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Cowbirds, conservation, and coevolution: potential misconceptions and directions for future research

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Abstract Avian brood parasitism is a model system for studies of coevolution and ecological interactions between parasites and their hosts. However, recent work may have led to misconceptions concerning the Brown-headed Cowbird (*Molothrus ater*), the most widely studied brood parasitic bird in the world, and its effects on host species. Potential misconceptions about this species that could affect management issues are as follows: cowbird populations are increasing; cowbirds are relatively new to North America; recently exposed hosts are defenseless against parasitism; cowbirds have caused widespread declines of songbirds; and cowbird control is always effective in increasing the size of endangered host populations. Potential coevolutionary misconceptions are that cowbirds are typically "host tolerant"; cowbirds evict host nestmates; and the mafia effect is widespread. It is important to clarify these issues because such misconceptions could hinder our understanding of parasite-host interactions, and thus obscure the direction of basic research and of management efforts taken to limit cowbird impacts on endangered species. We discuss these issues and suggest future research directions to enhance our understanding of this fascinating species.

Keywords Brown-headed Cowbird, coevolution, cowbird control, endangered species, host tolerant, mafia, *Molothrus ater*, nestling eviction

Introduction

The Brown-headed Cowbird (*Molothrus ater*) is one of the most maligned bird species in the world. The contempt many people have for cowbirds seems to relate to anthropomorphic views of its parasitic lifestyle, and the mortality it causes to the young of other species. For example, Dawson (1923) referred to the female cowbird as the "unchaste mother of a race gone wrong" and a "blight upon the flower of progress". Pearson and Burroughs (1917) stated that "the Red-eyed Cowbird is a handsomer bird than that feathered wretch, the [Brown-headed] Cowbird… but this fine apparel has no effect upon the bird's habits, which apparently are as reprehensible as those of her northern relative." More recently it has been suggested that any Brown-headed Cowbirds that show up in Europe "be instantly shot, without debate or delay" (Brewer, 1995), and the title of a paper that appeared in *Birding* was: "An open solicitation for cowbird recipes" (Schram, 1994).

There are approximately 100 species of avian brood parasites in the world (Robinson et al., 2013), so why is there so much vitriol directed toward this species? Besides moralistic views related to brood parasitism, attitudes towards cowbirds are also shaped by suggestions

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that they pose a widespread threat of extinction to other bird species (Mayfield, 1977), a view that has some validity, but only for a limited number of endangered species whose survival is threatened mainly by anthropogenic habitat destruction. The cowbird is a host generalist known to have parasitized 247 host species, at least 172 of which have successfully reared cowbirds (Lowther, 2012), and the generalist nature of the cowbird gives it the potential to impact the populations of some endangered songbird species. As a result, there is intense research interest in the Brown-headed Cowbird from conservation and management perspectives (Morrison et al., 1999; Smith et al., 2000; Ortega et al., 2005), in addition to research on its basic biology and coevolutionary relationships with its hosts (Rothstein and Robinson, 1998). In this paper, we describe potential misconceptions that have arisen concerning cowbird biology and how they affect both cowbird management and the study of cowbird-host coevolution, and we provide solutions and suggestions for future research. We begin with a short overview of publication trends concerning cowbirds to show how the focus on this species has shifted in recent decades.

The cowbird is the most intensively studied avian brood parasite in the world. A Biosis search in December 2012 yielded 1027 citations for "Brown-headed Cowbird" and only 372 for "Common Cuckoo" (*Cuculus canorus*). Prior to the 1980s, most publications on cowbirds focused on their basic ecology and relationships with hosts (Rothstein and Peer, 2005). This changed after three publications raised concerns that cowbirds were one of the primary causes of passerine species declines, including several endangered species. Brittingham and Temple (1983) reported that cowbird populations were increasing. However, their data on cowbird population trends were from the Christmas Bird Count (CBC) and these surveys can suffer from a number of confounding variables (Rothstein and Peer, 2005). In contrast, Breeding Bird Survey (BBS) data that are more rigorous and obtained following a much more standardized protocol have demonstrated a steady decline in cowbird numbers from 1966–2010, and substantial declines in most states with cowbird control programs (see below).

A second publication was by Terborgh (1989) who indicated that the decline of many North American species was due to four factors: loss of breeding habitat, loss of wintering habitat in the Neotropics, and increased nest predation and cowbird parasitism. This was followed by a third publication by Robinson (1992; see also Robinson et al., 1995) who reported extremely high rates of cowbird parasitism in Illinois and showed that many hosts experienced parasitism rates >80%. Robinson (1992) also found that the majority of these parasitized nests were also depredated, which resulted in population sinks for these songbirds in the small woodland patches studied (but see Bollinger et al., 1997).

These publications triggered an increase in studies in the 1990s through the early 2000s focusing on the effects of cowbird parasitism on songbird populations and also resulted in a shift in focus of cowbird studies from basic ecology and coevolution to management and conservation (Fig. 1; Rothstein and Peer, 2005). The increased profile of cowbirds as possible causal factors in the decline of passerine species culminated in three meetings that focused largely on management solutions for the "cowbird problem" (Morrison et al., 1999; Smith et al., 2000, Ortega et al., 2005). Interestingly, the publication trend has reversed since publication of the results of the last of these meetings (Ortega et al., 2005). The cowbird continues to be one of the most frequently cited species (Fig. 1), but a majority of the papers published on Brown-headed Cowbirds since 2005 have focused on basic biology, similar to the trends prior to the publications by Brittingham and Temple (1983), Terborgh (1989), and Robinson (1992). This may be

