The Brown-Headed Cowbird: A Model Species for Testing Novel Research Questions in Animal Ecology, Evolution, and Behavior

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Abstract

Although the brown-headed cowbird (*Molothrus ater*) is the most intensively studied brood parasite in the world, much of the research on cowbirds has focused on the negative effects of parasitism. Here, we argue that negative attitudes toward the cowbird have overshadowed opportunities this species provides for advancing our understanding of social behavior, physiology, evolution, and ecology and conservation of birds. Cowbirds are widely distributed, amenable to captive study, and easy to study in areas where they are abundant. Cowbird nestlings must communicate to unrelated host parents, but unlike some parasitic nestlings, they have no specialized adaptations for doing so. In some areas they often share nests with relatives, which may influence the degree of virulence host experience. The generalist strategy of the cowbird can be used to answer questions about the impact of high reproductive output on female cowbirds, maternal allocation of resources into eggs, and the consequences of exposure to a range of pathogens while visiting host nests. Cowbirds and their hosts provide a contrast to cuckoo-host systems because they are at an earlier stage of

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161

coevolution, and only a minority of hosts shows effective defenses against parasitism. Cowbirds serve as a model species for studying song learning as aspects of their complex vocalizations are dependent on experience to different degrees. Cowbirds also challenge assumptions of the link between mating systems and parental care because cowbirds are often socially monogamous. Finally, cowbirds are unique among brood parasites for their effects on endangered host species. In this chapter, we discuss the value of cowbirds as a model species in these areas and suggest avenues for future research.

9.1   The Cowbird as a Misconstrued Species

The brown-headed cowbird (*Molothrus ater*, hereafter "cowbird") is the most widespread obligate brood parasite in North America. Cowbirds are a coevolutionary contrast to parasitic cuckoos because they are of a more recent origin (Rothstein et al. 2002), and their interactions with hosts are at an earlier stage of coevolution. Because they are generalists and most of their hosts have evolved limited defenses against parasitism, cowbird parasitism has exacerbated the effects of habitat loss on populations of several endangered bird species (Rothstein and Peer 2005; Peer et al. 2013a). This, combined with a view that cowbirds are misconstrued as "lazy," makes the animosity directed toward cowbirds from laypeople and scientists alike unique among brood parasites (Peer et al. 2013b; Peer and Abernathy 2017).

The negative attitudes displayed toward cowbirds obscure the fact that the cowbird serves as a model species for the study of learning and social behavior, physiology, evolution, and ecology and conservation due to its brood parasitic lifestyle. Indeed, the cowbird is the most intensively studied brood parasite in the world in a range of biological disciplines in part because of its large geographic range, relatively high abundance, and the ease with which it can be studied in captivity. For example, in the past 15 years, there has been an average of 32 publications each year on the common cuckoo (*Cuculus canorus*), whereas there has been an average of 41 publications on the cowbird (Web of Science 2017). Prior to the 1980s–1990s, most research on cowbirds focused on their basic biology, but this changed when concern increased over the cowbird's role in declining neotropical migrant bird populations (Peer et al. 2013a). Rothstein and Peer (2005) clarified a series of myths concerning cowbirds and their relationship to endangered songbird hosts and found that in almost every case, habitat loss was a major factor in population declines. In this chapter, we emphasize this brood parasite as a model species in the hope of stimulating new research. We begin by examining begging behaviors by cowbirds, followed by cowbird physiology, cowbird–host coevolution, cowbird social behavior, and the ecological and conservation implications of cowbird parasitism; lastly, we suggest future research directions.

9.2   Cowbird as a Model System for Studying the Development and Evolution of Nestling Begging Displays

9.2.1   The Influence of Proximate Factors on Cowbird Begging Displays

Like all obligate brood parasites, cowbird nestlings face the challenge of communicating their needs to unrelated host "parents." Critical in this endeavor is their begging behavior, the combination of physical movements and vocalizations to solicit food from parents, as well as responding to appropriate stimuli, such as parental food calls given to elicit begging. Cowbirds typically exhibit a higher response rate to inappropriate stimuli and beg more intensely than host young (Hauber 2003a; Rivers 2009), suggesting that they have evolved an especially rapid begging response to initiate food solicitation more quickly than nestmates and to be first to receive food from parents (Rivers 2007). The cost of this rapid response is that it entails errors and begging at inappropriate times, which may be costly via wasted energy or increased rates of nest predation (Dearborn 1998; Haskell 2002).

Although nestling begging by nonparasitic species changes in response to short-term need (i.e., hunger; Clark 2002), only a handful of studies have evaluated the hunger-begging relationship in cowbirds (Hauber and Ramsey 2003; Lichtenstein and Dearborn 2004; Rivers 2007; Rivers et al. 2013, 2014) despite the prediction that parasites would exhibit a begging response that is invariant relative to short-term need (Lichtenstein and Dearborn 2004). Such studies have mostly found that begging intensity increases with short-term need in cowbirds (Hauber and Ramsey 2003; Lichtenstein and Dearborn 2004; Rivers et al. 2013, 2014). The lone exception came from Rivers (2007) who found that cowbird begging was not strongly influenced by food deprivation and supplementation; however, this could have resulted from a methodological approach whereby begging displays were averaged across a 90-min period during which hunger levels changed. Indeed, additional work with the same population found strong differences in begging intensity as short-term need varied (Rivers et al. 2013, 2014), suggesting that cowbird begging intensity may be an informative signal of need across populations.

Studies have also examined how begging displays change relative to the size of host offspring against which cowbirds compete for food. Cowbirds have fledged from the nests of >140 host species and have been raised by hosts ranging from 8 to 110 g, a >17-fold range that spans 12–210% of the mass of an adult cowbird (Peer and Bollinger 1997; Ortega 1998). Most studies have evaluated cowbirds competing against smaller hosts (Dearborn 1998; Lichtenstein and Sealy 1998) and confirmed that begging is more intense in cowbirds than in hosts. Host parents biased feeding to the largest nestling in the brood, which is typically a cowbird (Dearborn 1998; Lichtenstein and Sealy 1998; Rivers 2007). Only one study (Rivers 2007) quantified begging across the range of host sizes cowbirds encounter, finding that begging intensity was greatest when cowbirds competed against both small and large hosts, with a reduction in begging intensity in similar-sized host nests. This resulted from

constraints on the amount of food cowbirds obtained in hosts of different sizes. Although cowbirds outcompeted nestmates of small hosts, food acquisition of small hosts was constrained by low parental feeding abilities. In contrast, parents of large hosts provided adequate food, but cowbirds were outcompeted by larger host young. Cowbirds that competed against nestlings of similar size obtained the greatest amount of food and ultimately reduced begging (Rivers 2007).

