

SECTION II: THE BASIS FOR COWBIRD MANAGEMENT: HOST SELECTION, IMPACTS ON HOSTS, AND CRITERIA FOR TAKING MANAGEMENT ACTION

JAMES N. M. SMITH

THE PROBLEM

The Brown-headed Cowbird (*Molothrus ater*) uses many different hosts over its large range (Friedmann and Kiff 1985, Lowther 1993). Because of this fact, countless host populations are exposed to potential reproductive costs from cowbirds. The papers in this section deal with two key questions: (1) What are the magnitudes of these costs to specific host populations? (2) When is intervention necessary to protect vulnerable populations of hosts, and are there general rules of thumb to help managers decide that intervention is timely?

Before discussing these issues in more detail, I note that the costs imposed by cowbirds on hosts, and the occasional need to intervene to reduce these costs, are emotionally charged matters. To some managers of sensitive species (e.g., papers in Section III *this volume*), and to many members of the amateur birding community (Holmes 1993), cowbirds seem an obvious threat to populations of small songbirds, and one that can be readily ameliorated by trapping. However, four points in opposition to this view should be considered: first, the Brown-headed Cowbird is a native North American species (even though it has expanded its range greatly in the past) with certain intrinsic rights; second, the abundance of Brown-headed Cowbirds is low in areas of extensive forest; third, Brown-headed Cowbird numbers have recently declined over much of their range (Robinson et al. 1995a, Peterjohn et al. 1999, Wiedenfeld 1999); fourth, even where interactions with host individuals are strong, cowbirds may have little effect on host population dynamics (see below). Even people inclining to the view that cowbird impacts on host are often small (e.g., Rothstein and Robinson 1994), however, acknowledge that there are situations that justify strong management intervention.

ESTIMATING IMPACTS OF COWBIRD PARASITISM

THE RANGE OF COSTS IMPOSED BY COWBIRDS

Cowbirds impose a variety of costs on individual hosts (reviewed in Lorenzana and Sealy, this section): (1) egg removal (Sealy 1992) and (2) egg puncture (Peer and Sealy, this section), both of which can lead to desertion of clutches;

(3) occasional nestling removal (Tate 1967); (4) destruction of entire clutches or broods of hosts (Scott and McKinney 1994; Averill-Murray et al., this section); (5) reduced hatching success of host eggs (Peer and Bollinger 1999; Peer and Sealy, this section); (6) reduced survival of host young (Payne 1977, May and Robinson 1985, Payne and Payne 1998; Sedgwick and Iko, Chace and Cruz, this section); (7) increased energetic expenditure while rearing broods of nestlings and fledglings containing cowbirds (Smith and Merkt 1980, Woodward 1983) and perhaps consequent delays in renesting; (8) reduced post-fledging survival (Whitfield and Sogge, Sedgwick and Iko, this section); (9) reduced adult survival (Sedgwick and Iko, this section) and (10) reduced future fecundity (Lorenzana and Sealy, this section).

Brood parasitism always imposes costs on host individuals that get parasitized, but parasitism does not necessarily have any effect on the dynamics of host populations. Failure to appreciate this fact explains much of the lack of understanding between advocates and opponents of killing cowbirds in control programs. Costs due to parasitism, however, are likely to have consequences for populations if average reproductive success per host is already near the threshold level required to replace adult mortality in the absence of parasitism. If, on the other hand, hosts are reproducing at well above the level needed to replace adults that die, and host numbers are regulated by site-dependent mechanisms such as limited breeding habitat (Rodenhouse et al. 1997), parasitism merely removes host individuals that would otherwise emigrate or die before reproducing. Finally, host populations experiencing poor reproductive success because of frequent parasitism may remain stable because they are rescued by immigration from healthy populations elsewhere (Smith et al. 1996, Rogers et al. 1997). Only isolated populations cut off from immigrants are denied the possibility of rescue.

