# Reproductive success of the Brown-headed Cowbird: a prognosis based on Breeding Bird Census data

*Is there an optimal or "normal" cowbird/host abundance ratio?*

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RECENTLY THERE HAS been much interest in the reproductive biology and behavior of North America's only widely distributed obligate brood parasite, the Brown-headed Cowbird (*Molothrus ater*). Mayfield (1977) expressed grave concern that the Brown-headed Cowbird may now be the primary agent of extinction for Kirtland's Warbler and he speculated about the possibility of some sort of population control mechanism for it. Bull and Farrand (1977) have cited evidence that this cowbird is one of the primary causes for the elimination of the Tropical Parula (*Parula pitiayumi*) as a breeding species in the southwestern United States, and Elliott (1978) has documented the detrimental effects of an extremely high rate of cowbird parasitism in the Kansas grassland prairie, especially for the Dickcissel (*Spiza americana*). Elliott reports an astounding parasitism rate of 94.7% for the Dickcissel and an overall rate of 57.7%; not coincidentally, the Dickcissel is included on the *American Birds* "Blue List" for 1980, specifically owing to information received from the midwestern states, partially explained by sustained habitat losses for the species. Much recent scientific interest has centered around the documentation of host species as being either acceptors or rejectors and the evolution of such behaviors (Rothstein, 1975a, 1975b). However, relatively little work has been done concerning the population dynamics of the Brown-headed Cowbird in relation to the abundance of its host species. Unlike non-parasitic species, which may drive competing species to extinction, the success of the cowbird is dependent upon an abundance of hosts in order to reproduce and therefore cannot drive all of its hosts to extinction. As an obligate brood parasite it cannot exist without its hosts. This suggests that there may be an optimal, self-regulating ratio of cowbirds to hosts that represents an ideal balance between cowbird and host abundance. If cowbird numbers increase beyond this ratio the number of available host nests will decrease because the reproductive success of parasitised nests is lower than that of non-parasitised nests (Elliott, 1978). This reduction of available host nests would in turn be a limiting factor on the number of cowbirds that could "nest" thus reducing the number of cowbird young produced. This would, in turn, decrease the parasitism pressure and allow the host species to recover leading into an oscillation about the optimal cowbird/host ratio. One goal of this study is an attempt to explore this idea of an optimal or typical cowbird/host ratio.

UNLIKE MOST EUROPEAN brood parasites, *e.g.*, many European cuckoos, the Brown-headed Cowbird does not specialize on any one host. Instead, it is a generalist, parasitising >200 different species (Friedman, Kiff and Rothstein, 1977). As a generalist it apparently reaps the benefit of selection pressure for rejection behaviors of the host is very small for any one species. However, in any one area or habitat the number of different available host species may actually be quite small and under these circumstances the cowbird may be said to almost "specialize" on a very few species. In these cases the selection pressure for rejection might be considerable. In either case, generalist or specialist, there will necessarily be some selection pressure on the cowbird to discriminate between acceptor and rejector host species because there is a differential rate of reproductive success between the two groups. In turn, there will also be a selective pressure for the hosts to develop rejector behaviors. We might expect then, over time, that there will be some selection operating on both the cowbird and its hosts such that we might predict an increasing positive correlation between cowbird abundance and acceptor host abundance as well as an increasing negative correlation between cowbird abundance and rejector host abundance. At present the documented acceptors greatly outnumber the rejectors and we would certainly expect a very significant positive correlation between cowbird abundance and total potential host abundance.

In considering the above parameters of Brown-headed Cowbird reproductive success it seemed appropriate to attempt an evaluation of its abundance and the relationship to its host's abundance. This study reports the results of this evaluation using data from the annual Breeding Bird Census published by the National Audubon Society in *American Birds*.