One area that remains virtually unexplored is the extent to which proximate factors influencing begging displays (e.g., nestmate size) have long-term consequence on cowbirds that carry into adulthood. Although the long-term consequences of postnatal environments have received widespread attention in birds (Monaghan 2008), only one study has examined how rearing environments influence begging displays downstream in brood parasites (Liu et al. 2016). That study found that cowbird fledgling vocalizations resulted in changes to vocal motor pathway of the forebrain used for vocal imitation in adulthood (Liu et al. 2016). Fledgling cowbirds produced begging vocalizations similar to host nestlings with which they were reared, suggesting they matched host offspring vocalizations (Liu et al. 2016). Therefore, host-specific variation in natal environments may lead to changes in adult vocalizations, which could affect song learning and reproductive success. More research in this area is warranted.

9.2.2   The Influence of Ultimate Factors on Cowbird Begging Displays

Theory posits that three types of costs, predation (Haskell 2002), physiological (Chappell and Bachman 2002), and inclusive fitness (Godfray 1995), collectively shape the expression of offspring begging. Theoretical models of begging in brood parasites assume that parasitic young do not incur inclusive fitness costs because they are raised by unrelated hosts and compete against unrelated host young (Motro 1989; Godfray 1995; Holen et al. 2001). In turn, this leads to the expectation that cowbirds are only constrained by predation and physiological costs and therefore should exhibit more intense begging than nonparasitic young. Few studies have evaluated cowbird begging relative to a nonparasitic close relative, and most have failed to assess links between parental provisioning and cowbird and host begging in nests of different host species (Hauber 2003b; Madden et al. 2005; Rivers 2007). In contrast, two recent studies tested begging displays by cowbirds and red-winged blackbird (*Agelaius phoeniceus*) when both species were raised in standardized heterospecific environments while also evaluating host feeding (Rivers et al. 2013, 2014). Those studies focused on two cowbird hosts that harbor the majority of cowbirds within a heavily parasitized host community in Kansas (Rivers et al. 2012, 2014): the Bell's vireo (*Vireo bellii*), a species that only raises a single cowbird host when parasitized (Kosciuch and Sandercock 2008), and the dickcissel (*Spiza americana*), a preferred cowbird host that typically raises several of its own young when they share the nest with parasitic young (Zimmerman 1983). Despite providing markedly different rearing environments, both studies found that blackbird begging

displays were more intense than cowbirds in both host species, against theoretical predictions, raising questions regarding the upper constraints on cowbird begging displays (Rivers et al. 2012, 2014).

A related study conducted at the same location found that multiple parasitism was common within the host community and that >70% of cowbird offspring shared the nest with at least one other cowbird (Rivers et al. 2010, 2012). Genetic analysis revealed the likelihood that two cowbirds sharing a nest were full siblings was 40.4%, indicating that cowbird offspring often competed against close relatives (Rivers et al. 2012), and suggests that the begging of Kansas cowbirds may have been reduced via competition with close kin. Identical experiments were conducted in a separate population (Illinois) where cowbirds are typically reared without other cowbirds to test whether begging intensity was linked to population-level variation in within-brood cowbird relatedness as predicted by theory (Godfray 1995). In support of theoretical expectations, Illinois cowbirds begged more intensively in four distinct components of the begging display: latency to beg, begging score (a composite measure of begging posture and time spent begging), call rate, and call amplitude (Rivers and Peer 2016). Moreover, the two other factors that could explain population-level differences in begging intensity, predation and physiological costs, were similar in the two populations. Therefore, the results from these experiments support the hypothesis that begging intensity in Kansas cowbirds has been reduced by inclusive fitness costs arising from kin to kin competition in host nests. These results are especially noteworthy because they illustrate that the begging displays of an obligate brood parasite, a group that has been viewed as representing the pinnacle of selfishness in developing birds (Davies 2000), can be constrained in the same manner as nonparasitic offspring.

9.2.3 Cowbird Begging Displays and the Evolution of Virulence

Study of nestling virulence has been limited almost exclusively to investigations of directed killing of host young (nestmate killers; Rivers and Peer 2016), which occurs in honeyguides and some cuckoos (Davies 2000). Nestmate killers are not known to exhibit variation in host-killing behavior; in contrast, non-evictors do not cause harm to hosts through direct aggression but instead outcompete host young for food (non-evictors; Rivers and Peer 2016). Begging intensity is constrained, in part, by relatedness (Godfray 1995), so begging serves as the mechanism by which virulence is mediated in non-evicting parasitic young (Kilner 2005; Peer et al. 2013a). In turn, the expression of virulence is influenced by the same factors that shape the intensity of begging displays, including the degree of relatedness between parasitic offspring and their competitors (Kilner 2005; Buckling and Brockhurst 2008). Theoretical models have found that virulence is reduced when related parasites compete for limiting resources (Kilner 2005; Buckling and Brockhurst 2008), but nearly all empirical tests of this idea have been limited to microparasites (bacteria, viruses) that reproduce asexually and are behaviorally and structurally simple (Frank 1994; Rumbaugh et al. 2012). In addition, prior studies have failed to assess low- and high-

relatedness parasite populations to evaluate putative mechanisms responsible for how virulence changes over ecological and evolutionary timescales (Buckling and Brockhurst 2008). One exception is the study by Rivers and Peer (2016) that assessed the consequences of population-level variation in begging intensity by evaluating cowbirds in the two populations described above. They found that the more intense begging of cowbirds in the low-relatedness population resulted in >10% reduction in body mass of dickcissel nestlings after only 5 days. This difference was detected despite there being no differences between the populations in dickcissel body mass at hatching when experimental broods were created. Body mass at fledging has been linked to post-fledging survival (Naef-Daenzer et al. 2001), so the population-level differences in virulence observed have the potential to affect host offspring survival and recruitment. Cowbird densities are high throughout much of the Great Plains of the USA, so the relationship between parasite relatedness, begging intensity, and cowbird virulence may hold in other high-density areas and should be the focus of future work. More broadly, it is common for a range of brood parasitic offspring to compete against conspecifics in host nests (*Clamator* cuckoos: Martínez et al. 1998; *Vidua* finches: Schuetz 2005; *Anomalospiza* cuckoo finch: Stevens et al. 2013), so parasitic begging displays that are constrained by relatedness may be present in other species as well.