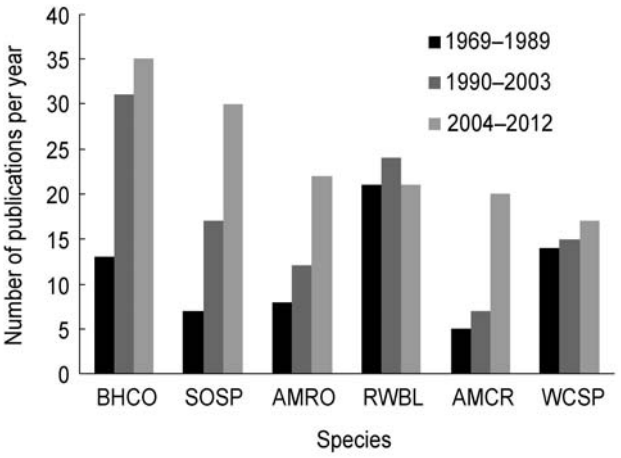

Fig. 1 Number of publications per year on the Brown-headed Cowbird and five other commonly studied North American passerine species (Song Sparrow [SOSP], American Robin [AMRO], Red-winged Blackbird [RWBL], American Crow [AMCR], and White-crowned Sparrow [WCSP]) over three time periods.

due to our paper (Rothstein and Peer, 2005) in which we discussed some of the misinformation concerning cowbird biology. We are hopeful that this is the case and that management-oriented cowbird research now focuses more on habitat, which is the most critical factor in preserving most bird populations that experience cowbird parasitism.

Conservation and cowbirds

Cowbird "myths"

Rothstein and Peer (2005) documented that much of what is believed concerning cowbirds and their effects on host populations, especially outside the research community, is largely exaggerated and in some cases false. Unfortunately, this misinformation persists today, which is evident in the Wikipedia article entitled "Cowbird" that reported the following when accessed February 18, 2013: "In some species the cowbird chick will use its large size to push the other chicks out of the nest." Similarly, the National Audubon Society's website (http://www.audubonbirds.org/species/Birds/Brown-headed-Cowbird.html) states "The young cowbird grows quickly at the expense of the young of the host, pushing them out of the nest..." Neither of these statements is true and below we address this misconception and others detailed by Rothstein and Peer (2005).

Myth 1: Cowbirds are increasing in abundance. This belief likely originates from the observation that cowbirds have become widespread in North America in recent history (Mayfield, 1965; Rothstein, 1994), but they were probably even more widespread and numerous prior to this (see below). In contrast to this pervasive dogma, cowbird numbers have declined by about 0.6% per year, in North America from 1966–2010 (Sauer et al., 2011; Fig 2), and the decline is especially pronounced in five of six states with long-term cowbird trapping programs (Fig. 3).

Myth 2: Cowbirds are new to North America. The five species of cowbirds likely originated in the tropics and subsequently moved into temperate regions (Rothstein et al., 2002). Although they are newer on the evolutionary time scale relative to other brood-parasitic groups, (Sorenson and Payne, 2001; Rothstein et al., 2002; Spottiswoode et al., 2011), cowbirds have been present for approximately 1 My in North America and are therefore not a new species there on an ecological time scale (Rothstein et al., 2002). It has often been suggested that the cowbird's range expansion is recent and in response to anthropogenic habitat alteration from European colonists (Mayfield, 1965). While the alteration of eastern forests has allowed cowbirds to now parasitize some forest interior species that probably had little contact with cowbirds 300–400 years ago, recorded history in North America is too brief to accurately reflect the complete history of cowbird-host interactions. Native Americans managed the landscape (Pyne, 1977), which

Fig. 2 Relative abundance of the Brown-headed Cowbird recorded survey wide during the Breeding Bird Survey from 1966–2010 (Sauer et al., 2011)