## METHOD

THE ANNUAL CHRISTMAS Bird Count has been used a number of times for the evaluation of winter population trends (*e.g.*, Brown, 1975, 1976; Stahlecker, 1975). However, for this study, it was necessary to know the population distribution during the breeding season and therefore the annual Breeding Bird Census (hereafter, B.B.C.) was used instead. This census does not seem to have been used for this type of study although Kroodsma (1977) did use the B.B.C., in a study of avifauna diversity of occupied habitats relative to wrens. Some reasons for this non-use may be the relatively few censuses that were reported until recently for any given year or, perhaps, the great variation in size of the census areas which range from a few tenths of an acre to hundreds of acres. Because the primary data of this study are ratios of cowbird abundance to host abundance the data should not be significantly affected by the variation in absolute size of the count areas. The small number of reports in the early years is indeed a problem.

The B.B.C. was initiated in 1937 and as of 1976 had completed 40 consecutive years. For this study my five sampling points were chosen: the late 1930s, the mid-1940s, the mid-1950s, the mid-1960s and the mid-1970s. The major problem encountered was the very small number of individual counts done in the early years. Thus, for both the 1930s and the 1940s it was necessary to use three years in order to find 25 counts that reported the number of breeding female Brown-headed Cowbirds and virtually all of them were from the northeastern states. It was not until the 1960s that the number of reports had increased to a point sufficient to insure any sort of representative sample across the country. The number of counts used for each decade are as follows: N = 25 for the 1930s, 1940s, and the 1950s; N = 50 for the 1960s and 1970s.

For every count the following information was recorded: (1) the number of breeding female Brown-headed Cowbirds; (2) the total number of potential hosts (Friedman *et al.*, 1977); (3) the number of acceptor hosts (Rothstein, 1975a); (4) the number of rejector hosts (Rothstein, 1975a); and (5) the area of the count plot. Then, for every decade, the number of breeding female Brown-headed Cowbirds was correlated with each of 2-5 above. Finally, for each census and every decade, the ratio of Brown-headed Cowbird to total potential hosts was calculated and a one-way analysis of variance done to determine if there were any significant changes across decades.

## RESULTS

THE MEANS FOR EACH decade of Brown-headed Cowbird to host ratios are presented in Table 1. A one-way analysis of variance (Downie and Heath, 1965) revealed no significant differences among the five groups (F. 1). We may therefore conclude that the ratio of cowbirds to hosts has not changed significantly since the 1930s. The Pearson product-moment correlation coefficients are presented in Table 2.

**Table 1. Ratio of Brown-headed Cowbirds to hosts for each decade sampled.**

| *Decade* | *1930* | *1940* | *1950* | *1960* | *1970* |
|---|---|---|---|---|---|
| N | 25 | 25 | 25 | 50 | 50 |
| Brown-headed Cowbird/host | .027 | .033 | .026 | .033 | .032 |

**Table 2. Pearson product-moment correlation coefficients for number of female Brown-headed Cowbirds correlated with host abundance and plot area.**

| *Decade* | *1930* | *1940* | *1950* | *1960* | *1970* |
|---|---|---|---|---|---|
| N | 25 | 25 | 25 | 50 | 50 |
| Acceptors | .79** | .25 | .42* | .53** | .34* |
| Rejectors | .40* | .31 | .54** | .25 | -.01 |
| Total hosts | .75** | .58** | .60** | .40** | .47** |
| Plot area | .66** | .47* | .62** | -.08 | .21 |

* $p < .05$
** $p < .01$

## DISCUSSION

AN EXAMINATION OF TABLE 1 clearly shows that there has been a remarkably constant ratio of Brown-headed Cowbird/hosts across all of the years considered. This ratio is approximately three breeding females/100 host pairs (nests). Although there seems to be some disagreement in the literature over how many eggs a female Brown-headed Cowbird lays in a five- to six-week breeding season, Harrison (1975) gives an estimate of 11-14 and Payne (1976) gives a range of 11.3-25.0 according to location. Let us take the number 10 for the sake of convenience and to be on the conservative side. Assuming, then, that a female cowbird lays 10 eggs, all in separate nests, this would result in a typical parasitism rate of 30% of the total available host nests. However, it is not uncommon for females to lay more than one egg in a given nest and thus the actual parasitism rate would be somewhat less than the 30%. If each cowbird laid two of her 10 eggs in nests already parasitised this would result in a parasitism rate of 24%. This is close to the figure of 21% reported by Hill (1976) based on an examination of 520 nests of 14 host species. It also agrees fairly well with the rate of 22.4% reported by Berger (1951) and the rate of 30.8% reported by Hergenrader (1962) but is considerably lower than the rate of 36.9% reported by Wiens (1963) and the remarkably high rate of 57.7% reported recently by Elliott (*op cit.*). In relation to Elliott's study we may note that the highest number of eggs laid by single female Brown-headed Cowbirds in Payne's study (1976) was in Oklahoma (25.0) and the lowest in northern Michigan (11.3). If we were to assume that females in Kansas laid 20± eggs instead of 10/breeding season then our predicted rate would jump to 48% (assuming only one nesting of the hosts)