9.3   Life History, Maternal Effects, and Parasites in Cowbirds

9.3.1   Reproduction and Life History

Female cowbirds are thought to be highly fecund and may lay 25–60 eggs per year (Scott and Ankney 1980), although genetic studies suggest this number is less (Alderson et al. 1999). Their reproductive strategy allows researchers to study the costs of egg production independent from parental care. These costs occur via resource limitation (energy/nutrition) or pleiotropic effects of elevated reproductive hormones over an extended period (Williams 2005; Nager 2006). For example, corticosterone (CORT) levels rise during egg production in birds (Wingfield and Farner 1978), and Dufty and Wingfield (1986) documented a prolonged period of elevated CORT during the breeding season in female cowbirds compared to females of other species. CORT is immunosuppressive when elevated for extended periods (Sapolsky 1992) and could lead to reduced immune function in female cowbirds (Merrill et al. 2013). There is increasing evidence that female cowbirds have adopted a fast pace-of-life strategy resulting in high annual reproductive effort, low levels of immune function (Merrill et al. 2013), reduced hematocrit (Keys et al. 1986), and low annual survivorship compared to male conspecifics and females of the related, nonparasitic red-winged blackbird (Ortega and Ortega 2009; Hahn and Smith 2011).

9.3.2 Maternal Effects

Maternal effects are any effect the maternal genotype or phenotype has on an offspring's phenotype (Wolf and Wade 2009). Females can influence offspring phenotypes in a non-genetic manner via differential allocation of resources such as hormones, antioxidants, antibodies, and other proteins and fats (Schwabl 1996; Grindstaff et al. 2003; Royle et al. 2011), as well as via differences in incubation behavior (DuRant et al. 2010) and resource provisioning to the chicks (Ghalambor et al. 2013). Because brood parasites such as cowbirds exhibit no parental behavior, they are limited in their capacity to influence the development of their offspring to pre-laying maternal effects that include (1) selecting among available hosts and depositing eggs in the nests of the highest-quality hosts, (2) adjusting resources to their eggs based on perceived differences in host nest conditions (*sensu* Merrill et al. 2017), or both. There is some evidence that female cowbirds discriminate among potential host nests and preferentially parasitize some species over others regardless of relative host abundance (Merrill et al. 2017). Moreover, there is some evidence that female cowbirds discriminate among nests within a species and preferentially parasitize nests with eggs that are small relative to the host species' average but only for host species with eggs larger than those of the cowbird (Merrill et al. 2017). Such selectivity could confer a competitive advantage to the cowbird in the nests of species which may challenge the cowbird chick for access to resources. There is also emerging evidence that female cowbirds adjust resources to their eggs based on environmental conditions and features of the host nest (Merrill personal observation). Maternal resource allocation likely influences the competitive capabilities of nestling birds, and this may be especially important for nestling cowbirds. Cowbird eggs have a short incubation period (Briskie and Sealy 1990); they beg more intensely compared to hosts (see above) and develop rapidly (Kilpatrick 2002). A nestling cowbird may compete for resources against many small nestmates or a few large nestmates depending on the host species. Maternal effects may thus be especially important for appropriately preparing the cowbird chick for its host nest. Schwabl (1996) proposed that females could differentially allocate testosterone levels among eggs, thereby manipulating the competitive abilities of the young in the nest, and while there is some support for this idea (Eising et al. 2001), there is no indication that cowbird chicks have consistently higher levels of testosterone compared to their hosts (Hauber and Pilz 2003; Hahn et al. 2005). Hahn et al. (2017), however, found that cowbird eggs had higher levels of yolk androgens in multiply parasitized nests, indicative of a potential response to elevated levels of nest competition from other cowbird nestmates. Moreover, Royle et al. (2011) found that levels of the antioxidant vitamin E in cowbird eggs positively covaried with levels of vitamin E in the eggs of the host red-winged blackbird. They proposed that these antioxidants are critical for combating elevated levels of reactive oxygen species resulting from high begging activities and accelerated growth rates of the nestling cowbirds and that female cowbirds should allocate antioxidants to their eggs at levels comparable to the host (Royle et al. 2011). These results suggest that female cowbirds may be capable of affecting their offspring via traditional (e.g., differential

allocation of egg resources) and nontraditional forms (e.g., host nest selection) of maternal effects.

9.3.3   Cowbirds as Hosts

Cowbirds have been recorded parasitizing nearly 250 species (Lowther 2013). Most avian species are host to numerous ectoparasites (Clayton and Johnson 2001) and potentially a suite of other parasites. The host-generalist nature of cowbirds may expose them to a much broader range of parasites and pathogens than their nonparasitic relatives. Hahn et al. (2000) found that cowbirds acquired lice from some hosts, although it is unclear if cowbirds are suitable long-term hosts for the majority of ectoparasites they encounter in host nests because many are host-specific (Clayton and Johnson 2001).

In support of the hypothesis that cowbirds should have more robust immune systems due to increased exposure, Reisen and Hahn (2007) and Hahn et al. (2013) examined responses to West Nile virus and innate immune function among cowbirds and related icterid species and found that cowbirds were the most immunocompetent species examined. However, Merrill et al. (2013) found that levels of immune function in cowbirds varied by sex and season and that during the breeding season females exhibited lower levels of bacteria-killing ability (BKA) and a reduced response to an injection of phytohemagglutinin (PHA) compared to male cowbirds and female red-winged blackbirds. Discrepancies among studies could be a result of different assays assessing different immune system components.

9.4   Coevolution

9.4.1   Cowbird–Host Coevolution

The interactions between cowbirds and their hosts differ from other parasite–host systems because they are at an earlier stage of coevolution (Rothstein et al. 2002). Cowbirds have been parasites for approximately 3–4 mya, whereas lineages such as the common cuckoo have been for 6–8 mya and *Viduidae* and *Anomalospiza* for 13 mya (Rothstein et al. 2002; Sorenson et al. 2004). This may account for one of the most enigmatic feature of cowbird–host interactions which is the widespread acceptance of parasitism by most cowbird hosts. Models suggest that when selection from parasitism is particularly strong, egg rejection can evolve rapidly (Soler 2014). However, there are many cowbird hosts that show no adaptive response to parasitism and yet raise none of their young when parasitized (Peer et al. 2013a, b). Cowbird hosts also show relatively little intraspecific variation in rejection response compared to Old World cuckoo hosts (Rothstein 1990).

