VESTIGES OF A PROPRIETARY INTEREST IN NEST'S BY THE BROWN-HEADED COWBIRD PARASITIZING THE KIRTLAND'S WARBLER

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SINCE the Brown-headed Cowbird, *Molothrus ater*, depends exclusively on other species to incubate its eggs and to care for its young, and since its fleeting visits to lay or remove eggs are rarely observed, we might be led to suppose its nesting drive to be fully extinguished by this time in its evolutionary history. However, I believe such is not quite the case. On the contrary, I believe the female cowbird in many instances gives a continuing and discriminating attention to the nests in which it lays its eggs, and consequently might be said to manifest, in moderate degree, a vestigial proprietary interest in those nests. I have never known the male cowbird to touch a nest.

This impression has developed gradually over the years of my study of the Kirtland's Warbler, *Dendroica kirtlandii*, a study that became in part also a study of the cowbird, since the reproductive lives of these two birds are so closely entwined.

Watching nest building intently. The cowbird's interest in the nest of the Kirtland's Warbler, as has been noted with other host species, first becomes apparent during nest building. At this time the female cowbird sits on an exposed perch some distance away and watches for extended periods while the warbler works. The span of attention of the cowbird is far longer than would be required merely to locate the nest. In a higher animal we might interpret this behavior as vicarious participation, and the term may not be totally amiss here. Certainly, the cowbird's involvement would seem to be deeper than that of a mere onlooker, if it is brought to ovulation as a result of this experience, as Hann has suggested (1937: 207).

Looking into the nest at intervals. Occasionally, when the owners of the nest are not present, the female cowbird walks up to the nest and peers into it. This may occur very early, even before the nest is finished. Hann (1941: 220) in his study of the Ovenbird, Seiurus aurocapillus, concluded that the "cowbird makes regular trips of inspection to nests." Once at a nest of the Kirtland's Warbler that was almost finished but had not yet received its first egg, I saw a cowbird walk up to the nest, poke its head through the overarching canopy of grass, look for a moment into the cavity, and then fly away. This occurred two hours after sunrise and thus much later in the day than the usual egglaying visit.

On another occasion, in the semidarkness before dawn I saw a cowbird walk to a nest, fly away, and then return 10 minutes later, laying an egg at one of the two visits. The dim light and the ground cover prevented me from being sure whether the egg was laid in the first or second visit. Then, on the following morning, which was still one day before the first warbler egg arrived, the cowbird returned and looked into the nest at seven, nine, and ten o'clock.

Doubtless, most of the cowbird's attention to nests centers in the building and egg-laying periods—that is, before incubation begins. At these times the cowbird is not likely to be opposed by the hosts, since small songbirds typically spend a very small part of these days near the nest. Also such cowbird visits are not likely to be recorded, for it is not often that a human observer will be watching a nest constantly from concealment at these stages.

Cowbird visits are probably less frequent after incubation begins. Now the nest is closely defended, and the cowbird is usually routed before it gets to the nest. Further, it appears hesitant in manner and more easily repelled in these broad-daylight visits than in the predawn, egg-laying visits. Hann (1937: 202) saw a cowbird push a shrieking Ovenbird right out of its nest in order to enter and lay an egg. But I saw a female Kirtland's Warbler put an unresisting female cowbird to flight three times in two days when the cowbird walked up to within a meter of the nest. This nest held young birds almost ready to leave.

Dubois (1956: 286) saw a female cowbird strike with its bill into the nest of a Song Sparrow, *Melospiza melodia*, injure one of the four nestlings and carry away another. This nest, like that of the Kirtland's Warbler, was on the ground. Dubois does not mention seeing the adult sparrows; so the nest was presumably undefended at the moment. I suspect that molestation of nests so late in the cycle is rare.

In my examples, the cowbirds were not banded, and therefore my inference that repeated visits to the same nest were made by the same cowbird is not proved. However, this inference is supported by the findings of others—particularly Friedmann (1929: 175), Nice (1937: 154), and Laskey (1950: 167)—that each cowbird has a definite home range. Also the idea that a host nest is normally the object of attention for one cowbird exclusively is supported by the fact that I have never found more than one cowbird egg laid in a day in a Kirtland Warbler's nest, although 52 per cent of parasitized nests in my study received more than one cowbird egg each (Mayfield, 1960: 148).

Here I have not considered egg-laying visits after the normal time—during incubation, with nestlings present, and in abandoned nests.

These "late" cowbird eggs comprise about 10 per cent of the total (Mayfield, 1960: 159), but I believe they indicate, not a continuing interest in nests, but an unpremeditated use, as might occur if a cowbird ready to lay an egg were to find the intended nest destroyed.

Visiting the nest repeatedly to remove eggs. The cowbird's continuing interest in the Kirtland's Warbler nest is shown by the fact that it removes more eggs than it lays, even though some parasitized nests do not lose any eggs; that is, a nest losing any eggs often loses several, presumably as a result of separate visits by the cowbird.

