbird parasitism (Hosoi and Rothstein 2000).

Cowbird control programs in which cowbirds are trapped and killed and eggs are removed from nests eliminate most selective pressure on hosts for defenses against parasitism. Although trapping and nest-manipulation programs meet their short-term goals by increasing productivity of endangered hosts (Kus 1999, Kostecke et al. 2005), they do not allow those hosts to incur costs that will lead to the initial evolution and fixation of anti-parasite behaviors. Ongoing control will lead to populations of hosts that require perpetual management, because they will never develop antiparasite behaviors. With the populations of many of those hosts—especially Kirtland's Warblers, Least Bell's Vireos, and Black-capped Vireos—increasing, it is time to consider scaling back control programs to determine whether hosts can defend themselves against parasitism. Rothstein (2004) has suggested that small populations are often parasitized more heavily

than large populations because the latter can swamp the parasite in a manner analogous to swamping of a predator when prey are clustered in time or space (e.g. Williams et al. 1993). Therefore, parasitism frequencies may decline significantly once populations become large.

For example, Least Bell's Vireos at Camp Pendleton experienced a 47% parasitism rate when there were only 27 pairs in the early 1980s (Griffith and Griffith 2000, Kus and Whitfield 2005), but now that there are $\geq 30\times$ as many Least Bell's Vireos (~800 pairs; Kus and Whitfield 2005), the cowbird population would likely have to show a 30-fold increase to continue to parasitize Least Bell's Vireos at a 47% rate. Likewise, the Black-capped Vireo population on Fort Hood has increased more than 20-fold since trapping began in 1988 (~85 to ~2000 pairs; Eckrich et al. 1999, Kostecke et al. 2005). Despite that, trapping has not been relaxed and even occurs during the nonbreeding season (Kostecke et al. 2005).

Allowing parasitism of—and, hence, renewal of selection pressure on—Black-capped Vireos, Least Bell's Vireos, and Southwestern Willow Flycatchers will allow antiparasite behaviors already present in those host populations to increase. For example, Least Bell's Vireos and Southwestern Willow Flycatchers desert parasitized nests—though in the case of Least Bell's Vireos, at a lower rate than their conspecific counterparts in the central United States, which have a longer history of parasitism (Parker 1999, Kus 2002). The situation with the Southwestern Willow Flycatcher is somewhat more complex, because it deserts parasitized nests as often as conspecifics with longer histories of contact with cowbirds (Rothstein et al. 2003, Sedgwick and Knopf 1988). There is strong evidence that nest desertion has a genetic component, even though it may be influenced by learning. Hosoi and Rothstein (2000) found that desertion was not correlated with parasitism, but rather with host habitat type. Hence, if selection is renewed and if population size and habitat are adequate, that behavior may spread through the population rapidly (see Rothstein 1975b). It is crucial to allow natural selection to take place—that is, to allow those vireos and flycatchers with defenses to produce more offspring so that, over time, the population becomes better defended against parasitism. Otherwise, those populations will forever depend on human intervention.

Rothstein et al. (2003) and Rothstein (2004) discuss additional reasons why cowbird control can sometimes be counterproductive to long-range conservation goals; for example, by distracting interest and funding from the most basic problem facing the cowbird hosts discussed here—namely, anthropogenic loss of habitat. Cowbird control was a wise management decision when all the endangered species we have cited above appeared to be on the brink of extinction, though it is not clear in some cases whether cowbird control was actually effective in boosting host population sizes. What is clear now is the wisdom of ceasing cowbird control, for at least a designated period, for taxa that have shown enormous population increases. Ceasing control for one to several years will not endanger the taxa, and such an action might demonstrate that control is no longer needed at all.

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CHAPTER 8

CONSERVATION SOLUTIONS FOR THREATENED AND
ENDANGERED COWBIRD (*MOLOTHRUS* SPP.) HOSTS:
SEPARATING FACT FROM FICTION

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ABSTRACT.—Brood parasitism by Brown-headed Cowbirds (*Molothrus ater*; hereafter “cowbirds”) reduces the reproductive output of individual hosts and has been the subject of considerable research and management activity. Many current management practices aimed at controlling parasitism are based on outdated perceptions. Among these are that cowbirds are increasing in range and abundance; cowbirds are relatively new to North America; cowbird parasitism reduces or limits population sizes of host species; new host populations are defenseless against parasitism; and cowbird control increases reproductive output and populations of hosts. Instead, cowbird numbers have declined significantly in recent decades. Cowbirds have been in North America for at least a million years, and their numbers likely peaked when mammalian megafauna were present during the Pleistocene. Thus, effects on hosts have occurred over a long period, and any recent extinction threats posed by cowbirds are likely attributable to anthropogenic changes. Because of this long history of contact with cowbirds, many hosts that nest in nonforested habitat have had long periods to evolve adaptations against parasitism, and evidence clearly demonstrates that they retain those defenses from past bouts of parasitism and, hence, are often well defended when parasitism is renewed. Cowbird parasitism is only one of many factors that can limit avian populations, and despite such factors, avian populations can still produce enough young to remain stable. There is no evidence that cowbirds are a serious threat to the survival of any passerines other than several taxa that are listed as federally endangered species. Cowbird control does not always translate into increased population sizes for those endangered species, and habitat loss is the most critical factor limiting their populations. Current management programs based on these outdated perceptions have shifted the focus away from the most critical issue threatening avian populations, namely anthropogenic habitat disturbance. A serious shortcoming of cowbird control programs is that they are open-ended; this is because local cowbird numbers in control areas are usually unchanged year after year as a result of extensive dispersal of new cowbirds into those areas. In some cases, control programs have become excessive and have been co-opted by special interests, particularly in Texas, where a broad statewide program to control cowbirds has been used to legitimize environmentally harmful actions that can hinder recovery of endangered species and affect avian diversity in general. We provide a series of questions that should be addressed before the initiation of cowbird control programs. Most importantly, we encourage managers to determine whether cowbirds are an important pressure on the host populations they oversee, whether resources used for control programs could have greater management benefits if used differently, and whether it is possible to define conditions that will indicate that annual cowbird control is no longer needed.