Three factors affect the cost of parasitism to a host population, and should therefore be considered when estimating this cost. First, the selection of hosts by cowbirds determines the degree to which particular hosts in a community are affected. Host selection by cowbirds is high-

ly variable, with the same host species often experiencing different levels of use in different places (Robinson et al. 1995a). Second, costs to individual hosts are generally low where female cowbirds are scarce relative to hosts (<1% of a host community). Finally, some taxa are intrinsically more vulnerable to cowbird parasitism than others. Larger hosts such as Red-winged Blackbirds (*Agelaius phoeniceus*; Røskaft et al. 1990) and Wood Thrushes (*Hylocichla mustelina*; Hoover and Brittingham 1993) are resistant to parasitism and show little cost unless a nest receives two or more cowbird eggs (Røskaft et al. 1990, Trine in press). Other hosts, such as vireos, generally suffer severely even when parasitized with one cowbird egg (Grzybowski et al. 1986; papers by Averill-Murray et al., Kus, and Chace and Cruz, this section). I now consider the papers in this volume.

HOST SELECTION BY BROWN-HEADED AND BRONZED COWBIRDS

Knowledge of local host selection is critical to estimating costs due to parasitism, as only hosts that are parasitized frequently are likely to show any population cost. The extensive survey of Halterman et al. found that, on average only 23% of host species were ever parasitized in eight western National Parks. Among the parasitized species, many were parasitized only once. In host species where over 20 nests were found, parasitism barely exceeded 10% for the four most commonly parasitized species: Bell's Vireo (*Vireo bellii*), Warbling Vireo (*V. gilvus*), Wilson's Warbler (*Wilsonia pusilla*), and Song Sparrow (*Melospiza melodia*). These data suggest that cowbirds living at low to moderate densities in extensive natural areas like large parks mainly use a few favored and suitable host species. In support of this pattern, Ellison found minimal parasitism of four species of sparrows in southern coastal California, while the California Gnatcatcher (*Poliophtila californica*) was parasitized frequently at the same site (Braden et al. 1997b). Peer and Sealy also found very little use of almost all suitable hosts by Brown-headed and Bronzed (*Molothrus aeneus*) cowbirds at a site in Texas where the two species are sympatric, and community-wide levels of parasitism were low. The Northern Cardinal (*Cardinalis cardinalis*) was preferentially parasitized (88% of all cases of parasitism) by both species of cowbird. Spautz found that the frequency of parasitism of Common Yellowthroats (*Geothlypis trichas*) varied strongly across habitats within a local area.

In contrast to these cases of strong host selection, Hahn et al. described seemingly unselective use of hosts in an area with dense cowbird pop-

ulations and frequent multiple parasitism of several hosts (see Strausberger and Ashley 1997 for a similar pattern). They marked female cowbirds individually and radio-tracked some of these. Their paper also reports the first DNA-based analysis of host selection by cowbirds, and is pioneering because host selection is related to the use of space by individual cowbirds. As in a previous molecular study by Fleischer (1985), Hahn et al. found that individual cowbirds at Millbrook, NY, behaved as host generalists. In summary, host selection is still a poorly understood aspect of cowbird biology, but selectivity may vary inversely with the female cowbird: host ratio within a landscape.

COSTS OF PARASITISM TO HOST INDIVIDUALS

Several papers in this section found that cowbirds imposed high costs on host individuals. Chace and Cruz and Averill-Murray et al. report large costs for the Plumbeous Vireo (*Vireo plumbeus*) and Arizona Bell's Vireos (*V. bellii arizonae*), respectively. In contrast, other papers report lower costs to individuals. Halterman et al. found that none of the many host species that they studied in eight western National Parks were parasitized frequently enough to reach their threshold (30% of nests parasitized) of concern about the population effects of parasitism. Whitfield and Sogge and Greene found generally high but spatially variable frequencies of parasitism across several study sites for Willow Flycatchers (*Empidonax traillii*) and Lazuli Buntings (*Passerina amoena*), respectively. At some sites and years, all the bunting nests that Greene found were parasitized. These small hosts seldom rear any of their own young when a cowbird egg hatches in their nests.