9.4.2   Why Do so Many Hosts Accept?

Numerous hypotheses have been proposed to explain acceptance of parasitism by cowbird hosts including (1) evolutionary lag, (2) evolutionary equilibrium, (3) mafia enforcement, and (4) source–sink population dynamics. Rothstein (1975) concluded that evolutionary lag was the best explanation for acceptance by cowbird hosts, and this continues to be the case (see Peer and Sealy 2004a). Hosts that reject cowbird eggs nest in open habitats or along forest edges and have had the longest time to coevolve with cowbirds (Peer et al. 2000; Peer and Sealy 2004a; Soler 2014). Rejecter species may also be more responsive to multiple parasitism that represents a greater threat (Lang et al. 2014), whereas accepters accept parasitism regardless of whether there is single or multiple cowbird eggs in the nest (Ward et al. 1996).

Although lag can account for some acceptance, there are hosts that have been parasitized for very long periods of time and yet accept parasitism (e.g., red-winged blackbird; Peer and Sealy 2004a). The evolutionary equilibrium hypothesis proposes that egg rejection entails costs which make acceptance of parasitism an option with greater net benefits. Potential costs include recognition errors, whereby hosts with eggs that resemble those of the cowbird accidentally reject their eggs, and rejection errors in which a host damages its egg when attempting to remove the thick-shelled cowbird egg. Recognition difficulties occur in grassland hosts and the northern cardinal (*Cardinalis cardinalis*), which have eggs resembling those of the cowbird (Peer and Sealy 2004a). Grassland birds reject non-mimetic eggs more frequently than cowbird eggs (Peer et al. 2000). Cardinal eggs can be similar to cowbird eggs, and cardinals are more likely to reject immaculate eggs that differ from their own, and they also eject some eggs with reduced ultraviolet reflectance (Abernathy and Peer 2016). Cardinal clutches have a high degree of intraclutch egg variation, and this, combined with the poor survival of cowbirds in cardinal nests, may indicate that rejection costs make acceptance of the optimal strategy (Abernathy and Peer 2016). Hosts with small bills risk rejection errors because they are incapable of grasp-ejecting cowbird eggs and instead must puncture-eject them. Because cowbirds lay thick-shelled eggs, host bills may bounce off the cowbird eggs into their own causing damage to them (Sealy 1996). However, these costs appear to be negligible in hosts such as the warbling vireo, which has a small bill and only loses 0.3 eggs for every cowbird egg ejected (Sealy 1996).

Another hypothesis for acceptance of parasitism is that hosts are forced to due to mafia tactics. A brood parasite revisits a nest it has parasitized, and if its egg has been rejected, it will destroy the nest contents (see Chap. 15). For this scenario to occur, the following must be true: (1) the parasite must revisit nests they have parasitized (Soler et al. 1995), (2) the parasite must be able to distinguish between its eggs and those of the host (Sealy and Underwood 2012), and (3) the host must be able to raise some of its young when parasitized because acceptance of a parasitic egg should be more beneficial than ejecting the egg and then having the nest subsequently destroyed (Soler et al. 1995). Hoover and Robinson (2007) simulated egg ejection by removing cowbird eggs from prothonotary warbler (*Protonotaria citrea*) nests and then used an experimental approach to allow cowbirds to reenter some nestboxes

or prevented reentry into others. They found that failure was significantly greater at nests that cowbirds could access compared to those they could not enter and concluded that cowbirds forced warblers to accept their eggs (Hoover and Robinson 2007).

The one criterion listed above that was satisfied in the Hoover and Robinson (2007) study was that warblers raise some of their young when parasitized. It was unclear whether the same females that laid the eggs revisited and destroyed the nest contents following cowbird egg removal. It is also unclear if female cowbirds can recognize whether their eggs have been ejected because of the similar appearance of warbler and cowbird eggs (Peer and Sealy 2004a). Although there is evidence female cowbirds can distinguish between cowbird and host eggs (Dubina and Peer 2013), differentiating between two similar eggs in a dark cavity might be difficult. Likewise, mafia tactics should evolve after a host begins ejecting the parasite's eggs. However, it would also be challenging for a female warbler to recognize a cowbird egg in her dark nest, and there is no evidence that warblers eject foreign eggs (Hoover 2003). There have been no other reports of mafia effects in cowbirds (McLaren and Sealy 2000).

One final possibility is that large-scale source–sink population dynamics may be responsible for the lack of defenses against cowbirds (Robinson et al. 2013). Because there are still large areas of cowbird-free forests in North America (Fry et al. 2011), many hosts reside in areas where there is no selective pressure for evolving defenses (Robinson et al. 2013). The lack of host defenses may not be a case of evolutionary lag; rather, it may reflect the extent to which evolution acts slowly in landscapes in which habitats are population sinks (Holt 1996). Much of the Midwestern USA, where cowbird parasitism is extensive, is also characterized by high nest predation rates (Robinson et al. 1995b). There is so little reproduction in these woodlots that defenses would evolve slowly because the few young produced would be swamped by young produced in large forests in which parasitism is rare (Barabas et al. 2004; Robinson et al. 2013). Paradoxically, the lack of host defenses may be an indicator of overall population health. As long as there are large unfragmented habitat patches that can act as population sources, there may be no need for management practices such as cowbird trapping.

9.4.3 What Do We Know About Hosts That Have Evolved Egg Rejection Behavior?

Hosts that have evolved rejection nest in open habitats and along forest edges, tend to be large with bills (>17 mm) that facilitate cowbird egg ejection, and have eggs that differ in appearance from those of cowbirds (Rothstein 1975; Peer and Sealy 2004a). Hosts reject eggs based on differences in size, background color, spotting, and ultraviolet reflectance (Rothstein 1982; Abernathy and Peer 2015, Chap. 22), but reduction of intraclutch egg variation does not appear to facilitate rejection (Abernathy and Peer 2014). Furthermore, some host species such as the cedar waxwing and yellow warbler (Rothstein 1976; Guigueno and Sealy 2011) do not

always eject when parasitized (see Chap. 25). These hosts decrease efforts to remove cowbird eggs when the costs of doing so are prohibitive relative to the risk and costs of being parasitized. Once a host evolves egg rejection, it may be retained up to several million years in the absence of parasitism (Rothstein 2001; Peer and Sealy 2004b; Peer et al. 2007, 2011a, b), although there are cases of phenotypic plasticity (Peer and Rothstein 2010; Kuehn et al. 2016) and partial but never complete loss of rejection (Peer and Sealy 2004b; Kuehn et al. 2014).