RESUMEN.—El parasitismo de cría por *Molothrus ater* reduce el éxito reproductivo de los individuos hospederos, por lo que ha sido el sujeto de considerable número de actividades de

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investigación y manejo. Muchas de las prácticas de manejo usuales que pretenden controlar el parasitismo se basan en percepciones anticuadas. Entre ellas, que *M. ater* está incrementando su rango de distribución y abundancia, que *M. ater* es relativamente nuevo en Norteamérica, que el parasitismo de *M. ater* reduce o limita los tamaños poblacionales de las especies hospederas, que las nuevas poblaciones de hospederos están indefensas contra el parasitismo, y que el control de *M. ater* aumenta el tamaño y la productividad de las poblaciones de los hospederos. Sin embargo, el número de *M. ater* ha declinado significativamente en décadas recientes. *M. ater* ha estado en Norteamérica por al menos un millón de años, y sus números pareciera que tuvieron un máximo en el Pleistoceno, cuando la megafauna de mamíferos estaba aún presente. En consecuencia, los efectos sobre sus hospederos han existido durante un largo período, y cualquier riesgo de extinción reciente propuesto que involucrara a *M. ater*, podría ser atribuido a cambios antropogénicos. Debido a esta larga historia de contacto con *M. ater*, muchos hospederos de hábitats no boscosos han tenido un largo período para desarrollar adaptaciones en contra del parasitismo. Además, existe evidencia clara de que retienen aquellas defensas desarrolladas durante eventos pasados de parasitismo y que, frecuentemente, están bien defendidos cuando el parasitismo se renueva. El parasitismo por *M. ater* es sólo uno de los numerosos factores que pueden limitar las poblaciones de aves, y a pesar de dichos factores, estas poblaciones pueden aún producir suficientes juveniles como para permanecer estables. No existe evidencia de que *M. ater* sea una seria amenaza para la supervivencia de ningún Passeriforme excepto aquellos pocos taxa que están en la lista de especies en peligro a nivel federal. El control de *M. ater* no siempre se traduce en un incremento en el tamaño poblacional de aquellas especies en peligro, y la pérdida de hábitat es el factor más crítico que limita dichas poblaciones. Los programas de manejo usuales basados en aquellas percepciones anticuadas han desviado el foco alejándolo del más crítico problema que amenaza las poblaciones de aves, nos referimos a los disturbios antropogénicos del hábitat. Un serio defecto de los programas de control de *M. ater* es que no tienen fin. Esto es debido a que los números de *M. ater* en áreas de control se mantienen prácticamente constantes año a año como resultado de una amplia dispersión de nuevos individuos hacia dichas áreas. En algunos casos, los programas de control se han convertido en excesivos y han sido adoptados por intereses especiales, particularmente en Texas, donde un amplio programa que abarca todo el estado para el control de *M. ater*, ha sido utilizado para legitimar prácticas ambientales dañinas que pueden obstruir la recuperación de especies en peligro y afectar la diversidad de aves en general. Nosotros proponemos una serie de cuestiones que deben ser abordadas antes de iniciar los programas de control de *M. ater*. Más aún, alentamos a los responsables del manejo para que determinen si los *M. ater* son una presión importante sobre las poblaciones de hospederos que ellos vigilan, si los recursos usados en los programas de control de *M. ater* podrían resultar en manejos más beneficiosos al ser invertidos en forma diferente, y si es posible definir las condiciones que indiquen que el control anual de *M. ater* no es más necesario.

THE BROWN-HEADED COWBIRD (*Molothrus ater*; hereafter "cowbird") is one of the most frequently cited species in modern North American ornithology. Most of the citations in the 1900s involved studies directed at the breeding biology of other species but that became cowbird studies when nests were parasitized. There were relatively few studies directed at cowbirds *per se* until the 1970s—perhaps, in part, because of Herbert Friedmann's (1929) landmark cowbird monograph, the most comprehensive single-species study written to that date, which may have discouraged further inquiry. Most cowbird research in the 1970s and 1980s dealt with basic research on the evolutionary and behavioral questions posed by brood parasitism (e.g. Rothstein 1975, 1978, 1982).

There was very little attention paid to cowbirds as a conservation issue, except for work involving the Kirtland's Warbler (*Dendroica kirtlandii*) in Michigan and the Least Bell's Vireo (*Vireo bellii pusillus*) in California (Mayfield 1960, 1973, 1977, 1978; Goldwasser et al. 1980). Discussion relating parasitism to the decline of those two taxa dates to the 1920s. The first cowbird control program began in 1972 to aid the Kirtland's Warbler after a population decline from 1961 to 1971 coincided with an apparent increase in levels of cowbird parasitism (Mayfield 1972, Shake and Mattsson 1975).

In the 1980s, three publications focused conservation attention on cowbirds. Brittingham and Temple (1983) presented evidence that cowbirds had increased throughout the 1900s and

that forest birds nesting near edges suffered high rates of cowbird parasitism. Terborgh (1989) influenced conservation policy by presenting evidence that many North American passerines were declining, not just a few endangered species, and that the declines were attributable to four causes: (1) loss and degradation of breeding habitat in North America, (2) loss and degradation of wintering habitat in the Neotropics, (3) increases in nest predation, and (4) increases in cowbird parasitism. Finally, Robinson (1992) showed that most nests of some species nesting in small woodlots in Illinois were parasitized. In particular, data on Wood Thrush (*Hylocichla mustelina*) showed 100% parasitism in some populations, and indicated that most Wood Thrush populations in central Illinois were reproductively failing.

Those three studies helped stimulate an international symposium on migrant birds in 1989, where further evidence of population decline, reproductive failure, and cowbird parasitism was presented (Hagan and Johnston 1992). This galvanized attention on the threat posed by cowbirds to North American passerines and resulted in a marked increase in cowbird research in the 1990s. Although citations suggest that the cowbird was a frequently studied North American passerine from 1969 to 1989 (Fig. 1), it became the most frequently cited species from 1990 to mid-2003, when cowbird research expanded greatly.

This intense focus on cowbirds and conservation led to the first national cowbird symposium in 1993, the results of which were published in Smith et al. (2000). Results of a cowbird workshop in 1997 appeared in Morrison et al. (1999). The present monograph is the product of a symposium on cowbirds held at the American Ornithologists' Union meeting in Champaign-Urbana, Illinois, in 2003. This symposium focused on the ecology of cowbird control, with papers that mixed new findings on natural factors that control cowbird populations with studies of the actual results of cowbird control on the reproductive success of threatened and endangered species.

Here, we synthesize current information about the role of cowbird control in bird conservation, starting with common misconceptions about cowbird ecology and ending with a list of factors that should be considered as part of all cowbird control programs.