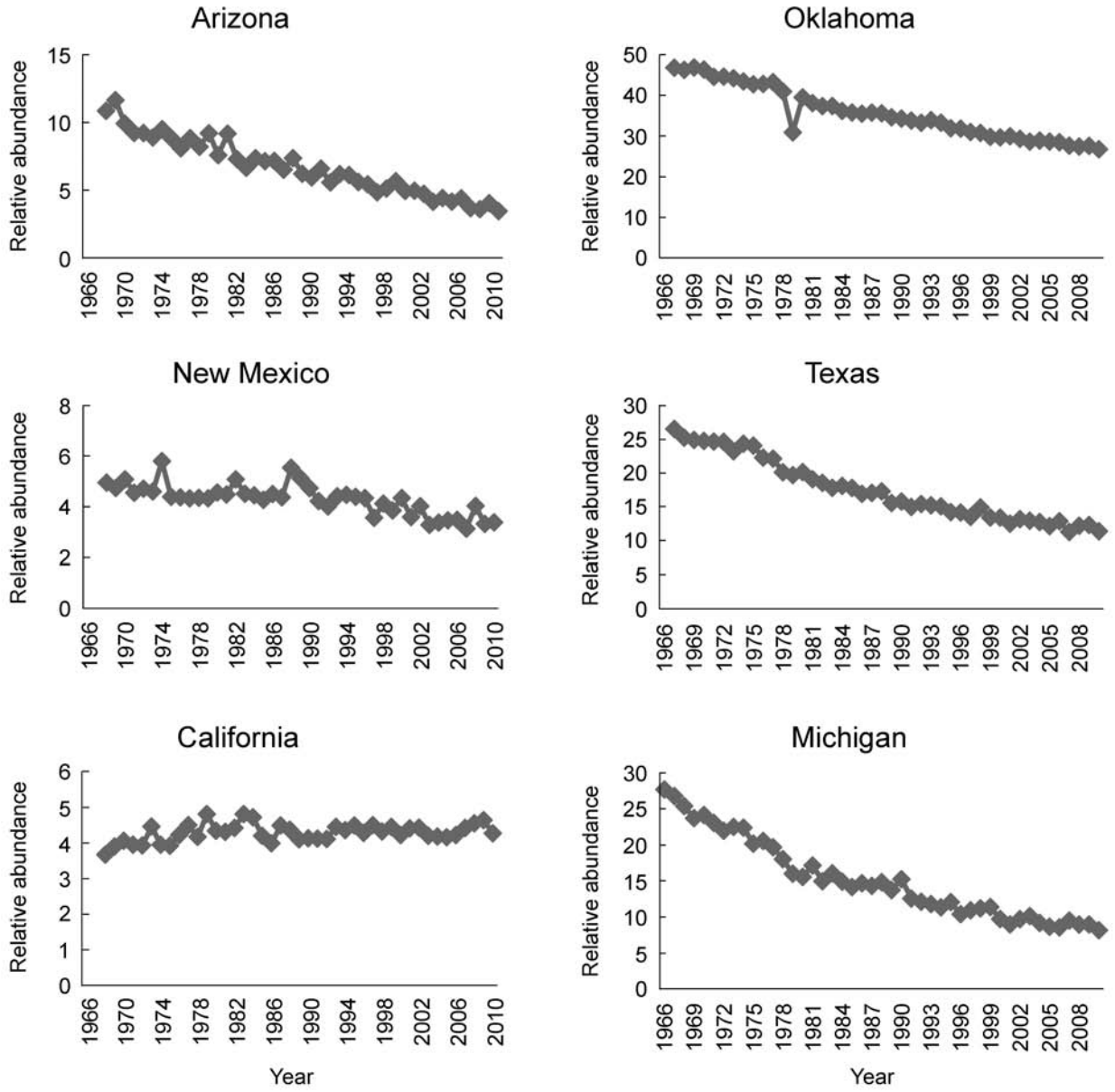

Fig. 3 Relative abundance of the Brown-headed Cowbird recorded during Breeding Bird Survey data from 1966–2010 in six states with active cowbird control programs (Sauer et al., 2011)

likely created habitat for cowbirds in the eastern forests and cowbirds and other grassland species were present there when colonists arrived (Askins, 2000). Indeed, the continuous extent of forest coverage in eastern North America that Europeans described as they moved west was a recent phenomenon. European diseases rapidly spread westwards and decimated Native American populations largely eliminating their ecological impacts so that by the time European explorers arrived in much of eastern North America a century or two later, forests had become more continuous and dense than they had been before the continent was discovered by Europeans (Mann, 2005).

More importantly, cowbirds may have been much more widespread during the Pleistocene (up to 10000–15000 ya), when North America's landscape contained one of the most diverse megafauna on the planet (Pielou, 1991). Bison, oxen, horses, llamas, camels, mammoths, mastodons were common and given the cowbird's association with large ungulates, North America would have been a cowbird paradise during this period (Rothstein and Peer, 2005). Lastly, there is

fossil evidence of cowbirds in North America dating to 500000 ya and fossils of two extinct probable cowbird species from the Pleistocene (Pielou, 1991; Lowther, 1993). Based on this evidence, cowbirds have been parasitizing hosts in North America for a long period and any host species that could not sustain parasitism went extinct. To the extent that cowbirds are a current threat to host populations, the causation must therefore be due to recent anthropogenic changes (e.g., habitat destruction) and not to cowbirds being a new ecological or evolutionary pressure (Rothstein and Peer, 2005).

Myth 3: Parasitism always limits or reduces host population sizes. Populations are limited by numerous factors such as food supply, habitat, predators, and parasites (Newton, 1998). The only hosts that are now imperiled by cowbirds are endangered species that have also experienced significant population reductions due to loss of habitat (Rothstein and Peer, 2005). Cowbird parasitism is exacerbating declines of endangered species due primarily to habitat losses because few populations remain and most or all are heavily parasitized. However, nest predation must also be considered when assessing the relative impacts of cowbirds on threatened and endangered hosts. For example, while parasitism rates are high in some areas, these same nests are also likely to be depredated (Robinson, 1992; Robinson et al., 1995).

Myth 4: New hosts lack defenses against parasitism and are prone to extinction when coming into contact with cowbirds. It has been suggested that hosts that have come into contact with cowbirds in recent history are at risk and may be in need of intervention (Mayfield, 1965; Reed, 1999). Because of the habitat changes in the North American landscape and range shifts of hosts and cowbirds described above, many host lineages have become exposed to parasitism in the past few centuries. However, relatively few of these host populations that appear to have been initially exposed to cowbirds in the several hundred years of recorded history in North America are actually new hosts. Many of these host lineages evolved defenses during past bouts of parasitism, and are still well-defended against renewed parasitism because the defenses are retained for long periods of time in the absence of parasitism (Rothstein, 2001; Peer and Sealy, 2004a; Underwood et al., 2004; Peer et al., 2007, 2011a, 2011b). For example, the endemic Island Scrub-Jay (*Aphelocoma insularis*) occurs on Santa Cruz Island, California where there are no brood parasites, yet it ejects 100% of experimental parasitism (Peer et al., 2007). Molecular clock data indicate the Island Scrub-Jay split from its mainland ancestors 140000 to 151000 ya, and therefore has maintained ejection for an extensive time period in the absence of selection pressures (Peer et al., 2007). Similarly, egg rejection in the absence of parasitism has likely been retained for substantially longer periods in the Loggerhead Shrike (*Lanius ludovicianus*; 1.1–1.8 My) and the Bohemian Waxwing (*Bombycilla garrulus*; 2.8–3.0 My) (Peer et al., 2011a, 2011b). Support for the persistence of host defenses that evolved in the past and have been retained after cowbird parasitism ceases also comes from data on desertion of naturally parasitized nests. The habitat in which a host nests, which in all likelihood reflects its past exposure to past cowbird parasitism, is a better predictor of desertion in response to parasitism than is the history of a host's recent contact with cowbirds (Hosoi and Rothstein, 2001). These data (see also Rothstein, 2001; Peer and Sealy, 2004a) indicate that host populations that are newly exposed to cowbirds in recent history are unlikely to be prone to extinction solely because of this exposure, although some of these populations may have weaker defenses than conspecific lineages with a continuous history of exposure (Briskie et al., 1992; Gill and Sealy, 2004). Nevertheless, resource managers often ignore this point. For example, it is widely assumed that endangered hosts in California are endangered due to cowbird parasitism (Goldwasser et al., 1980; Laymon, 1987) because they are defenseless and never experienced parasitism before cowbirds colonized most of California in the early 1900s (Rothstein, 1994).