Most estimates of individual costs, including many of those found here, are based on comparisons of fledgling production in parasitized and unparasitized nests, and this estimate is subject to biases (Lorenzana and Sealy). Only the paper by Sedgwick and Iko here measured the effect of parasitism on seasonal reproductive success, and made the useful comparison of production from parasitized nests, unparasitized nests, and all nests. Finally, Sedgwick and Iko calculated the first estimate of the lifetime cost of cowbird parasitism to individual hosts. Parasitized females raised 45% fewer young than unparasitized females over their life spans.

The meta-analysis by Lorenzana and Sealy is a welcome application of this technique to studies of brood parasitism. They summarized several of the most detailed studies of parasitism and calculated effect size for the numbers of host fledglings lost through parasitism. Losses varied in a coherent pattern with host size, with

smaller hosts losing more fledglings per attempt than larger hosts.

COSTS OF PARASITISM TO HOST POPULATIONS

It is much more difficult to estimate the effects of parasitism on host populations than effects on host individuals. To estimate costs to populations requires a demographic analysis of the effects of parasitism on host population growth. The paper by Sedgwick and Iko in this section is one of the most detailed demographic analyses of the consequences of parasitism conducted to date. They found that an average frequency of parasitism of 23% was insufficient to have a detectable influence on Willow Flycatcher population growth in eastern Oregon. Their paper is also a benchmark for predicting the effects of higher levels of parasitism on endangered populations of Southwestern Willow Flycatchers (*Empidonax traillii extimus*; see Whitfield and Sogge, this section).

Most estimates of the population-level costs of parasitism have employed formal demographic modeling. The pioneering study by May and Robinson (1985) used difference equations to model population costs. Their results suggested that costs to populations could be severe, especially in short-lived hosts.

Current approaches usually employ matrix models (e.g., Greene, and Citta and Mills, this section), which are readily available in software packages for analyzing population viability. These models make simplifying assumptions (such as stable age distributions and density-independent vital rates) that may make field biologists uncomfortable, but they generate useful insights. Greene's stochastic and deterministic models both predict that isolated local populations of buntings are vulnerable to extinction when parasitized. In a second study of this host species, Greene et al. (this section) used landscape models to estimate the amount of habitat where the Lazuli Bunting may be exposed to frequent cowbird parasitism. They found that virtually the entire range of the bunting in the state of Montana consists of good cowbird habitat, and concluded that the buntings are regionally at risk of extinction. However, temporal and spatial variation in parasitism levels were both high (Greene, this section), and nearby source populations may reduce the risk of extinction below that suggested by the models, which did not incorporate dispersal.

In a novel use of matrix models, Citta and Mills explore how cowbird control options affect population growth in cowbirds. They found several interesting results. First, cowbird population growth is very sensitive to the survival rate of cowbird eggs in host nests. Second, kill-

ing adult cowbirds in the breeding season does little to reduce cowbird numbers in the future, an empirical result found by most cowbird removal programs. Modeling suggests that removals outside the breeding season would be more effective at reducing cowbird population growth, but Citta and Mills consider winter removals to be impractical because of the high dispersal capability of the cowbird (see also Rothstein and Cook in press). Finally, the costly management practice of removing cowbird eggs from host nests (see Kus, this section) may do little to reduce cowbird population growth. Citta and Mills also note that habitat alteration may be a more effective way of managing cowbirds than removal programs (see also papers in section III, *this volume*).