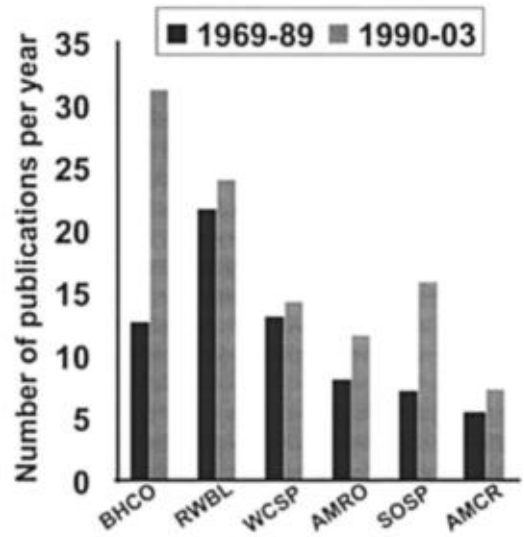


FIG. 1. Number of publications per year listed by Biosis for two time periods for the Brown-headed Cowbird and five other commonly studied songbird species. Note that the cowbird has shown the largest increase since 1990 but was one of three most studied passerines before then (1969–1989). Species abbreviations are as follows: BHCO = Brown-headed Cowbird (*Molothrus ater*); RWBL = Red-winged Blackbird (*Agelaius phoeniceus*); WCSP = White-crowned Sparrow (*Zonotrichia leucophrys*); AMRO = American Robin (*Turdus migratorius*); SOSP = Song Sparrow (*Melospiza melodia*); AMCR = American Crow (*Corvus brachyrhynchos*).

FACT AND FICTION ABOUT COWBIRDS

Recent work on cowbirds has shown that some major beliefs that heightened the cowbird's profile as a potential threat to North American passerines are simply not true or have much less validity than was previously assumed. Below, we discuss the merits of seven commonly held assumptions about cowbirds.

(1) *Cowbirds are increasing their range and abundance.*—Cowbirds colonized major parts of North America between 1900 and 1960. Those areas include California, Oregon, Washington, southern British Columbia west of the crests of the Sierra and Cascades mountain ranges, the Maritimes of Canada, and the southeastern United States (Rothstein 1994). Colonization of the southeast continues today but at a very slow rate, and expectations that the Shiny Cowbird (*M. bonariensis*) would invade North America

via Florida (Cruz et al. 1998, 2000) have not materialized (Smith and Sprunt 1987).

The perception of rising cowbird numbers is based primarily on Brittingham and Temple's (1983) suggestion that Christmas Bird Censuses show increasing cowbird populations throughout the United States during the 1900s. However, Brittingham and Temple's (1983) data (their fig. 1) did not show abundance but showed instead the percentage of Christmas Bird Counts in 11 southern states for which cowbirds were reported as a function of time, a result subject to a number of confounds. For example, increased numbers of count participants could result in increases in a species' detections, even if the species maintained a constant abundance. Breeding Bird Survey (BBS) data show that cowbirds declined 1.2% per year in North America when averaged across the years 1966–2003 ($P < 0.01$; Sauer et al. 2004). The relative abundance of cowbirds in 2003 (~10 individuals per BBS route) was only 61% of the abundance in 1966 (~16.5). Breeding Bird Survey data show that even states in the southeast, where cowbirds are still colonizing new areas, are showing only very gradual increases in cowbird abundance. Cowbirds have declined greatly in the other areas colonized in the 1900s, such as the Pacific Northwest and the Canadian Maritime Provinces.

For the six states that currently have cowbird control programs, cowbird abundance has been constant in two (California and New Mexico) but has declined in the other states (Fig. 2). The latter are particularly interesting because the declines started before cowbird control programs were initiated. For example, cowbird control began in Texas in 1988 (Summers and Norman 2003), but by that time cowbird abundance had declined to 12 per BBS route from its Texas peak of 19–20 birds per route from 1967 to about 1977 (from data in Sauer et al. 2004). So cowbird control may have been addressing a problem that had already been partially resolved by a major decline in cowbird numbers. Breeding Bird Survey data on cowbird trends were first presented at the 1993 cowbird workshop, but the notion that cowbirds are still increasing persists, despite a steady decline over the succeeding decade. Although cowbirds have declined in most parts of North America, there are a small number of areas where they are increasing, such as the Central Valley of

California, and cowbird effects in these latter regions may require closer scrutiny.

(2) *Cowbirds have increased their range in the past 250–300 years.*—Cowbirds have certainly increased their range within the past 250–300 years, following a period in which they were mostly restricted to the Great Plains, where they associated with roaming bison (*Bos bison*) herds. However, cowbirds were probably found in isolated pockets in eastern North America. After Europeans had colonized North America and had begun clearing the eastern forests, the cowbirds' eastward expansion progressed rapidly (Friedmann 1929, Mayfield 1965). They colonized the eastern one-third of the United States by the early 1800s, the Canadian Maritime provinces by the 1900s, the southeastern United States by the late 1950s and early 1960s, the Pacific Slope of the United States by the 1900s, and northwestern Canada by the 1950s (Rothstein 1994).

The notion that cowbirds are newcomers to the eastern one-third of North America in the very recent past is questionable because the extensive, mostly unbroken forests that early European explorers found developed only after Europeans had made contact with Native Americans. Those contacts led to epidemics of diseases, such as smallpox, that spread rapidly across much of North America, resulting in a reduction of Native American populations, by some estimates, to 15% or less of their original size decades or even centuries before Europeans had reached much of the continent (Dobyns 1983, Thornton 1987). Native Americans routinely burned parts of the eastern forests for agriculture and to increase the abundance of game, such as bison, deer, and elk (Pyne 1997). But after the Native American population was severely reduced, their ecological effects were likewise reduced, and forests became denser and more continuous. So it is likely that cowbirds were in eastern North America when Europeans first arrived. In fact, a number of other grassland bird species were present in the East (Askins 1993, 2000), which also makes it likely that cowbirds are not newcomers to eastern North America.