Myth 5: Cowbird control programs always increase reproductive output and host population sizes. The reproductive success of individual hosts increases when cowbirds and their eggs are removed from nests, but this alone does not always yield larger host population sizes. One of the best examples of this is Kirtland's Warbler (*Setophaga kirtlandii*), a species that may have always been rare due to its nesting only in jack pine (*Pinus banksiana*) forests 6–24 years after fires (DeCapita, 2000). In the recent past, it was impacted by fire suppression policies (Mayfield, 1992). After the 1971 census, the number of singing males declined to 201, down from 502 in the 1961 census (U.S. Fish and Wildlife Service, 2012a). A cowbird control program was implemented in 1972 in which adult cowbirds were killed and their eggs removed from warbler nests (DeCapita, 2000). More than 153000 cowbirds have been killed in over 40 years of trapping (U.S. Fish and Wildlife Ser-

vice, 2011). However, the number of singing warbler males remained steady near 200 until about 1990 when they began to increase (U.S. Fish and Wildlife Service, 2012a). Thus, despite the fact that almost all cowbirds were removed from the nesting habitat and parasitism frequencies were close to 0% for almost 20 years, there was no increase in warbler numbers, indicating that cowbirds were not responsible for the stagnation in warbler numbers, otherwise the population should have rebounded. The increase starting in 1990 is directly attributable to a fire (Mack Lake) that burned out of control in 1980 and created large amounts of new suitable habitat. In fact, by the time the warblers began to increase in 1990, the great majority of warblers were nesting on this newly created habitat, which raises the ironic likelihood that the species might have gone extinct even with cowbird control had this accidental fire not occurred!

Beginning in 1991, Kirtland's Warbler numbers have steadily increased and the 2012 census recorded a record high 2090 singing males (U.S. Fish and Wildlife Service, 2012a). This warbler was once restricted to nesting in 13 counties in Michigan (Mayfield, 1992) and has now expanded its breeding range into Wisconsin and Canada (U.S. Fish and Wildlife Service, 2012b). What has changed since 1991? Not cowbird parasitism, because the cowbird control program has been operating since 1972. Instead, new habitat has been created allowing the population to expand beginning with the 10500 ha Mack Lake burn in 1980 (DeCapita, 2000). The population has also benefited due to increased wintering habitat in the Caribbean (Haney et al., 1998; but see Sykes and Clench, 1998). Cowbird parasitism may have caused the warbler's decline between 1961 and 1971; however, the failure of the warbler population to increase after cowbird control began shows that declining habitat availability could have been the primary cause. Cowbird control was a wise management decision in the early 1970s, but subsequent events fail to support the hypothesis that cowbird control saved the Kirtland's Warbler from extinction despite such claims (e.g., Terborgh, 1989; DeCapita, 2000; Wiens et al., 2012; Wilson et al., 2012). While these claims may be true, analysis of the evidence does not support this level of certainty (Rothstein and Peer, 2005).

A similar outcome was observed in the Southwestern Willow Flycatcher (*Empidonax traillii extimus*) cowbird control program. Flycatcher populations have not increased in spite of cowbird removal and this is probably due to the fact that most of the riparian habitat in which these birds nest has been eliminated (Rothstein and Peer, 2005). Endangered Least Bell's (*Vireo bellii pusillus*) and Black-capped Vireo (*Vireo atricapilla*) populations have increased following cowbird control, but in each case habitat was also increased (Rothstein and Peer, 2005).

There are claims that Kirtland's Warblers will be reliant on cowbird control in perpetuity (U.S. Fish and Wildlife Service, 2012a; Wiens et al., 2012). No cowbird control programs have been stopped, and there exists little impetus to do so. Rothstein and Peer (2005) suggested that experimental reduction of cowbird control was warranted now that some endangered songbird populations have significantly surpassed their mandated population goals and may be able to sustain parasitism. Such a reduction was initiated at Fort Hood, Texas where cowbird control began in 1988 to benefit the Black-capped Vireo, and to a lesser extent the Golden-cheeked Warbler (*Setophaga chrysoparia*; Hayden et al., 2000). The 2011 census estimated that there were between 4000 and 6000 male vireos (Cimprich and Hemibuch, 2011, unpubl. report), which is at least twice the mandated population goal for the species (Kostecke et al., 2010, unpubl. report). Cowbird control was experimentally relaxed on a portion of the site from 2006–2010 and as would be predicted, parasitism frequencies increased in areas where cowbirds were no longer killed (Kostecke et al., 2010, unpubl. report). However, the critical data are whether there was an effect on the numbers of individuals breeding at the population level. Additional experimental relaxation of cowbird control is needed to determine whether enlarged endangered host populations can sustain it.

There are numerous negative aspects associated with cowbird control that we have reviewed previously (see Rothstein and Peer 2005) including the possibility that cowbirds may be keystone species, management decisions being based upon reports rather than peer-reviewed science, trapping and killing non-target species, profit motive, and special interest groups that promote the haphazard killing of cowbirds. While controlling cowbirds in 1972 to aid the Kirtland's Warbler was the prudent decision based on evidence available at the time, it is highly unlikely that the warbler would be seriously affected at the population level after several years without cowbird control to assess the continued need for this intervention. We should determine whether it is necessary to continue to kill one native species to aid

another species, otherwise the situation is not different than haphazardly killing predators such as hawks, owls, or snakes because they consume other animals. Indeed, given the high nest predation rates on these endangered songbirds (e.g., Cimprich and Comolli, 2010, unpubl. report), one could rightfully ask why there is not more focus on eliminating nest predators. Cowbird culling is likely favored because cowbirds are disliked (whereas predators such as hawks are often admired) and dead ones in the hand likely provide immediate satisfaction that progress is being made. In contrast, habitat restoration is long-term and the results are not immediate. Similar lethal management approaches with nuisance blackbird species have also failed (Peer et al., 2003; Blackwell et al., 2003). In short, while controlling cowbirds was an appropriate decision in the early days of several endangered species recovery programs, we contend that much and perhaps most funding devoted to current control programs would be better utilized in habitat management. A management practice implemented to benefit one or just a few species should not be substituted for habitat management that can be beneficial to entire communities.