Since this ratio has been so consistent across time it may represent an optimal balance between parasite and host In the long run, assuming that the Brown-headed Cowbird selects nests randomly, this 24% may be spread over, possibly 100 host species and thus the parasitism rate/species would be only 0.24%. However, in localized areas there may be only a few potential host species and the nests of some species may be more accessible than others such that, in the short run, the local parasitism rate for certain species may be considerably higher than the 0.24%. In fact, Elliott (*op. cit.*) reported a local rate of 94.7% for the Dickcissel If this small localized population contains most of the nesting pairs for any one particular species (*e.g.*, Kirtland's Warbler) then there is a very real danger that parasitism may be a primary cause of extinction.

Elliott (*op. cit.*) found an extremely high density of Brown-headed Cowbirds and thus an extremely high rate of parasitism in the Kansas grassland prairie. He also found that multiple parasitism was the rule rather than the exception There is, however, a suggestion that this very high density is maladaptive for the Brown-headed Cowbird as the cowbird fledgling rate was lower at the higher densities than it was at the lower densities. If this is true then the lower densities will be selected for and the tendency will be towards a lower cowbird density and a lower parasitism rate. Even if the Brown-headed Cowbird fledgling rate is not higher at the lower densities the very high rate of parasitism may so severely reduce the resident host population that the available host nests will be greatly reduced thus limiting the reproductive potential of the Brown-headed Cowbird and lowering both the cowbird density and rate of parasitism.

An examination of the correlation coefficients reveals a number of interesting patterns. The number of cowbirds always correlates significantly, not surprisingly, with the number of acceptor nests and total available nests. The r's for rejector species show a trend across years from significant to nonsignificant. In the 1930s and 1950s they were positively correlated but in the 1960s and 1970s the number of cowbirds does not bear any consistent relationship to the number of rejector species. Could this represent the beginning of Brown-headed Cowbird discrimination of rejector hosts?

*Field Sparrow nest with cowbird egg/pencil drawing by Joan Poole.*

BECAUSE OF THE SMALLER Ns and the sampling problems mentioned above I think that we should view the correlations from the 1930s and 1940s as somewhat suspect and I would like to consider in detail only the correlations for the 1960s and 1970s. If we do this it becomes clear that: (1) the number of Brown-headed Cowbirds is positively related to the total number of nests available and to the number of acceptor hosts available; (2) the number of cowbirds is not related to the number of rejector species present; and (3) the number of cowbirds is not correlated with the area of the count plots. The latter, nonsignificant, correlations with area support the theory that available nests are the limiting factor for the Brown-headed Cowbird, not individual territory size or food supply both of which should be correlated with the area of the count plots.

In summary, it appears that, in most areas, the density of nesting Brown-headed Cowbirds is approximately 3/100 available host nests and that this ratio has remained constant over the last 40 years. The carrying capacity of Brown-headed Cowbirds in any one area is controlled and limited by the total number of available host nests. Thus, for the species as a whole, there is a self-regulating population control mechanism over a large area. It is likely that the total population of cowbirds will continue to increase as it is still expanding its range. However, with the exception of very special cases such as Kirtland's Warbler, the cowbird should not be the primary agent of species extinction, although Elliott (*op. cit.*) has shown that it may have a very significant effect on species which are widely distributed.

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