(3) *Cowbirds are relatively new to North America.*—These recent range expansions, and perhaps the fact that most extant cowbird species are in the Neotropics, have created the perception that cowbirds are completely new to much of North

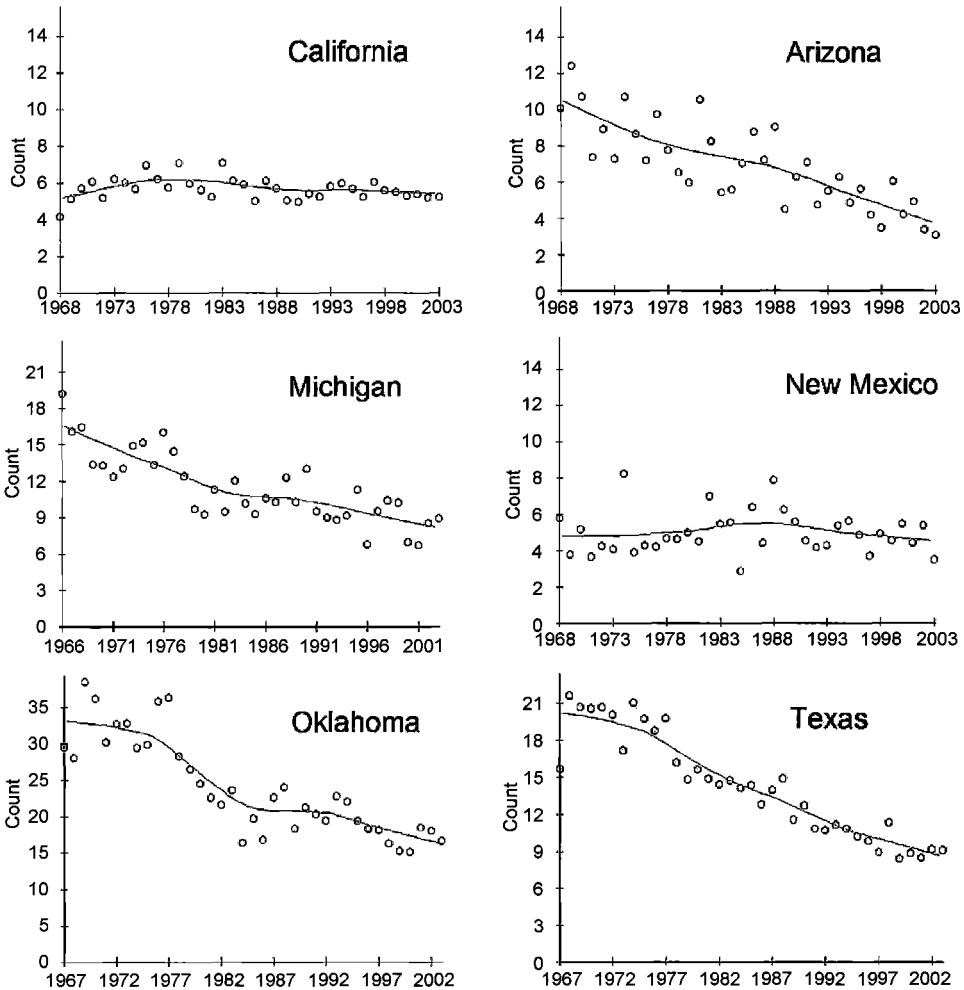


FIG. 2. Relative abundance trends for the Brown-headed Cowbird in six states with cowbird control programs, based on Breeding Bird Survey data (Sauer et al. 2004). Note that cowbird abundance has remained fairly constant in California and New Mexico but has declined in the other four states and that these declines began before the control programs in each case. The axes differ among states because of different levels of abundances across states and because the Breeding Bird Survey began later in western states than in eastern ones (1966 vs. 1967 or 1968).

America. If cowbirds really are new to parts or all of North America, they could pose significant threats to our avifauna because processes that can lead to widespread songbird extinctions over relatively rapid ecological time scales may now be occurring. In addition, we would expect host species to be relatively defenseless against cowbird parasitism if cowbirds are recent arrivals to North America, because they would not have had time to evolve antiparasite adaptations.

However, cowbirds are ancient residents of North America in terms of ecological time scales. DNA sequence data (Lanyon 1992, Lanyon and Omland 1999, Rothstein et al. 2002) indicate that the Brown-headed Cowbird diverged from the Neotropical Shiny Cowbird, its sister species, about a million years ago. It is likely, then, that cowbirds have been present in North America for at least a million years, because it is probable that allopatric speciation is responsible for

cowbird diversity. Additionally, cowbird fossils dating to 10,000 to 500,000 years ago have been found in California, Oregon, New Mexico, Texas, Kansas, Florida, and Virginia (Lowther 1993). There are also Pleistocene fossils of two extinct blackbirds that are thought to be cowbirds (Pielou 1991). Thus, North America's parasitic bird fauna may be less diverse today than in the recent geological past.

A widespread, abundant, and, perhaps, more diverse cowbird community is consistent with the cowbird's affinity for large mammals and the fact that North America supported perhaps the world's greatest diversity of large mammals only 15,000–20,000 years ago. There were bison, oxen, horses, llamas, camels, mammoths, and mastodons. All these large browsing and grazing mammals must have made North America into a veritable paradise for cowbirds. Even in the absence of fossil evidence for cowbirds and their likely mammalian associates, it would be very risky to use the cowbird's distribution at the time Europeans began to describe North America as an indicator of its historical distribution. One of the most persistent trends that arises from the study of Pleistocene plants and animals is that present-day distributions are usually poor guides to distributions that prevailed in the recent geological past (Pielou 1991). The inescapable conclusion from the fossil record and cowbird biology is that cowbirds have been widespread across North America for a long time.

It is clear from Pleistocene and more recent history that cowbird effects on hosts have occurred over a long period and that all species that could not sustain any parasitism whatsoever went extinct long ago. Therefore, any threats that cowbirds pose today must be attributable to recent ecological changes and almost certainly to anthropogenic factors.

(4) *Cowbird parasitism reduces or limits population sizes of host species.*—Avian populations can be limited by many factors in addition to brood parasitism, including breeding and wintering habitat, predation, disease, lack of food, or adverse weather (Newton 1998). Despite these limits, avian populations can often produce enough young to maintain stable populations locally; in addition, many populations are regulated by regional source-sink dynamics, wherein overproduction of young on some sites maintains populations at sites

with low reproductive success (Donovan et al. 1995). Thus, effects from brood parasitism will not necessarily endanger a local population, unless the losses affect a substantial portion of the population. Hosts that are threatened by complete extinction because of cowbirds are those that have had significant reductions in their populations because of habitat loss, which can exacerbate the effects of cowbird parasitism by leaving a small number of populations that are all heavily parasitized. Another factor to consider is that small fragmented populations in some landscapes may be limited by both cowbird parasitism and nest predation. For example, although cowbirds parasitized nearly 100% of Wood Thrush nests in small Illinois wood lots, most of those nests failed because of nest predation (Robinson 1992). So those populations would be sinks, even without cowbird parasitism. Because cowbirds are native to North America, they might easily have limiting effects on some host species or populations, as may be the case with the widespread Song Sparrow (*Melospiza melodia*; Smith et al. 2002). But as pointed out above, any extinctions caused by cowbird parasitism alone would have occurred many thousands of years ago.