Cowbirds and coevolution

Cowbirds are not "host tolerant"

To our knowledge, this anthropomorphic term was first used by Johnsgard (1997) to describe parasitic nestlings that share nests with their hosts and do not evict or kill them. The term "host tolerant" has been used in the scientific literature to indicate that cowbirds and other parasitic species could potentially kill host nestlings, but refrain from doing so because of indirect benefits that nestlings may provide (e.g., Kilner et al., 2004; Kilner, 2005; Grim, 2006). It has also been used to describe hosts tolerating brood parasitism (Svensson and Råberg, 2010), which has only served to increase confusion. The term "host tolerant" is misleading for two reasons. First, it implies that parasitic offspring have evolved the ability to kill host offspring yet refrain from doing so because of indirect benefits gained by parasitic nestling (e.g., Kilner et al., 2004; Kilner, 2005; Grim, 2006). Unlike some lineages in which parasitic nestlings directly kill host offspring (i.e., most Old Word cuckoos [via eviction], and honeyguides and New World cuckoos [by stabbing]), there is no evidence that cowbirds have the capacity to kill host young. Therefore, the use of host tolerance tacitly implies that cowbirds can kill nestmates when there is no evidence to suggest that it is a feasible scenario. Second, there is a large number of hosts that raise fewer than one offspring when parasitized, and many that nearly always raise only the cowbird and none of their own young when parasitized (n = 36 species; Table 1). In these cases, host offspring are killed indirectly by the cowbird's behavior that stems from hatching sooner than hosts and intensive begging for food, and are not "tolerated" by the cowbird. When these host species occasionally raise their own young in parasitized nests, the cowbird egg usually does not hatch because it is infertile or is laid too late in the host's incubation period (e.g., Grzybowski, 1995). Hosts such as these are ones for which control is appropriate in at least some situations. When endangered passerines such as Black-capped Vireos, Least Bell's Vireos, and Southwestern Willow Flycatchers are parasitized they usually raise only cowbirds. Clearly, this is not "host tolerance" because the result is the same as if the nestling parasite had actively killed the host young as in "host intolerant" cuckoos and honeyguides.

In addition, Rasmussen and Sealy (2006) reviewed observations of hosts feeding fledgling cowbirds. Their findings plus those of Robinson (1992) revealed that only a cowbird fledgling was being fed in 84% of 127 cases. In spite of possible biases in these data (e.g., cowbird fledglings were more observable), they provide strong circumstantial evidence that any host offspring that fledged often die shortly thereafter. Rasmussen and Sealy's (2006) and Robinson's (1992) data include 41 host species not listed in Table 1, which means at least 45% of the hosts known to raise cowbirds (n = 172) usually or at least occasionally raise only cowbirds, or if their nestlings do fledge they die shortly after leaving the nest. Interestingly, a number of these hosts are larger than cowbirds (Western Meadowlark [*Sturnella neglecta*], Red-winged Blackbird [*Agelaius phoeniceus*], Brewer's Blackbird [*Euphagus cyanocephalus*], Brown Thrasher [*Toxostoma rufum*], Wood Thrush [*Hylocichla mustelina*]) or similar in size (Northern Cardinal [*Cardinalis cardinalis*], Eastern Towhee [*Pipilo erythropthalmus*], Rose-breasted Grosbeak [*Pheucticus ludovicianus*], Black-headed Grosbeak [*P. melanocephalus*]). This is further evidence that the use of the term "host tolerant" is unwarranted. For both of these reasons, we recommend that the term host tolerant should not be used for cowbirds and other species that do not directly kill host young through eviction or stabbing behaviors.

Table 1 Hosts of the Brown-headed Cowbird that have been recorded to raise < 1 of their own young when parasitized (n = 36 species)