The models in this section reveal that we still lack reliable estimates of some key demographic parameters needed to model the impacts of parasitism reliably. The most difficult parameter to estimate is juvenile survival after fledging. Even the careful work of Sedgwick and Iko found that local juvenile survival was far too low (0.11) to fill local territorial vacancies, presumably because open Willow Flycatcher populations in Oregon exchange dispersers frequently. Higher estimates of juvenile survival are available for island populations where water barriers frustrate dispersal. The mean proportion of juvenile Song Sparrows surviving from 30 days to breeding age on Mandarte Island, BC, was 0.37 ($N = 15$ years, Arcese et al. 1992). Such estimates, however, may not apply well to open populations on the mainland. Until we have the methods to measure juvenile dispersal and survival accurately in the field, all population models of the effects of parasitism will have considerable uncertainty associated with their predictions.

A final way to estimate population and community-level costs is by manipulative experiment. De Groot et al. showed that trapping female cowbirds markedly reduced the frequency of local nest failure in the Song Sparrow, but trapping did not increase numbers of breeding sparrows the next year (M. J. Taitt and J. N. M. Smith, unpubl. data). Costs to a host population may be higher than those calculated from differential production of fledglings from parasitized and unparasitized nests, if cowbirds commonly induce total nest failure in a species, as they seem to in the Song Sparrow (De Groot et al.; Arcese and Smith, in press). There are additional reasons to think that cowbirds contribute to source-sink dynamics in this species in the Pacific Northwest (Smith et al. 1996, Rogers et al. 1997). Data are needed to test if cowbirds markedly increase rates of total nest failure in species other than the Song Sparrow. Until it is

confirmed that cowbirds frequently depredate nests in a range of host species, De Groot et al.'s result should not be used to justify broad-scale cowbird removal programs. Appropriate data can be obtained from pilot removal programs or by comparing sites with variable abundance of cowbirds (Arcese and Smith in press).

De Groot et al. also report the first systematic attempt to measure community-wide impacts of cowbirds. They used a long-running cowbird removal program to test the idea that cowbirds alter quantitative patterns of host abundance in communities. Such effects are apparently present, but relatively weak, in pine forests of the Lower Peninsula of Michigan.

Two types of management decisions should flow from accurate assessments of population costs that are due to cowbirds. First, new habitat restoration or cowbird removal programs should be initiated to reduce newly recognized and severe population costs. Second, if cowbird pressure on a host population is low, or has decreased below a threshold of concern (see below), any management action already in progress should be scaled down so that scarce funds are matched to current conservation priorities. The Southwestern Willow Flycatcher population on the South Fork of the Kern River (Whitfield and Sogge, this section; Whitfield et al., section III; Whitfield in press, Rothstein and Cook in press) may be a case of the latter type. Despite several years of cowbird trapping, and consequent large reductions in the local frequency of parasitism, there has been little recovery of flycatcher numbers. Despite the lack of a population response at the South Fork Kern River, cowbird control efforts to protect this subspecies elsewhere are being expanded (Rothstein and Cook in press).

De Groot et al.'s study is also of interest in this context. Costs of parasitism to individual Kirtland's Warblers (*Dendroica kirtlandii*) were high before 1972 (Walkinshaw 1983), and led to the initiation of a 26-year cowbird removal program to protect the warbler population (DeCapita in press). De Groot found that trapping was remarkably effective and removed virtually all cowbirds locally. However, she found only 0.016 female cowbirds per suitable host (De Groot, unpubl. point count data) in jack pine (*Pinus banksiana*) habitat in Michigan > 10 km distant from trapping areas. This value is low enough to suggest that cowbirds are no longer abundant enough regionally to pose a serious threat to the warbler population. Cowbird numbers have declined in the region since 1960 (Peterjohn et al. in press) and it may be time to cease killing cowbirds in part of the Kirtland's Warbler's breeding habitat. Such an action

would test whether current cowbird removal programs to protect the warbler are still needed and would be timely, given recent suggestions that winter habitat, not reproductive output, limits warbler numbers (Haney et al. 1998).