(5) *New host populations are defenseless and therefore prone to extinction.*—Mayfield (1965) and Reed (1999) have argued that "new" host populations have not evolved defenses and may be in need of cowbird control. However, because cowbirds were probably more common in the past and most songbird lineages have experienced parasitism, we would expect them to have evolved antiparasite behaviors. But what happened to those defenses as the cowbird range contracted after the Pleistocene? It is often assumed that adaptations are lost once they no longer have any use. However, Peer et al. (2005) show that defenses against brood parasitism usually occur only in response to parasitism and are usually retained for long periods without parasitism because they are essentially cost free when not expressed. Passerine populations that occur in the absence of brood parasites demonstrate levels of parasitic egg rejection similar to levels expressed by conspecific or congeneric populations sympatric with parasitic birds (Bolen et al. 2000, Rothstein 2001, Peer and Sealy 2004a, Peer et al. 2005). Likewise, Hosoi and Rothstein (2000) found that a species' nest desertion tendency is related to the costs it

suffers from parasitism and to its habitat type (with forest vs. nonforest serving as an indicator of past or present sympatry with cowbirds). There is little or no overall trend indicating low levels of defense in populations that have only recently been exposed to cowbirds. Besides adding to our evidence that cowbirds had a much broader distribution and affected many songbird populations in the past, presence of defenses in populations recently exposed to cowbirds within historical times also indicates that these defenses are not costly to maintain in the absence of parasitism. This clearly suggests that not every newly exposed host population is defenseless and in need of cowbird control.

Among endangered hosts that are the subject of cowbird control, only Kirtland's Warblers demonstrate a virtual lack of defenses against parasitism. They nest in forests and may have just come into contact with cowbirds within the past 250–300 years. By contrast, the other three endangered host species for which there is extensive cowbird control—the Black-capped Vireo (*Vireo atricapilla*), Least Bell's Vireo, and Southwestern Willow Flycatcher (*Empidonax traillii extimus*)—all nest in open areas and likely have had much longer contact with cowbirds, which enabled them to evolve antiparasite behaviors (Rothstein et al. 2003). Indeed, a population of Willow Flycatchers that has become parasitized only recently within historical times demonstrates higher levels of defenses against parasitism than some populations that have been parasitized for longer periods (Rothstein et al. 2003). Despite the widespread occurrence of nest desertion and the retention of it and egg rejection in host populations that no longer experience parasitism, it is worth noting that very few North American species show egg recognition behavior (Rothstein 1975, Peer and Sealy 2004b), which is the most efficient defense against brood parasitism. The scarcity of this defense means that cowbird parasitism can be the final cause of extinction for some species reduced to small fragmented populations by habitat loss.

(6) *Cowbird parasitism reduces reproductive output of individual hosts.*—Despite a recent suggestion that cowbirds may behave altruistically by allowing host young to survive because more nestlings lead to higher feeding rates (Kilner et al. 2004), reduction in reproductive output of individual hosts is one item of conventional wisdom that holds true. Cowbird parasitism

and associated host egg removal invariably reduce the reproductive success of hosts, though the costs vary. Hosts smaller than cowbirds and those with relatively long incubation periods are affected the most (reviewed in Peer et al. 2005; Lorenzana and Sealy 1999).

(7) *Cowbird control increases reproductive output and populations of hosts.*—Although cowbird control always increases the reproductive output of heavily affected host populations, this increase in output does not always lead to an increase in numbers of adult breeders. The Kirtland's Warbler was the subject of the first cowbird control program (Shake and Matsson 1975), initiated in 1972 after a census in 1971 revealed only 201 singing males (Mayfield 1972), compared with ~500 in 1961. Over the next 18 years, cowbirds were removed from the Kirtland's Warbler breeding grounds; however, the number of singing males remained at ~200. Numbers of males did not increase significantly until 1990, when 776 singing males were recorded (Weinrich 1996); in 2002, 1,050 males were recorded (M. E. DeCapita pers. com.). The increase followed an out-of-control prescribed burn in 1980 at Mack Lake that burned 10,500 ha. In the process, a large amount of suitable habitat was created for this habitat specialist that nests in jack-pine (*Pinus banksiana*) forests 6–24 years after fires (DeCapita 2000). The initial increase in numbers was entirely attributable to more individuals breeding at the Mack Lake site, which suggests that habitat was the most important factor limiting population growth. Wintering habitat may also have been limiting, and it too increased around the time of the Mack Lake burn (Haney et al. 1998; but see Sykes and Clench 1998).

Cowbird control was believed to be a good idea in 1971, and though it has been suggested that cowbird control saved the Kirtland's Warbler from extinction (Terborgh 1989, Kepler et al. 1996), there is no conclusive evidence confirming this suggestion. For example, Kirtland's Warblers did not decline in the absence of cowbird control from 1971 to 1972, and it requires an odd coincidence to suggest that the Kirtland's Warbler was headed toward extinction only to be saved by cowbird control just when its population happened to be at the carrying capacity it would have for the next 18 years. Parsimony would suggest that the Kirtland's Warbler population was already stabilized at carrying capacity when cowbird control began.

There have also been no apparent increases in Southwestern Willow Flycatcher populations as a result of cowbird control at seven Arizona sites after 5–8 years of control and at three California sites after >10 years of control (Kus and Whitfield 2005), even though the number of young produced has increased (Rothstein et al. 2003). Southwestern Willow Flycatchers nest in riparian habitat, most of which has been lost in the Southwest (U.S. Fish and Wildlife Service 2002), so lack of suitable habitat may be limiting this species.

Unlike Kirtland's Warblers and Southwestern Willow Flycatchers, populations of Least Bell's Vireos increased rapidly following initiation of cowbird trapping (Griffith and Griffith 2000). However, the population increase began before trapping started, and a key population continued to decline despite cowbird control efforts (Rothstein and Cook 2000). Black-capped Vireos also increased, likely because of cowbird control, but unlike other federally endangered hosts, Black-capped Vireos occur within the pre-European center of cowbird abundance. Clearly, this host has coexisted with cowbirds in recent times, which suggests that control was required because of human-induced factors. Although the large population increases in both Black-capped and Least Bell's vireos are sometimes attributed to cowbird control alone (Griffith and Griffith 2000, Kostecke et al. 2005), they have also benefited from increases in habitat. For example, extensive wildfires on Fort Hood in February 1996 (Goering 2000) resulted in a large increase in Black-capped Vireo habitat (Kolozsar and Horne 2000), the result being that by 2003, Black-capped Vireo abundance was higher on the 1996 burn areas than on other study areas on Fort Hood (Cimprich 2003).