To get a measure of the total loss, it is not sufficient simply to count eggs as they appear and disappear. Too many are removed before they are seen by anyone. Therefore, I prefer to deduce the losses by comparing a sample of parasitized nests with a sample of nests that have not been molested by cowbirds, as follows:

Eggs in Kirtland's Warbler Nests
(142 nests)

Warbler eggs in 67 nests not parasitized Warbler eggs per nest not parasitized	d 310 4.63
Warbler eggs in 75 parasitized nests Warbler eggs per parasitized nest	205 2.73
Warbler eggs lost per parasitized nest	1.90
Cowbird eggs in 75 parasitized nests Cowbird eggs per parasitized nest	125 1.67
Warbler eggs lost per cowbird egg gain	ned, $\frac{1.90}{1.67}$ 1.14
(Nests were included only if clutches plete because seen on at least two days	

Removing eggs only from nests it is using. It is significant that the cowbird's drive to remove eggs is directed only at nests in which it has laid or will lay its own eggs. Even though there are other Kirtland's Warbler nests in the vicinity, these other nests almost never lose eggs without the destruction of the entire clutch at one time, a kind of destruction not attributed to the cowbird. Therefore, the cowbird normally seems not to seek eggs for themselves but takes eggs only from nests it is using for its own.

Removing only the hosts' eggs. The cowbird does not remove eggs at random, but is able to discriminate between its own and the hosts' eggs, some of which are treated as other birds might be expected to treat "foreign objects." I have 13 definite instances where cowbirds

removed eggs from nests containing both cowbird eggs and Kirtland's Warbler eggs, and each time the cowbird took only warbler eggs. In these instances the cowbirds were confronted with choices among a total of 23 warbler eggs and 19 cowbird eggs. The odds against 13 correct choices without an error are 3,000 to 1 by chance alone.

Probably the cowbird discriminates on a basis of size rather than color or pattern. Both kinds of eggs are whitish and lightly speckled, but the warbler egg is smaller. At the nest of the Ovenbird the cowbird has more difficulty in distinguishing the hosts' eggs, which are nearer the size of its own. But even here Hann (1937: 204) noted the loss of only four cowbird eggs as against 30 Ovenbird eggs lost. The mean size of Brown-headed Cowbird eggs in Kirtland's Warbler nests is 20.9 by 16.5 mm. (N=24); of Ovenbird eggs, 20.3 by 15.6 mm. (N=48, Hann, 1937: 172); of Kirtland's Warbler eggs, 18.1 by 13.9 mm. (N=154).

Never emptying the nest completely. I have never known the cowbird to take the only egg present in a Kirtland's Warbler nest. Long ago Burroughs (1887: 30) noted that the cowbird takes an egg only when the nest contained "two or more eggs," and Hann (1941: 212) found this to be true also in nests of the Ovenbird. However, it is only fair to point out that few Kirtland's Warbler nests were found so early and watched so closely that a first egg might not have been laid and removed unseen.

This subtle distinction by the cowbird may have survival value, because songbirds are more likely to desert if the nest is emptied than if its contents are merely reduced; on the other hand, an inattentive host might not be aware of the loss of an only egg if it were replaced by a cowbird egg before the host's next visit.

Destroying several eggs in a crowded nest. I have a small number of examples suggesting that a cowbird removing eggs from a crowded nest may create havoc in it. Not surprisingly, these instances are few, because the cowbird is most active early in the egg-laying stage and because full clutches are likely to be under incubation and therefore defended. (The Kirtland's Warbler normally begins incubation on the next-to-last egg.)

In nests that had complete sets of eggs when cowbirds visited them to lay and to remove eggs, the results were as follows:

Cowbird Damage to Full Clutches of Kirtland's Warbler Eggs (7 nests)

	Warbler eggs	Cowbird eggs
Before cowbird damage	32	1*
After cowbird damage	8	9
Cowbird eggs added, 8		
Warbler eggs destroyed, 24		

^{*} One nest held a cowbird egg laid earlier.

The resultant set of eggs in each instance was a clutch of one to four eggs, that is, about the usual number to be found in a nest at the usual time of a cowbird's visit. Excluded from this table were four other full clutches that received additional cowbird eggs without loss.

SUMMARY

The Brown-headed Cowbird still retains vestiges of a nesting drive shown in ways suggesting a proprietary interest in the Kirtland's Warbler nests it parasitizes, as follows:

- 1. Watching nest building intently.
- 2. Looking into the nest at intervals.
- 3. Visiting the nest repeatedly to remove eggs.
- 4. Removing eggs only from nests it is using.
- 5. Removing only the host's eggs and not its own.
- 6. Never emptying the nest completely.
- 7. Destroying several eggs in a crowded nest.

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