9.4.4 Other Responses by Hosts to Cowbird Parasitism

Smaller hosts may respond to parasitism by desertion or by burying the cowbird egg in the nest lining. Our understanding of nest desertion and how often it is a *bona fide* response to parasitism is lacking in cowbirds. Desertion of naturally parasitized nests is more common than desertion of experimentally parasitized nests, suggesting that observing a cowbird at the nest may make a host more responsive (Strausberger and Burhans 2001). Hosoi and Rothstein (2000) found that hosts nesting in non-forested habitat were more likely to desert parasitized nests than those in forests.

9.4.5 Cowbird Response to Host Defenses

There has been little selection on cowbirds to modify the appearance of their eggs in response to host discrimination. Numerous hosts lay eggs that resemble cowbird eggs, especially those nesting within the core of the cowbird's range, and many of these hosts are more likely to eject non-mimetic eggs. One study examined hosts that nest largely outside of grasslands but found no evidence of mimicry (Underwood and Sealy 2008). Cowbirds may cause rejecters to misimprint on and accept cowbird eggs as their own by parasitizing naïve individuals, but it is unclear if this is a by-product of high local cowbird abundance or an evolved strategy (Strausberger and Rothstein 2009). A response to host egg discrimination occurs in the brown-headed cowbird's sister species, the shiny cowbird, which has wider eggs where a favored host uses egg width to detect parasitic eggs (Mason and Rothstein 1986). Finally, cowbirds may multiply parasitize hosts, and this may be a strategy to increase host acceptance (e.g., Gloag et al. 2012).

In contrast to egg appearance, eggshell structure has been modified in at least two ways. First, while not a defense against host egg rejection, cowbird eggshells have greater porosity that appears to enhance embryonic respiration and allow cowbird nestlings to hatch sooner than most hosts (Jaeckle et al. 2012). Second, cowbirds lay eggs with thick shells which resist host egg puncture (Spaw and Rohwer 1987) and may reduce damage to cowbird eggs when contacting host eggs during laying (Rothstein 1990). Less than one-third of the rejecter hosts in North America are known to puncture-eject, which suggests that thick eggshells evolved for another reason, perhaps to protect the cowbird egg during laying, with resistance to puncture-ejection being a benefit for the few hosts that demonstrate it.

9.5   Song, Mating and Spatial Systems, and Social Behavior

9.5.1   Spatial Behavior

Most birds choose a breeding habitat that meets the needs of their young and themselves. But cowbirds can uncouple breeding and feeding activities by carrying them out in different places (Rothstein et al. 1984; Chace et al. 2003), which allows them to exploit a larger range of habitats than nonparasitic birds (Rothstein 1994). For example, in the Sierra Nevada of California cowbirds occupied breeding habitat where egg laying and mating take place in forests and meadows from sunrise until late morning/early afternoon and then congregated at feeding sites (Rothstein et al. 1980, 1984). Commuting distances between breeding and feeding sites ranged up to 7 km in the Sierra (Rothstein et al. 1984) and up to 16 km in New Mexico (Curson and Mathews 2003), so a single feeding area can be visited by cowbirds breeding over a large area (Anderson et al. 2012). Cowbirds are social at afternoon feeding sites, but both males and females are alone or in small groups in breeding areas where they respond aggressively to playback of sex-specific vocalizations (Dufty 1982; Rothstein et al. 1988; Yokel 1989). This alone does not mean that cowbirds are territorial because breeding ranges can overlap (Rothstein et al. 1984). However, the aggression suggests some attempt to defend breeding areas.

Cowbirds are highly interactive in the morning, and vocalizations typically occur when >1 individual is present. Unlike most passerines, male cowbirds sing close to others (<1 m) while facing them, so it is often possible to determine the individual to whom a song is directed. Males sing to and court females in the morning if no other males are present, and males sing to each other if no females are present. However, if a male is courting a female and other males arrive, nearly all subsequent songs will be between males (Rothstein et al. 1988). Copulations occur only if no other cowbirds are nearby (Gorney-Labinger and Rothstein 2002), but female choice is likely influenced by the numbers of songs males direct toward them at other times and in male counter-singing sessions. Experiencing male song stimulates female reproductive activity in captivity (West et al. 2002) but it is unknown whether this occurs in the wild.

9.5.2   Song Development and Function

Cowbirds have played a major role in understanding vocal development and function in birds, a subject that has provided insights into the development of human speech (Brainard and Doupe 2002). Similarities between human and songbird vocal development include a sensitive period early in life and the need for auditory feedback. Partly because of their easy adjustment to captivity, cowbirds have enabled researchers to study the extent to which different aspects of vocalizations are dependent on experience. A long-standing need in bird song research was a way to assess female choice. Although males in most passerines respond aggressively to field playbacks of male song, playbacks elicit little change in females. This problem

was partially solved by King and West (1977) who found that captive female cowbirds deprived of male contact respond to playback of male song with the lordosis posture, i.e., copulation solicitation display (CSD). These results led to the discovery that administration of estradiol could cause females of many species to respond to male songs with CSDs (Searcy and Marler 1981).

The vocalization type with which female cowbirds were first tested is perched song (PS), which is primarily used when males are near conspecifics (Rothstein et al. 1988). It has introductory notes below the frequency of most bird song followed by components above the frequency of most species' songs. The basic structure is innate (King and West 1977), but males build repertoires by copying the PS types of older males (O'Loghlen and Rothstein 2010a, 2012a). PS is accompanied by a display involving wing spreads, bowing and tail cocking, and often ending in bill wiping (O'Loghlen and Rothstein 2010a, b). These movements are coordinated with the production of sound (Cooper and Goller 2004), are innate (Hoepfner and Goller 2013), and are more intense when directed at a male (O'Loghlen and Rothstein 2010b, 2012b). Video and sound of a male displaying and singing elicits stronger CSD responses than sound alone (O'Loghlen and Rothstein 2012b).