JUSTIFYING COWBIRD CONTROL: A HIERARCHICAL APPROACH

POTENTIAL NEGATIVE EFFECTS OF COWBIRD CONTROL

There seems little doubt that cowbird control has had population-level benefits for some endangered host species, particularly Black-capped and Least Bell's vireos. This has led many people to believe that because cowbird control is sometimes beneficial and is relatively easy to do, it should always be applied when

a host is affected by parasitism. We have even heard it suggested that if control does not aid a targeted host population that is at risk, reducing cowbird numbers will help some birds somewhere (S. I. Rothstein pers. obs.). Such views ignore brood parasitism as a natural process that occurs on every continent save Antarctica. No one would argue that we should blithely decide to adopt a policy of killing snakes and accipiter hawks because reduction of those predators is sure to aid songbirds. Just as removal of those predators could have unanticipated negative effects on biodiversity and ecosystem functions, so too could the wholesale removal of cowbirds as suggested by some (Ortego 2000), who have advocated killing large numbers of cowbirds concentrated at huge winter roosts. Cowbirds might limit, for example, the populations of host species that are particularly good competitors and that might otherwise threaten the survival of less-competitive passerines. We suggest that many people are ready to kill off cowbirds at a moment's notice because they apply human behavioral standards to an animal that makes its living by killing someone else's young (i.e. they simply do not like cowbirds).

On the other hand, we must accept that any killing is unethical to some people. Therefore, an inadequately justified control program that attracts attention could create a public opinion backlash that could jeopardize control programs that are worthwhile. Those of us interested in the recovery of endangered host species can only consider ourselves lucky that cowbird control has not yet come across the radar screen of animal-rights activists. These individuals are against any killing of animals, even if it is essential to save endangered species, as in the program described in Rothstein (2004) that involved killing non-native black rats (*Rattus rattus*) that were threatening seabirds on one of California's Channel Islands.

Although there are good reasons to doubt the wisdom of cowbird control programs that simply kill cowbirds for the benefit of hosts in general, it may make good sense to control cowbirds when there is a rare host species whose survival is endangered by parasitism. But here, too, we see good reason for careful deliberation before cowbird control programs are initiated, because unfettered control can have serious negative consequences that may retard the recovery of an endangered host. The most serious problem with

a poorly justified cowbird control program comes from the fact that funds for endangered species recovery are severely limited. Funds expended on control programs often mean fewer funds directed at more critical management issues, such as habitat increase or other issues that may be far more important than cowbird control. This is especially critical when cowbird control becomes a routine part of the management toolbox for an endangered species that experiences widely varying rates of cowbird parasitism on different populations. For example, Southwestern Willow Flycatchers experience very different rates of parasitism in different areas, yet cowbird control was started, in some cases, without collection of baseline data on parasitism rates (Rothstein et al. 2003). Part of the problem is that people like active attempts to deal with issues. Cowbird control is active, and the numbers of cowbirds killed can become a surrogate for real measures of progress, such as increasing numbers of hosts. For example, articles on the internet touting the success of a program in Texas that encourages private landowners to trap and kill cowbirds to aid songbirds have titles like "Cattle and Songbirds Live in Harmony" (Krause 2002) and measure the success of the program in terms of cowbirds killed. This program requires no assessment of threats to songbirds in areas affected by the landowners' cowbird control nor any follow-up to determine benefits to host populations. In fact, when such articles discuss benefits, they misleadingly refer to increases in Black-capped Vireos that preceded the private-landowner trapping program. Although every cowbird killed could be beneficial in some situations, a facile quantitative measure of success, like numbers of cowbirds killed, decreases the incentive for examination of the ultimate measure of success, which is the extent to which numbers of a targeted host species increase.

To exacerbate things, interests with clear profit motives, such as ranchers and developers whose activities damage or destroy habitat, often have strong lobbies that advocate for their actions and for using cowbird control as mitigation for those actions. By contrast, there is no profit-motivated lobby calling for a reduction of cowbird control or a more careful analysis of its need. Ironically, the availability of cowbird control as a putative mitigation measure for negative effects on habitat can actually facilitate habitat loss or degradation.

The issue of profit also comes into play in another manner, because a great deal of cowbird control is done by private contractors such as consulting firms. As is typical of businesses, these firms advocate the value of their product, namely cowbird control. There is nothing wrong with private individuals profiting from an action, such as cowbird control, that the government deems beneficial, but evidence for the benefits should ideally come from individuals who do not profit from the control, and often that is not the case. Indeed, evidence that cowbird control has benefited an endangered host at the population level should be subjected to peer review, yet there is not a single paper clearly showing population-level benefits of cowbird control in a peer-reviewed journal.

Even when cowbird control is done by non-profit nongovernmental organizations, the money flowing into the organization for control efforts can create an incentive to continue cowbird control indefinitely. A similar situation may prevail even if the control program is run by a governmental agency, which may be reluctant to give up its line-item funds used to control cowbirds. It is hard to document the unimpeded momentum that cowbird control programs assume, because agencies are not going to admit that there is an incentive to maintaining their budgets at existing levels and private for-profit contractors who control cowbirds are unlikely to assess whether their services are still needed. But our discussions with people involved in cowbird control make it obvious that little or no serious thought is given to cessation or lessening of control efforts. The unstoppable nature of control programs is sometimes even stated explicitly, as in the draft recovery plan for the Least Bell's Vireo (U.S. Fish and Wildlife Service 1998), which proposes cowbird control in "perpetuity." In fact, no major cowbird control program has ever been ended (there are some minor ones that ran out of money).

Yet another negative consequence of cowbird control is that trapping invariably catches large numbers of nontarget species. Griffith and Griffith (1994), for example, reported 8,453 captures of ~1,500 individuals of nontarget species during a single year of cowbird trapping at Camp Pendleton. That can be detrimental, because species other than cowbirds have higher mortality rates in traps and can suffer breeding failure because of time spent away

from their nests. Lastly, a potential negative effect of overuse of cowbird control is the development of "resistance." Cowbird trapping is a potent selective pressure, and any trait that makes it less likely for cowbirds to enter traps will spread rapidly. Cowbirds may also learn to avoid the decoy traps used in control programs, as one of us (S.I.R.) has seen with the development of alarm responses to Potter traps. We have also found that some cowbirds can escape from decoy traps, and this too is a trait that may spread more rapidly as trapping becomes more widespread. Cowbird trapping is a worthwhile management tool, but its overuse may make the development of resistance more likely and potentially negate its usefulness when cowbirds really do need to be controlled.