Host species	Number of young raised (n)	Reference
Acadian Flycatcher (*Empidonax virescens*)	0.1 (74)	Whitehead and Taylor, 2002
Willow Flycatcher (*E. traillii*)	0.0 (11)	Ward and Smith, 2000
Least Flycatcher (*E. mimimus*)	0.0 (8)	Tarof and Briskie, 2008
Dusky Flycatcher (*E. oberholseri*)	0.0 (13)	Ward and Smith, 2000
Eastern Phoebe (*Sayornis phoebe*)	0.32 (19); 0.1 (7); 0.67 (?)	Rothstein, 1975; Hill, 1976; Hauber, 2003
Say's Phoebe (*S. saya*)	0.1 (1)	Hill, 1976
Warbling Vireo (*Vireo gilvus*)	0.1 (24)	Ward and Smith, 2000
Bell's Vireo (*V. bellii*)	0.0 (1)	Hill, 1976
Black-capped Vireo (*V. atricapilla*)	0–0.2 (?)	Grzybowski, 1995
White-eyed Vireo (*V. griseus*)	0 (?)	Hopp et al., 1995
Yellow-throated Vireo (*V. flavifrons*)	0.6 (8)	Rodewald and James, 2011
Plumbeous Vireo (*V. plumbeus*)	0.52 (51); 0.9 (20)	Chace et al., 2000; Goguen and Curson, 2012
Cassin's Vireo (*V. cassinii*)	? [a]	Goguen and Curson, 2002
Blue-headed Vireo (*V. solitarius*)	0.0 (7)–0.14 (20)	James, 1998
Horned Lark (*Eremophila alpestris*)	0.0 (14)	Hill, 1976
California Gnatcatcher (*Polioptila californica*)	0.0 (9); 0.63 (27); 0.5 (8)	Lorenzana and Sealy, 1999
Blue-gray Gnatcatcher (*P. caerulea*)	0.0 (20); 0.1 (129)	Kershner et al., 2001; Curson unpubl. data in Lorenzana and Sealy, 1999
Brown Thrasher (*Toxostoma rufum*)	0.0 (1)	Hill, 1976
Sprague's Pipit (*Anthus spragueii*)	0.0 (3) 0.0 (10)	Davis and Sealy, 2000; Davis, 2003
Common Yellowthroat (*Geothlypis trichas*)	0.11 (9)	Stewart, 1953
Northern Cardinal (*Cardinalis cardinalis*)	0.0 (7)	Berger, 1951
Black-headed Grosbeak (*Pheucticus melanocephalus*)	0.5 (15)	Ward and Smith, 2000
Indigo Bunting (*Passerina cyanea*)	0(5); 0.37 (277)–0.40 (140)	Phillips, 1951; Payne and Payne, 1998b
Dickcissel (*Spiza americana*)	0.0 (13)	Hill, 1976
Black-throated Sparrow (*Amphispiza bilineata*)	0.20 (?)	Johnson and van Riper, unpubl. data in Hauber, 2003
Clay-colored Sparrow (*Spizella pallida*)	0.4 (22)	Davis, 2003
Baird's Sparrow (*Ammodramus bairdii*)	0.6 (37)	Davis, 2003
Grasshopper Sparrow (*A. savannarum*)	0.5 (4); 0.92 (13)	Hill 1976; Davis and Sealy, 2000
Savannah Sparrow (*Passerculus sandwichensis*)	0.11 (9) 0.1 (23)	Davis and Sealy, 2000; Davis, 2003
Lark Bunting (*Calamospiza melanocorys*)	0.0 (13)	Hill, 1976
Lark Sparrow (*Chondestes grammacus*)	0.2 (9)	Hill, 1976
Song Sparrow (*Melospiza melodia*)	0.3 (26)	Ward and Smith, 2000
Chestnut-collared Longspur (*Calcarius ornatus*)	0.6 (74)	Davis, 2003
Western Meadowlark (*Sturnella neglecta*)	0.0 (1); 0.64 (28)	Hill, 1976; Davis and Sealy, 2000
Red-winged Blackbird (*Agelaius phoeniceus*)	0.4 (17)	Hill, 1976
Pine Siskin (*Carduelis pinus*)	0.2 (16)	Hill, 1976

[a] Raise ≥ 1 host young in only 12.5% (n = 8) to 37.5% (n = 8) of parasitized nests (Goguen and Curson, 2002).

Cowbirds rarely if ever evict host nestmates

Dearborn (1996) videotaped a Brown-headed Cowbird nestling pushing a nestling Indigo Bunting (*Passerina cyanea*) from a nest and concluded the cowbird exhibited nestmate eviction behavior. In addition, Twomey (1945) described two nests from which nestling buntings were "pushed" and "ejected" by nestling cow-

birds, although it is unclear whether the evictions were witnessed or if nestlings were observed on the ground after falling from the nests. In part, based on these observations, several authors have suggested that nestmate eviction may be typical of cowbird nestlings (Oppel et al., 2004; Fauth and Cabe, 2005; Broom et al., 2008), despite this behavior having been documented only once. Based on additional videotaped nests we have reviewed and a thorough analysis of the events immediately prior to the bunting falling from the nest Dearborn (1996) described, we contend that nestmate eviction is not a regular behavior of cowbird nestlings.

We analyzed video from 47 parasitized nests of six common cowbird hosts. Yellow Warbler (*Setophaga petechia*) nests (n = 35) that contained a single cowbird nestling with 1–4 warbler nestlings (mean = 2.3 warblers/nest) were videotaped in western Montana from 1996–2004 (M.J. Kuehn pers. comm.). No cases of nestling eviction occurred during the 26 h of recording. One or more warbler nestlings disappeared from four nests, and a single cowbird nestling disappeared from a fifth nest. In two of these nests, warbler nestlings disappeared from nests that had become tilted. One of these two nests was videotaped after two of the three warbler nestlings disappeared. The female warbler lowered her body to brood and placed her foot on the warbler nestling. She re-positioned herself to keep from sliding down the tilted nest. Both nestlings moved suddenly in response to the female and a warbler nestling fell from the nest. At the third nest, a female cowbird visited while the female warbler was brooding and forced the adult warbler onto the nest rim, which allowed the cowbird to remove a warbler nestling. We were unable to document the cause of the disappearance of the warbler nestling at the fourth nest. An American Kestrel (*Falco sparverius*) removed the cowbird from the nest from which only a cowbird nestling disappeared.

As part of a study on nestling provisioning, K. Ellison (pers. comm.) videotaped 12 parasitized nests in the grasslands of southwest Wisconsin from 1998–2008 for 1344 h: Eastern Meadowlark (*Sturnella magna,* n = 7 nests), Bobolink (*Dolichonyx oryzivorus,* n = 1), Song Sparrow (n = 1), Savannah Sparrow (*Passerculus sandwichensis,* n = 2), and Henslow's Sparrow (*Ammodramus henslowii*, n = 1). Broods in these nests ranged from 1–3 cowbirds, with and without host young. No nestmates, host or cowbird, were evicted by cowbird nestlings. If eviction is typical of cowbird nestlings our assessment of cowbird behavior for > 1300 h of video in 47 parasitized nests should have revealed additional instances of nestmate eviction. However, our extensive review found no evidence of eviction leading us to conclude that this is not a widespread behavior.