Male cowbirds also perform flight whistles (FW) composed of two to four mostly pure tone syllables (Rothstein et al. 1988) that are used in long-distance communication, in flight, or by a perched male that has landed or is about to fly away. FWs show extraordinarily well-defined spatial dialects, and this is another reason cowbirds have been key in birdsong studies (Rothstein and Fleischer 1987). FW dialects often differ in overt ways such as the three-syllable FW found in the Mammoth Lakes area of the Sierra Nevada, California, and the adjacent four-syllable FW found at Convict Lake. FW dialects occur throughout the cowbird's range (Rothstein and Fleischer 1987; O'Loghlen and Rothstein 2002a). See Fig. 1 for examples of male vocalizations.

Although oscine passerines show intraspecific song variation, it was thought that cowbirds would be an exception and have innate unvarying vocalizations due to their brood parasitism. But the high degree of variation in FWs suggests that learning is involved (O'Loghlen and Rothstein 1993, 1995, 2010a, b). Most cowbirds do not complete vocal development until they are 2 years old because adult males stop singing when female cowbirds stop laying, which limits the opportunity for young birds to memorize song during their hatch year (O'Loghlen and Rothstein 1995). Yearling males are sexually mature (Gros-Louis et al. 2006) and perform FWs but do not have complete local FWs until the second year (O'Loghlen 1995).

Adult males within a FW dialect have PS repertoires assembled from a pool of about ten song types (O'Loghlen and Rothstein 2002a, b). Some PS occurs over areas that encompass multiple FW dialects, but adults within a FW dialect have greater PS sharing than with males from other dialects (O'Loghlen 1995). As with FWs, PS repertoires of many yearling males are deficient and have a larger proportion of unique song types (O'Loghlen and Rothstein 1993, 2002a, b). Yearling males that hatched early in the previous breeding season may perform the appropriate FW and PS types having experienced local song types as juveniles (O'Loghlen and Rothstein 2002b).
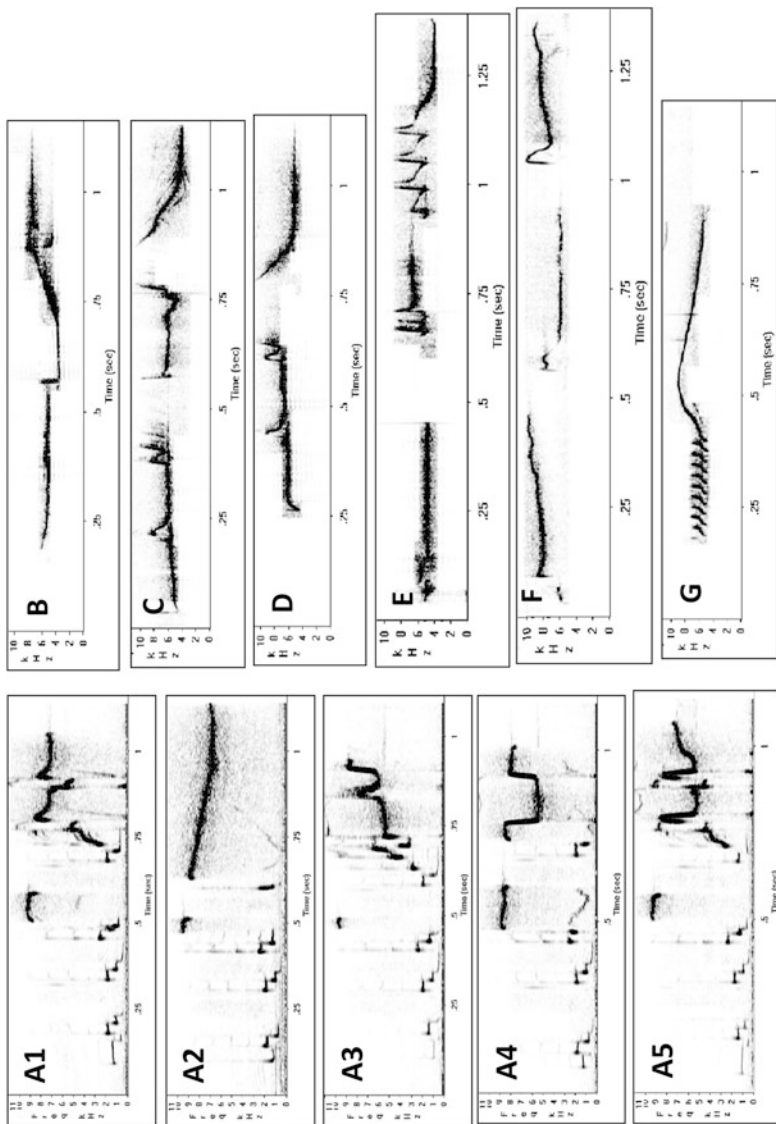
Fig. 1 Perched songs (PSs) and flight whistles (FWs). Panels A1–A5 are the PS types in the repertoire of a single male from Santa Barbara, CA. Panels B–G are FWs done in different populations. Note that PSs always follow distinctive structural rules, very low frequency elements followed by mush higher sounds whereas FWs have a much narrower frequency band but are variable in duration and sound type (usually modulated pure tones but with some FWs containing buzzes or trills). FW B is the type done in the Santa Barbara, CA area. FWs C, D, and E are from the Convict, Mammoth and Lee Vining dialects of the eastern Sierra of California (Rothstein and Fleischer 1987; O'Loghlen and Rothstein 2010a). FWs F and G show further diversity and are from dialects in Oklahoma and Washington State

9.5.3   Mating System

Although cowbirds do not provide parental care, observations and genetic studies show that most cowbirds are monogamous, but there are populations that exhibit polygyny (Teather and Robertson 1986; Alderson et al. 1999) and promiscuity (Elliott 1980). Female choice among potential mates clearly occurs because females choose the time and place of mating by attracting a male by broadcasting their chatter or rattle call, which explains why chatter playbacks attract males (Rothstein et al. 1988). Females also use this call to signal aggression when sung to by males and when competing with other females (Dufty 1982).

Indirect evidence indicates that female choice is based on male genetic quality. In an experiment in which a female's consort was removed, females tended to form a pair bond with an already-mated male suggesting that "widowed females" did not chose new mates randomly (Yokel and Rothstein 1991). Age is one indicator of genetic quality because all male consorts were at least 2 years old (Yokel 1989). Yearling males and some adults fail to mate, but all females breed (Fleischer et al. 1987). Females can identify adult males (>2 years old) by their shinier black plumage and absence of brownish underwing coverts (Ortega 1998). These coverts are revealed if males spread their wings during a PS (O'Loghlen and Rothstein 2010a, b), which makes the display an honest signal of age and may explain why it evolved. The FW type and PS repertoire furnish additional evidence of age since adult males are more likely to have vocalizations that match a local dialect (O'Loghlen and Rothstein 1993, 2002a, b).