The aforementioned private-landowner cowbird control program in Texas is the most egregious example of the negative effects of a single-minded focus on cowbirds. It began in the late 1990s at the initiative of the Central Texas Cattlemen's Association (CTCA), which has exclusive and free grazing rights on Fort Hood. The CTCA developed the program during a period when its grazing rights were in danger of being restricted or eliminated because of the results of research (Cook et al. 1998) sponsored by Fort Hood. Black-capped Vireos had already increased after a decade or so of cowbird trapping, but Cook et al.'s (1998) study of grazing and cowbirds led them to conclude that "The need for [cowbird] trapping [at Fort Hood] is largely a result of a continuous and loosely regulated grazing system on the installation." Instead of limiting grazing, CTCA proposed to aid Fort Hood's conservation program by encouraging its members and others to kill cowbirds outside Fort Hood because some cowbirds likely feed on private land near the fort. This proposal developed into a state-sponsored partnership with the Texas Parks and Wildlife Department (TPWD) that defused efforts to address grazing problems on Fort Hood. The partnership program has now spread to other parts of Texas and requires a minimal amount of initial training but no assessment of whether the cowbirds being trapped affect sensitive bird populations, no follow-up as to whether local bird populations change as a result of cowbird trapping, no recordkeeping as to number of cowbirds killed and number of nontarget species caught and possibly harmed in cowbird

traps, and no follow-up as to whether participants are correctly distinguishing between cowbirds and nontarget species.

The program has been featured in a number of online articles that tout the benefits of partnerships between government and private parties and the compatibility of grazing and conservation. These articles, a public-relations bonanza for ranchers, falsely credit the increased numbers of Black-capped Vireos to the private-landowner trapping program. They further mislead the public by suggesting that it is cowbirds and not anthropogenic habitat loss that is the real problem. To make matters worse, the articles omit mention that grazing can have major detrimental effects on the environment, especially when it is done at levels that are too high. There is an extensive literature on the negative effects of grazing on western landscapes (e.g. Belsky 1992, Fuhlendorf and Smeins 1997); by focusing only on cowbirds, the articles give the impression that cowbird control negates the only negative effect of grazing. Besides the extensive literature on grazing from throughout the United States, research on Fort Hood itself shows detrimental effects on habitats, such as decreased vegetation cover (Sanchez et al. 2000). Keddy-Hector (2001) suggests that grazing interests have inflicted a range of other negative effects on Fort Hood. He argues that "habitat improvement" plans for the base increase acreage suitable for grazing by destroying habitat of the Golden-cheeked Warbler (*Dendroica chrysoparia*), a second endangered passerine on Fort Hood; that grazing damages archaeological sites and greatly increases rates of soil erosion; and that cattle interfere with military training operations and are a hazard to public safety because they cause motor-vehicle accidents. Keddy-Hector (2001) suggests that catering to grazing interests means that "Cows and cow people win. Our military, the general public, endangered species, water quality, and game and fish and wildlife lose." To the extent that Keddy-Hector's characterization of the situation is accurate—and much of what he states is backed up by Fort Hood's own data—it is all made possible by the fact that it is easy to trap and kill cowbirds. Thus, although cowbird control negates one of the detrimental consequences of grazing (i.e. an increase in cowbirds), the ease of control deflects attention from the other detrimental consequences of grazing.

IMPORTANT FACTORS TO CONSIDER BEFORE
INSTITUTING COWBIRD CONTROL

As scientists, we would like to think that our management is science-based. Ideally, research should separate those habitat and demographic conditions that call for cowbird control from those for which control is not necessary. We list below a set of questions that any manager contemplating a cowbird control program should ask. Our questions are based on recommended management actions in the recently completed recovery plan for the Southwestern Willow Flycatcher (U.S. Fish and Wildlife Service 2002). This plan is one of the most thorough for any endangered species and the most in-depth plan for a passerine.

(1) *Am I legally compelled to control cowbirds?*—Part of the problem with the excessive focus on cowbird control in states like Texas and California is legal in nature. The Endangered Species Act (ESA) mandates mitigation for harmful effects inflicted on endangered species, including harm done to a species' habitat. Cowbird control is a commonly instituted mitigation measure in southern California, but it is mandated in such a routine manner that there is little attempt to determine whether it is really needed. Cowbird control is commonly mandated for any actions that harm riparian habitat, regardless of whether the affected habitat could or does support an endangered species. Although such mitigation appears to satisfy the ESA, it may do nothing to aid endangered species. In such cases, the ready availability of cowbird control as a mitigation measure means that other, more effective actions, such as habitat preservation or restoration, may not be mandated and that cowbird control can be used to legitimize habitat loss. When this happens, control is clearly detrimental to recovery efforts.

(2) *Are cowbirds the proximate problem limiting a host's population?*—Before undertaking cowbird control, one should intensively study the reproductive behavior and demography of the focal species. For some species, cowbird parasitism is obviously not the proximate limiting factor, and for them, cowbird control, or at least control with no other action, is not a suitable remedy. For other species, such as the Southwestern Willow Flycatcher, cowbird parasitism may be a problem in some populations but not in others.

(3) *What are the demographic thresholds that should trigger cowbird management for local populations?*—Cowbird control should be instituted only after baseline data show parasitism rates to be above a critical level (U.S. Fish and Wildlife Service 2002). This is especially critical for some endangered species that experience very different rates of parasitism in different parts of their range. Smith (1999) recommended that management should be considered if parasitism is >60% for two or more years but also discussed some considerations that would lower or raise this threshold. For example, he recommended that the critical parasitism level for management considerations be lowered to >50% for species listed as threatened or endangered. Rothstein et al. (2003) recommended that cowbird control should be considered for endangered species such as the Southwestern Willow Flycatcher if parasitism on a local population exceeds 20–30% for two or more years (see also U.S. Fish and Wildlife Service 2002). However, Rothstein et al. (2003) also recommended applying this guideline with flexibility, considering data on local populations (e.g. current population trends). For example, parasitism rates of 30% or even higher might not have warranted cowbird control for a large Southwestern Willow Flycatcher population in New Mexico that grew between 1997 and 1999 despite parasitism rates of 11–27%. Although monitoring nests to collect baseline data on parasitism rates can be costly, it can save funds in the long run if the data show that control is not necessary. Source-sink dynamics is another consideration that calls for flexibility. For example, a sink population that experiences high parasitism rates in a small habitat patch might still be a sink even after cowbirds are eliminated, because of the problems experienced by small populations with extensive edge effects. Any cowbird management efforts for such a population might be a waste of resources if there are healthy source populations.