RULES OF THUMB FOR MAKING MANAGEMENT DECISIONS

One rule of thumb used in this section is that parasitism is of concern (and a host population may need protective management) when the frequency of parasitism exceeds 30% (Halterman et al.). This rule originates from a paper by Mayfield (1977), who also noted in the same paper that Ovenbirds (*Seiurus aurocapillus*) reproduced well despite 50% parasitism. It is of interest that only two of the papers in this section (Averill-Murray et al. and Chace and Cruz) reported average frequencies of parasitism of over 50% across a region. Recent simulations by Grzybowski and Pease (in press) have revealed that the relationship between percent parasitism and seasonal reproductive success (seasonal fecundity) of hosts is complex, and that 30% of nests parasitized is probably much too low to be a threshold of concern in most populations.

I therefore close with a suggested rule of thumb for managers to consider when contemplating action to reduce the costs of cowbird parasitism. I choose what might seem to be a high threshold for four reasons. First, there are few good examples of severe costs of parasitism to host populations (as opposed to high costs to host individuals, which are frequent). Second, some recent cases where moderate to high costs to individuals have been studied in detail in the field, they have had little or no effect on host populations (Smith and Arcese 1994, Rogers et al. 1997; Sedgwick and Iko, this section). Third, simulations by Grzybowski and Pease (in press) suggest that passerines can often tolerate frequencies of parasitism exceeding 50%. Finally, two studies where parasitism lowered mean host productivity so markedly that local populations were sinks (Robinson et al. 1995b, Rogers et al. 1997) reported frequencies of parasitism of 65–95%. My suggested rule of thumb is:

Managers should consider initiating cowbird management programs when the frequency of parasitism in a sample of 30 or more nests gathered in a locality in each of two or more years, consistently exceeds 60%.

Only one study in this section (Averill-Murray et al.) meets this criterion. It may be no coincidence that the Arizona Bell's Vireo that they studied is a race of the only cowbird host that has shown consistent and large increases in local

numbers after effective cowbird removal (Kus, this section; Griffith and Griffith in press; but see Rothstein and Cook in press).

My suggested rule, however, should be modified if one or more of the following additional factors applies. If one or more of factors 1–5 below apply, a lower threshold of concern, perhaps > 50%, is appropriate.

1. The habitat of the host is so poor, or so restricted in extent, that even unparasitized females are reproducing poorly.

2. The host species belongs to a particularly vulnerable taxon (e.g., vireos).

3. The population of concern is spatially isolated and appropriately listed as threatened or endangered (Kus, and Whitfield and Sogge, this section).

4. The host's local or regional population has been in a prolonged state of decline (e.g., Whitfield and Sogge, this section).

5. There is frequent multiple parasitism (e.g., Hahn et al. this section).

If, however, factors 6–8 below apply, they would raise the threshold of concern.

6. There is a period early in the year when the host can reproduce in the absence of cowbirds, as often seen in birds of the U.S. southwest (e.g., Finch 1983; Braden et al. 1997b; El-lison, this section).

7. The host has a widespread distribution and generally healthy populations in much of its range, so that local populations performing

poorly are likely to be rescued by immigration (Robinson et al. 1995b, Brawn and Robinson 1996, Rogers et al. 1997).

8. Host numbers are increasing locally in the absence of management action.

A final and fairly common situation is that both brood parasitism and nest depredation are frequent locally (e.g., Brawn and Robinson 1996, Rogers et al. 1997). Since cowbirds can behave like nest predators (see above), there is a possibility that cowbird management may solve both problems simultaneously. In other cases, predator management, not cowbird control, may be the appropriate management action.

In conclusion, the papers in this section offer many insights into host selection by cowbirds and the costs of parasitism. I encourage readers to distinguish costs severe enough to lower numbers of adult hosts in the future, which are of considerable management significance, from those that merely reduce the breeding success of individual hosts without changing host numbers the following year. Managers will generally need detailed local data on host populations and parasitism levels to make wise decisions. Even with such data, careful judgement will still be needed in deciding when to initiate or terminate cowbird management programs.

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