Young males memorize the local FW and PS types done by older males. Yearling males are attracted to playback of adult vocalizations in the spring (Snyder-Mackler and White 2011) but do not perform the local FW and PS types until they are 2 years old (O'Loghlen and Rothstein 1993). Females hear more songs from dominant males (Rothstein et al. 1986), and the amount of singing correlates with male reproductive success in captivity (Gros-Louis et al. 2006). Song development in young males is also affected by older females that exert more influence on the vocal development than juvenile females (Miller et al. 2008). In nature, females experience FWs and PS repertoires of local males, and males respond to female chatter calls with FWs. CSD experiments in the lab show that females find the local FW and PS types more stimulating than those from other dialects (O'Loghlen and Rothstein 1995, 2003).

A further indication of the importance of male vocalizations occurs during copulation. Males produced FWs as they fly to a chattering female and rush through their vocal repertoire as they mount the female, which allows females a final assessment of a male's vocalizations. Mating males perform these loud vocalizations with virtually no intervening silence, something done only during copulations (Gorney-Labinger and Rothstein 2002) and thus advertise copulations, as in other animals (Hauser 1993).

9.5.4   Studies Conducted in Captivity

Because cowbirds readily adapt to captivity, complex questions about social behavior can be tested by mixing birds in various combinations. However, these results can be difficult to relate to natural situations where cowbirds move large distances and experience social dynamics that cannot be replicated in captivity. For example, White et al. (2012) found that captive male cowbirds introduced to different individuals developed different behaviors than males in static groups which never occur in nature. Captive groups have also been used to assess whether individuals show assortative mating (Freeberg et al. 2008) by mixing birds from distant locations, but such mixing is unlikely in nature, and distant populations that show assortative mating in captivity may be linked genetically by a series of populations found between the distant localities (Fleischer and Rothstein 1988). It is unclear how captive studies relate to events in nature as even large cages cannot replicate the social flux that cowbirds experience (Rothstein et al. 1984). Moreover, captivity alters behaviors and endocrine systems (Calisi and Bentley 2009). The most meaningful results are likely when captivity is used to test explicit questions prompted by field studies (O'Loghlen and Rothstein 2003).

9.6   Cowbirds as Tests of Hypotheses Concerning the Impact of Brood Parasites on Host Population Dynamics

9.6.1   Effects of Cowbirds on Host Fitness

Parasitism by cowbirds reduces host fitness in nearly all species parasitized (Ortega 1998). These fitness costs result from multiple behaviors including (1) host egg removal (Sealy 1992); (2) damage to host eggs during laying by cowbirds (see above); (3) early hatching and rapid development of cowbird nestlings, which enables them to monopolize the food delivered by their foster parents (see above); (4) the choice of mostly smaller host species, which means that the larger cowbird nestlings monopolize food delivered to the nest (see above); and (5) loud begging by cowbird nestlings, which may increase conspicuousness of nests to some predators and decrease food delivered to host nestlings (Dearborn 1999). These costs are multiplied in nests that receive more than one cowbird egg per nest, a common occurrence in parts of North America with high cowbird densities (Robinson 1992; Rivers et al. 2010). There is evidence that raising cowbirds may be more costly for adults than raising their own young, which suggests that cowbird nestlings may cause parents to work harder to feed them (Hoover and Reetz 2006) and to renest more often because females that raise a cowbird are more likely to initiate a second brood than those that raise a brood without a cowbird possibly to recoup the losses after raising a cowbird (Louder et al. 2014).

The extent to which cowbirds threaten host populations varies greatly among hosts, habitats, years, landscape cover, and regions (Robinson et al. 1995a). Small hosts such as flycatchers (family Tyrannidae) that have slow developmental rates

and small clutches tend to fledge very few host young when parasitized (Peer et al. 2013a), whereas larger hosts such as wood thrushes (*Hylocichla mustelina*) can raise their young alongside cowbirds and only incur costs in regions where parasitism levels are extremely high such as the Midwest (Robinson et al. 1995b). Host species with small ranges and fragmented remaining habitat patches are likely to be particularly threatened by cowbird parasitism because they lack refugia from parasitism (Smith et al. 2000; Wilsey et al. 2013). Cowbirds have also been blamed for causing population declines in widespread species, even those in which exposure to cowbirds varies throughout their breeding ranges (Mayfield 1977).

One mechanism that has been hypothesized to cause these long-term declines is an increase in the proportion of "sink" habitat (*sensu* Pulliam 1988) in landscapes in which breeding habitat is fragmented and therefore exposed to cowbird parasitism (Donovan et al. 1995; Robinson and Hoover 2011). Small forest fragments surrounded by agriculture and pasture have abundant cowbird feeding habitat in close proximity (Thompson 1994). These areas tend to have very high cowbird populations (Cummings and Veech 2013) and parasitism levels (Robinson et al. 1995b), which can drive host productivity below levels necessary to compensate for mortality (Donovan et al. 1995). Because cowbirds search for nests in areas that can be up to 16 km from where they feed (see above), only a few foraging sites such as pastures, stockyards, or agricultural fields can support cowbird populations in large proportions of the landscape (Morse and Robinson 1999, but see Stoklosa et al. 2014). Decreases in nesting success resulting from cowbird parasitism have been implicated in creating sink habitat (Robinson and Hoover 2011; Robinson et al. 2013). These regions, however, also typically have very high levels of edge-associated nest predation (Donovan et al. 1997), which can make it difficult to disentangle the effects of losses to cowbird parasitism from losses to nest predators. Nevertheless, there is little doubt that the combined effects of predation and parasitism create steep source–sink habitat gradients and that these gradients are related to habitat fragmentation (Robinson and Hoover 2011).

Some host species have complex and seemingly adaptive "decision rules" that enable them to avoid areas with high nest predation rates and return to areas where most nests escape predation (Hoover 2003). Most hosts, however, do not have comparable decision rules with respect to cowbird parasitism. They are just as likely to return to an area where they raised cowbirds than to an area where they raised their young as long as those nests escaped predation (Hoover 2003). Therefore, cowbird parasitism may threaten populations because habitats with high cowbird parasitism, but low rates of nest predation, continue to attract and retain breeding populations of hosts, even if parasitism drops nesting success below the source–sink threshold. These habitats have been called "ecological traps" (*sensu* Gates and Gysel 1978), which can be operationally defined as attractive sink habitat (Robinson and Hoover 2011).