(4) *What are the explicit goals of a cowbird control program?*—If a cowbird control program is initiated, we recommend development of explicit goals that define conditions that will end the control program and periodic (3–5 years) peer reviews that judge the program's efficacy. Because current cowbird control programs are not associated with clear increases for at least one high-profile endangered host,

the Southwestern Willow Flycatcher, it may be advisable, in some cases, to design control programs as experiments that include critical assessments of efficacy through comparison of host population trends with and without cowbird control (U.S. Fish and Wildlife Service 2002). Because enlarged host populations may experience lowered levels of parasitism, even in the absence of cowbird control, managers should re-evaluate the need for continued cowbird control if a host population has increased. Analyses of the results of cowbird control programs should proceed in a scientific manner by considering alternative explanations for increases in host populations after cowbird control was initiated. Typically, such analyses attribute the increases entirely to cowbird control, even though all three endangered species that have increased after cowbird control began (albeit 18 years later in the case of the Kirtland's Warbler) also experienced large increases in habitat (DeCapita 2000, Cimprich 2003).

(5) *Can landscape-level features reduce parasitism rates?*—The effect of landscape-level distribution of habitat on cowbird abundance and parasitism rates has been shown clearly in forest birds (Robinson et al. 1995a, b; Thompson et al. 2000). Cowbirds require both habitat with breeding hosts where they can deposit eggs and open habitat for foraging in the afternoon (Rothstein et al. 1984, Thompson 1994, Goguen and Mathews 1999). Foraging habitat is often limiting in forested landscapes, which reduces local cowbird densities and can lead to reduced parasitism rates (Verner and Rothstein 1988). Distance from breeding to feeding areas can also be important, because extensive movements by female cowbirds seems to result in lower numbers of eggs laid (Curson et al. 2000). Understanding such large-scale processes in grassland ecosystems is more difficult, because complex factors interact to determine the relative quality of foraging habitat for cowbirds in open country (Morris and Thompson 1998). Another landscape-level factor is the availability of livestock that may serve as foraging associates for cowbirds. As has been described for Fort Hood and is even likelier for more heavily forested landscapes, removing of livestock or restricting grazing during the passerine breeding season may be the best approach for dealing with cowbird parasitism.

(6) *Can we model demography well enough to determine whether cowbird control can be ended if*

host populations increase?—An important possibility to consider, but one that has been ignored by managers of endangered host populations, is that the population-level effect of cowbirds may decline drastically once an endangered species increases. When cowbird control began at Camp Pendleton, there were ~50 pairs of Least Bell's Vireos with a 50% frequency of parasitism (Griffith and Griffith 2000). A 50% parasitism frequency could endanger any Least Bell's Vireo population, because this bird almost never fledges any of its own young from a parasitized nest, so cowbird trapping was an appropriate management action in the 1980s. But today, there are at least 1,000 Least Bell's Vireo pairs at Camp Pendleton, a 20-fold increase since the early 1980s; and the parasitism frequency would still be only 50% if cowbirds also showed a 20-fold increase in the absence of trapping. If cowbirds maintained their original abundance, the parasitism frequency on the greatly enlarged Least Bell's Vireo population would be roughly a 1/20th what it was before cowbird control began, because the same number of cowbirds would be distributing the same number of cowbird eggs among 20× as many Least Bell's Vireo nests. A similar situation might prevail for the Kirtland's Warbler in Michigan, which has undergone a nearly 10-fold increase in numbers, from 200 Kirtland's Warbler pairs to nearly 2,000 (DeCapita 2000), since cowbird control began. How much would cowbird numbers increase in areas with these recovering endangered species? It is very unlikely that cowbirds in these situations would show the same increase in numbers that these endangered species have shown.

Because they are host generalists, cowbird numbers are affected by many factors besides the numbers of a single host species. Although there is a positive relationship between cowbird numbers and overall host numbers, the correlation is weak and not linear and is even absent sometimes (Jensen and Cully 2005). Data from the San Pedro River in southern Arizona may be informative here. Cattle were barred from grazing in and along the river in January 1988 (Krueper et al. 2003). There was an immediate increase in the amount of riparian habitat that spring, and improvement continued over the next several years. By 1990, the relative abundance of Yellow Warblers (*D. petechia*) had increased 5-fold compared with baseline

data collected in 1986. Abundance of Common Yellowthroats (*Geothlypis trichas*) increased 11-fold, whereas cowbird abundance showed a 2.3-fold increase, so the population-level effects of cowbird parasitism would have decreased after elimination of grazing and consequent improvement in habitat. We can determine whether increased numbers of endangered species would experience decreased rates of cowbird parasitism that are not a threat to their survival only by ending cowbird control for several years and subsequently determining parasitism rates in the absence of control. Determining whether the need for cowbird control is as great today as it was when control programs were initiated would be practicing the sort of adaptive management that governmental agencies are supposed to pursue. But the pressures discussed above that maintain the momentum for cowbird control seem to preclude any change in policy (i.e. any attempt to practice adaptive management).

(7) *If cowbird control is necessary, can we do a better job of it?*—We have already cited a number of improvements to cowbird control programs, such as explicit statements of goals that define conditions that will end the control program, and analyses that consider alternative explanations for increases in host populations after cowbird control was initiated. Efforts are needed to ensure that the effects that cowbird control has on nontarget species are minimized, though low levels of unavoidable negative effects on nontarget species should not deter cowbird trapping if control is well-justified.

Lastly, managers should initiate public education programs to inform the public about the justification for controlling cowbirds and about other measures that can reduce cowbird numbers, such as suspending bird-feeding activities and cattle grazing during the passerine breeding season. If cowbird control elicits complaints that it is wrong to kill one native bird to help another, managers should explain that control is viewed as a short-term management tool necessitated by increased rates of parasitism, or drastically reduced host populations that are threatened by loss of reproductive potential, or both. Managers should explain that action against one native bird to aid another reflects no value judgment as to the worth of one species over another but instead reflects society's commitment, as expressed in the Endangered

Species Act, to maintain levels of biodiversity. That commitment includes cowbirds too—a point that seems to have been missed in the volunteer cowbird-control program in Texas.

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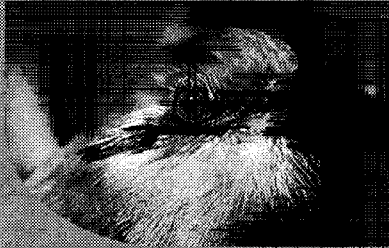
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