In addition to assessing the potential for eviction behavior in other hosts, we reviewed the video provided by Dearborn (1996), which included approximately eight minutes prior to the eviction (D.C. Dearborn, pers. comm.). After reviewing the video several times, we have concluded that the behavior of the cowbird caused the bunting to fall from the nest; however, this was not a clear case of directed nestmate eviction as observed in most parasitic cuckoos. First, the behavior of the bunting contributed to its fall from the nest because it moved onto the back of the cowbird. This significantly increased the likelihood that it could fall from the nest when the cowbird elevated, especially considering the size of the cowbird nestling relative to the bunting (18.2 g vs. 7.6 g, respectively; Dearborn, 1996). Second, the cowbird's response to a bunting on its back is consistent with observations of cowbirds competing for food against nestmates during begging scramble: when a nestmate contacts a cowbird nestling and prevents it from begging, the cowbird separates itself from the nestmate through similar movements witnessed in the video (J.W. Rivers, pers. obs.). Importantly, we have observed that once cowbird nestlings are no longer impeded by their nestmates they typically stop moving, which is in contrast to evicting cuckoo nestlings that continuously search the nest to evict all nestmates (Payne and Payne, 1998a; Payne, 2005). The cowbird in the Dearborn observation exhibited none of these behaviors. Finally, the cowbird made no attempt to get underneath the host nestling as is typical for evicting cuckoos (Payne, 2005). Although it is possible that cowbirds and cuckoos could have evolved eviction differently, we would expect nestmate eviction to be similar between cowbirds and cuckoos given the limited motor skills of altricial nestlings.

We suggest that citing Dearborn's (1996) observation as evidence that nestmate eviction is an evolved behavior typical of cowbird nestlings is misleading; instead, Dearborn's observation apparently represents a rare set of circumstances. Others have cited it as evidence of the rarity of nestmate eviction in cowbirds and have suggested that cowbird nestlings "apparently refrain from [nestmate eviction] behavior on most other occasions" (Kilner et al., 2004). Surprisingly, other authors have promoted the idea that cowbirds may "strategically

evict" nestmates from nests (Broom et al., 2008). We suggest that categorizing cowbirds in either manner is misleading.

Dearborn's observation is similar to a swallow nestling that was cross-fostered into a magpie nest and then proceeded to evict magpie eggs just as a nestling cuckoo would (Alvarez et al., 1976). Dawkins (1976) suggested that it might be incipient fratricide, but there have been no other reports of this behavior. It appears that a similar series of events has occurred in the cowbird, where a closer examination of a single case of nestmate eviction appears to be only an anomalous incident. Nevertheless, the absence of evidence for a behavior does not prove the absence of that behavior and we encourage future research into the possibility of nestmate eviction in cowbird nestlings.

Farming and mafia

It has long been known that female Brown-headed Cowbirds remove host eggs in conjunction with parasitism (Friedmann, 1963), possibly to enhance incubation of the parasitic egg (Peer and Bollinger, 1997, 2000; Sealy et al., 2002) and also for food (Sealy, 1992). Reports of cowbirds destroying nest contents go back many years as well (Du Bois, 1956), but only recently has it been recognized that female cowbirds may regularly destroy unparasitized nests to induce re-laying by hosts when a female finds a nest at which incubation is too advanced to allow her egg to hatch (Smith and Arcese, 1994; Arcese et al., 1996; Hoover and Robinson, 2007). Egg destruction behavior is known to occur regularly in Shiny and Bronzed Cowbirds that do not typically remove host eggs from parasitized nests like the Brown-headed Cowbird (Peer and Sealy, 1999; Nakamura and Cruz, 2000; Fiorini et al., 2009). The increased use of video surveillance has revealed that the destruction behavior is more widespread in Brown-headed Cowbirds than previously believed (Elliott, 1999; Granfors et al., 2001; but see McLaren and Sealy, 2000), and it has even been shown to occur in captive males (Dubina and Peer, 2013). Nevertheless, these video studies also show that cowbirds are responsible for only a small proportion of nests that are destroyed. For example, even though cowbirds were abundant, they were responsible for only one of 25 videotaped predation events at a study site in Missouri (Thompson et al., 1999). If cowbird destruction of unparasitized nests is a major factor in songbird breeding dynamics, then unparasitized nests should have higher predation rates than parasitized nests but this is often not the case (Rothstein, 1975; Kus, 1999; Whitfield and Sogge, 1999). Similarly, if cowbird nest destruction is a major factor, then destruction should decline when cowbird removal programs occur but this has not occurred (Walkinshaw, 1983; Stutchbury, 1997; Whitfield and Sogge, 1999; Whitfield, 2000). In addition, it is worth noting that other passerines not regularly thought to be predators, such as Red-winged Blackbirds (*Agelaius phoeniceus*), Yellow-headed Blackbirds (*Xanthocephalus xanthocephalus*) and Gray Catbirds (*Dumetella carolinensis*) sometimes depredate nests (Belles-Isles and Picman, 1986; Sealy, 1994; Cimprich and Moore, 1995). Thus, while cowbirds destroy nests, this behavior is not unique to them and it is unclear how important it is to host population dynamics.

Mafia behavior in which brood parasites destroy the nest contents of hosts that reject their eggs (Zahavi, 1979) was first reported experimentally by Soler et al. (1995) in Great-spotted Cuckoos (*Clamator glandarius*), and was recently reported in Brown-headed Cowbirds through a series of elegant experiments (Hoover and Robinson, 2007). However, there have been no additional reports of mafia behavior occurring in cowbird hosts (e.g., McLaren and Sealy, 2000). Additional studies are necessary because this may be a localized phenomenon.

Mafia behavior also has a theoretical difficulty in that most host species that reject cowbird eggs do so at frequencies of nearly 100%. If mafia behavior is widespread, it should have kept rejection behavior from becoming fixed in host species but clearly it has not done so. It would also be expected that hosts most likely to be victimized by mafia behaviors should be those with the longest period to coevolve with cowbirds, but those hosts also are the most likely to be rejecters (Peer and Sealy, 2004b), whereas the only cowbird host in which mafia behavior has been reported, the Prothonotary Warbler (*Protonotaria citrea*), is a forest species that has probably experienced limited parasitism for most of its history.