Management plans that reduce habitat fragmentation to lessen cowbird parasitism have become a core element in landscape-level conservation (Llewellyn et al. 1996; Beissinger et al. 2000). Preservation of very large, mostly forested tracts reduces both nest predation and cowbird parasitism in the Midwest (Robinson et al. 1995b).

Such large tracts may act as source habitat that produces surplus individuals that recolonize small patches in which local populations are not viable in the absence of immigration (Donovan et al. 1995; Robinson et al. 1995b). For critically endangered host species, cowbird control has also been recommended as a more direct method of reducing the negative consequences of cowbird parasitism (Smith et al. 2000), although this approach is not without controversy (Rothstein and Peer 2005).

9.6.2   Role of Cowbirds in the Conservation of Endangered Host Populations

Cowbird parasitism has been at least partly blamed for the endangerment of several songbird species or subspecies that have small remaining populations in geographical ranges in which cowbird habitat dominates large proportions of the remaining landscape (Smith et al. 2000). Cowbird trapping has been used and has been shown to increase nesting success for the Kirtland's warbler (*Setophaga kirtlandii*), least bell's vireo (*Vireo bellii pusillus*), southwestern willow flycatcher (*Empidonax traillii extimus*), and black-capped vireo (*Vireo atricapilla*) (Smith et al. 2000). At least some of these populations recovered or stabilized after cowbird control was initiated. Kirtland's warblers and black-capped vireos, for example, experienced parasitism levels of well over 50% of nests, levels that the populations were unlikely to sustain over long timescales. As such, they appear to be conservation-dependent species (Rockwell et al. 2012; Wilsey et al. 2013). All of these endangered species, however, also have small population sizes resulting from extreme habitat loss and disturbance, which reduces habitat quality and likely also increases nest predation, and may suffer from winter habitat loss as well (Rothstein and Peer 2005; Rockwell et al. 2012). Many population recoveries were associated with improved habitat management at the same time that cowbird control was being practiced. The recovery of the Kirtland's warbler, in particular, may have been driven more by an accidental habitat burn that greatly enlarged the amount of suitable breeding habitat rather than by cowbird control per se (Rothstein and Peer 2005; Rockwell et al. 2012). Therefore, cowbird control appears to work best in association with intensive habitat management and may not be necessary once populations have recovered and occur over wide enough area to have refugia from cowbird parasitism (Rothstein and Peer 2005). Some species, however, may still require more focused cowbird control efforts, especially in landscapes dominated by cowbird feeding habitat such as rangelands in which the entire landscape matrix provides feeding habitat, including much of the habitat occupied by the endangered hosts themselves (Smith et al. 2000; Brodhead et al. 2007; Wilsey et al. 2013).

9.6.3   Landscape Management

The most sustainable long-term strategy for reducing the negative effects of cowbird parasitism on their hosts is to reduce habitat fragmentation by enlarging habitat

patches (Brunswig et al. 2016). This strategy would potentially benefit hosts by increasing their populations, decreasing cowbird populations via a reduction in afternoon feeding habitat, and increasing "interior" habitat that is far from cowbird feeding areas that might act as source habitat. Although evidence for this strategy is mixed (see above), this approach should also reduce excessive levels of nest predation associated with edge-adapted predators such as raccoons (*Procyon lotor*) and feral species. For landscapes such as Eastern North America, the most important element of any conservation strategy would be to maintain the large forested areas in regions such as those in the Appalachians that can act as source habitat where there are few cowbirds. Landscape-level management that reduces the negative effects of habitat loss and fragmentation may eliminate the need for large-scale cowbird control.

Concluding Remarks and Future Directions

The cowbird is an ideal species for examining questions regarding host–parasite coevolution, maternal effects and physiology, song learning and patterns of cultural transmission, and ecology and conservation due to its life history as a generalist brood parasite. Avenues for future research in host–parasite coevolution include continuing to investigate alternatives to evolutionary lag for the widespread acceptance of parasitism by cowbird hosts. Many hosts have been exposed to parasitism for relatively long periods and yet do not appear to respond adaptively. Further examination of cowbird counter-strategies including multiple parasitism, farming, and whether mafia behavior is a widely used strategy is needed. Studies of cowbird nestlings when competing against large hosts across a range of age differentials will elucidate how early hatching by cowbirds enhances survival when raised by a large host. We also need to determine how rearing environments influence adult phenotype, which components are robust against early competitive environments, and whether these relationships differ from nonparasitic relatives. Additional experiments on whether cowbird begging is linked to population-level factors, including within-brood relatedness, are also needed. Equally valuable are studies of whether cowbirds discriminate between conspecific and heterospecific young to modulate begging.

Data on hormonal and immunological profiles of cowbirds would increase our understanding of the trade-offs of individual life history strategies. Experimental manipulation of egg production would be an effective way to examine costs of egg laying, including CORT levels, immune function, oxidative stress, and telomere length. Another major question is the reason female cowbirds in diverse regions lay eggs at the same rate of ~ 0.7 per day.

The degree to which cowbirds are territorial, especially at low densities, is still unclear. We know that male song stimulates female reproductive activity in captivity (West et al. 2002), but we need to determine if this occurs in nature. Testing whether female sexual responses are influenced by differences

(continued)

in yearling versus adult male plumages would provide valuable information on female choice. Similarly, indirect evidence indicates that female choice is based on male genetic quality, and testing this hypothesis with direct genetic evidence is needed. Additional studies are also necessary to assess variation in population levels of social and genetic monogamy.

One promising approach to cowbird management is to use trapping programs as experiments to identify factors that limit breeding populations. We need better data on adult survival from marked host populations because relatively small increases in survival estimates for forest hosts can have a profound effect on the source–sink threshold and therefore the extent to which parasitism limits populations. Once understood, we will have a better understanding of the levels of landscape management needed to create sustainable regional populations. We also need to use large-scale habitat management projects as experimental tests of the effects of landscape fragmentation on cowbird parasitism. We need a better understanding of the role of different kinds of landscape matrices in providing cowbird feeding habitat, and we need to study whether cowbirds themselves may have source–sink habitats based on host community composition and the average nesting success of their hosts.

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Cover illustration: Common cuckoo, the best studied brood parasite, fed by a robin. Photo by Oldřich Mikulica

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