Future research directions

Cowbirds and conservation

The strongly negative attitudes many people have towards cowbirds have resulted in a perception that ef-

forts should be made to eliminate as much cowbird parasitism as possible for as many host species as possible. While it might be correct to apply this mindset to endangered species that are in imminent risk of extinction, these ideas are imprudent when applied to cowbird hosts in general because we might as well also eliminate other factors that affect bird populations such as nest predators. It is unclear whether cowbirds have widespread effects on bird communities, but even if they do, that alone would provide no clear mandate for management actions because it is probable that common bird species in any ecosystem affect the numbers of other bird species through basic and natural ecological processes as competition for food or nest sites. Cowbird effects on rare species, however, may be another matter. Basic demographic theory shows that a generalist parasite like the cowbird can drive such species to extinction, however, it is important to be mindful that any threatened species that is endangered by cowbird parasitism suffers mainly from anthropogenic effects on its habitat. Any efforts to limit cowbird impacts should be coupled with efforts to improve and enlarge suitable habitat.

Given the crises they were experiencing 20–40 years ago, decisions to implement cowbird control programs for Least Bell's Vireos, Black-capped Vireos, Kirtland's Warblers and Southwestern Willow Flycatchers were prudent at the time. However, attitudes over the years have led to views that these control programs need to be continued with little or no thought given to the possibility of ending management intervention. This attitude is especially unfortunate when applied to the first three of these four species because all of them now have large populations in some parts of their range that might experience much smaller cowbird impacts if cowbird control were suspended than the impacts suffered when these host populations were much smaller. It is clear that cowbirds would pose no threat to the survival of the main population of the more than 2000 pairs of Kirtland's Warblers that currently breed in Michigan if cowbird control were to be suspended for several years to determine whether the level of impact cowbirds would have on these enlarged populations was a serious threat. We suggest that cowbird control be suspended in places where there are large populations of Least Bell's Vireos, Black-capped Vireos, and Kirtland's Warblers. At the same time, cowbird control could still be conducted to protect small populations of these species. Funds saved by determining that cowbird control need not be conducted in perpetuity for large host populations could enhance efforts to aid these species in other ways because funding for endangered species is severely limited. The efficacy of the Endangered Species Act in the United States depends on its ability to limit or mitigate actions that could harm listed species because the act provides only limited funds to aid these species. In fact, much of the funding that is available is mandated as mitigation for actions that have harmed or are likely to harm these species. Funds currently spent on cowbird control are likely a significant proportion of all of the available to aid endangered host species.

We have previously reviewed changes that should be made in the way cowbird programs are instituted and continued over time (Rothstein and Peer, 2005). In addition, our previous review was based in part on the USFWS recovery plan for the Southwestern Willow Flycatcher (U.S. Fish and Wildlife Service, 2002), which is accessible online at http://www.fws.gov/southwest/es/arizona/SWWF_RP.htm and contains official federal policy guidelines for cowbird issues related to the flycatcher which can, we suggest, be applied to other endangered hosts. To emphasize research needs related to management efforts, we emphasize two points. First, a link between cowbird control and an increase of one targeted population of an endangered host species should not by itself be taken as sole justification for instituting control actions on all populations of this species because cowbird parasitism is spatially variable. This variation has been evident for at least a half century (Friedmann, 1963) and is especially important, among endangered host species, for the Southwestern Willow Flycatcher, which has both heavily and infrequently parasitized populations (Rothstein et al., 2003). This endangered species also illustrates our second suggestion for management-related research. Among populations of this species that have experienced moderate-to-high levels of cowbird parasitism, there have been about as many host increases as decreases after control programs were instituted. Therefore, experiments should be conducted with some flycatcher populations targeted for control efforts and some not. This would enable agencies to determine whether cowbird control effectively increases population sizes of this host and whether management resources should be devoted to cowbird control.

Cowbirds and coevolution

Numerous topics concerning the coevolutionary re-

lationships between cowbirds and their hosts deserve future research attention (see Rothstein and Robinson, 1998). Among those we have addressed is mafia behavior and whether it is a strategy regularly employed by cowbirds. Specifically, following the intriguing results of Hoover and Robinson (2007), the next step is to determine whether an individual female that parasitizes a nest revisits and destroys its contents when its egg has been ejected. Moreover, there have been no further reports of mafia behavior and so it appears it is not widespread. It is also unclear how cowbirds can determine whether their eggs have been ejected in the dark cavity nests of Prothonotary Warblers (S. Robinson, pers. comm.). And because cowbirds are host generalists, the cowbirds that were parasitizing Prothonotary Warblers must also be using other hosts in the community. Are they employing mafia behavior with those hosts too? It would be unusual if they were employing this strategy with only a single host and one that accepts or deserts, but does not eject. Additional experiments need to be conducted with more hosts and researchers should be permitted to publish studies that fail to find a mafia effect even though such results would be regarded as less exciting than studies showing supporting evidence.

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牛鹂的保护与协同进化：潜在的误解和未来的研究方向

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摘要：鸟类巢寄生是研究寄生者与宿主之间相互作用及其协同进化的模式系统。然而，近来开展的一些工作却使人们对褐头牛鹂（*Molothrus ater*）这一世界上研究最多的寄生性繁殖鸟类产生了误解，特别是在到底该鸟对其宿主鸟类是否会产生危害这一认识上。这些潜在的误解包括：褐头牛鹂是一种新出现在北美的寄生鸟类，其种群正在快速增加；新近被牛鹂寄生的宿主没有防御行为，因此牛鹂寄生导致了目前雀形目鸟类的普遍减少，而对牛鹂的控制管理有效增加了濒危宿主鸟类的种群。而关于协同进化方面的误解则包括：牛鹂是典型的“相容性寄生鸟类”；牛鹂雏鸟会拱掉巢内宿主卵或雏鸟；牛鹂具有“黑手党”报复行为。这些误解由来已久，已严重影响了我们对牛鹂这一神奇寄生鸟类及其协同进化过程的认识。为此，本文对所有这些误解一一做了说明，并对未来的研究方向进行了展望。

关键词：褐头牛鹂，协同进化，牛鹂控制管理，濒危物种，宿主相容性，黑手党效应，*Molothrus ater*，拱雏行为