CHANCE DISTRIBUTION OF COWBIRD EGGS

By Harold Mayfield

The Brown-headed Cowbird (*Molothrus ater*) often places just one egg in the nest of a host but sometimes deposits two, three, or even more. Since about 60 per cent of parasitized nests contain but a single cowbird egg each (Friedmann, 1963:12), one might suppose that the cowbird tends to use a nest but once and does otherwise only under special circumstances, as when a different nest is not available or when two or more cowbirds cross paths unwittingly. On the other hand, a field observer, finding several cowbird eggs in a nest, might suppose that cowbirds find some nests particularly attractive and return to lay in them repeatedly.

Which of these two opposing suppositions is true? Or is neither of them true? Intuitively, one would think that an intelligent creature, such as a bird, would exercise some choice—seeking out different nests for each egg if possible or returning repeatedly to a preferred nest if possible. Obviously one course will tend to increase the ratio of nests with one cowbird egg, and the other course will tend to increase the ratio of nests with more than one cowbird egg. Any exercise of choice whatsoever, or any instinctive tendency to seek out or avoid certain nests, will cause the proportion of nests with one egg, two eggs, three eggs, and so on to be different from that predicted by chance alone.

If a given number of cowbird eggs are laid at random among a given number of nests, the pattern of distribution to be expected can be calculated easily. The probability that a nest will get 0, 1, 2, 3, . . . cowbird eggs is given by each successive term in the Poisson series, as follows:

$$e^{-c},\ ce^{-c},\ \frac{c^2e^{-c}}{2!},\ \frac{c^3e^{-c}}{3!},\ .\ .\ .\ .\ ,\ \text{where } c = \frac{\text{number of cowbird eggs}}{\text{number of nests in sample}},$$

that is, the cowbird eggs per nest in the sample, the average expectation, or the sample mean; and $e = 2.71828\ .\ .\ .$, the base of natural logarithms. The number e^{-c} for any value of c can be read directly from a table of exponentials. The sum of all the numbers in the series is 1, because the sum of all the probabilities is certainty. To express each probability, not just as a fraction, but as the number of nests in a category, each member of the series may be multiplied by N, the number of nests in the sample, thus:

$$Ne^{-c},\ cNe^{-c},\ \frac{c^2Ne^{-c}}{2!},\ \frac{c^3Ne^{-c}}{3!},\ .\ .\ .$$

It was Preston (1948) who first considered the distribution of cowbird eggs in this light. He examined five reports on host nests and found that the distribution of cowbird eggs in each sample was not as close to that predicted by chance as when he analyzed just the parasitized segment of the sample and considered the distribution of subsequent cowbird eggs after the first in each nest. Here the observed pattern was remarkably close to the predicted pattern in all five studies. He concluded (p. 115) "the first cowbird egg in a nest is *not* placed at random, but all subsequent ones *are*."

For his analysis he used data from the following studies: Friedmann (1929:248) on the Louisiana Waterthrush (*Seiurus motacilla*) in several Eastern localities; Hann (1937:202) on the Ovenbird (*Seiurus aurocapillus*) in southern Michigan;

TABLE 1

DISTRIBUTION OF COWBIRD EGGS

Observer	Host		Cowbird eggs per nest 0	1	2	3	4	5 or more	No. nests	No. cowbird eggs	P[1]
Berger	20 Michigan hosts	Observed	388	53	36	15	6	2	500	204	0.001
		Calculated	332.5	135.7	27.7	3.7	0.4	0			
Hann	Ovenbird	Observed	20	10	8	2	2	0	42	40	0.15
		Calculated	16.2	15.4	7.3	2.3	0.6	0.1			
Jacobs	Kentucky Warbler	Observed	73	44	15	2	0	0	134	80	0.75
		Calculated	73.8	44.0	13.1	2.6	0.4	0			
Mayfield	Kirtland Warbler	Observed	62	36	29	9	1	0	137	125	0.06
		Calculated	55.0	50.2	22.9	7.0	1.6	0.3			
Nice	Song Sparrow	Observed	125	69	26	3	0	0	223	129	0.40
		Calculated	125.0	72.3	20.9	4.0	0.6	0.1			
Norris	14 Pennsylvania hosts	Observed	164	45	21	7	0	0	237	108	0.001
		Calculated	150.3	68.5	15.6	2.3	0.3	0			
Southern	Red-eyed Vireo	Observed	29	41	21	6	3	4	104	136	0.25
		Calculated	28.1	36.8	24.1	10.5	3.4	1.1			
Walkinshaw	Field Sparrow	Observed	482	135	42	5	0	0	664	234	0.001
		Calculated	466.8	164.5	29.0	3.4	0.3	0			

[1] P is the approximate value of the significance probability for chi-square test of goodness-of-fit. Probability of 0.05 or larger is taken to indicate adequate fit.

Jacobs (*in* Friedmann, 1929:248) on the Kentucky Warbler (*Oporornis formosus*) in southwestern Pennsylvania; Nice (1937:159) on the Song Sparrow (*Melospiza melodia*) in central Ohio; and Norris (1947:90) on 14 western Pennsylvania hosts taken together.

I encountered similar circumstances in my study (Mayfield, 1960:153–155) of the Kirtland Warbler (*Dendroica kirtlandii*). In my sample of complete sets of warbler eggs, the cowbird eggs were distributed as though there were an element of chance but perhaps some other factor also. However, if I considered just the parasitized subsample, I found the subsequent cowbird eggs, after the first in each nest, to be laid almost exactly according to chance.

Proceeding in the same way, I have examined also the data from three other studies yielding samples of sufficient size for statistical analysis: the work of Berger (1951:28) on 20 hosts taken together in southern Michigan; the investigations of Southern (1958:196–197) on the Red-eyed Vireo (*Vireo olivaceus*) in northern Lower Michigan; and those of Walkinshaw (unpublished) on the Field Sparrow (*Spizella pusilla*) in southwestern Michigan.

Discussion of tables 1 and 2.—A comparison of the actual distribution of cowbird eggs with that predicted by chance in each of the studies just mentioned is presented in table 1 and table 2.

Except for two of the examples introduced by Preston, I have avoided using any study in which the original sample of host nests was smaller than 100. Of the nine examples used, seven were studies of individual host species; but two, the reports of Berger (1951) and Norris (1947), were of a different kind, namely, a grouping of all the hosts in a locality. I have had some hesitance about attempting to use such groups for comparison, recognizing that they contain in varying proportions

Table 2

DISTRIBUTION OF SUBSEQUENT COWBIRD EGGS

Observer	Host		Subsequent cowbird eggs per nest 0	1	2	3	4 or more	No. para-sitized nests	Sub-sequent cow-bird eggs	P[1]
Berger	20 Michigan hosts	Observed	53	36	15	6	2	112	92	0.30
		Calculated	49.3	40.5	16.6	4.5	0.9			
Friedmann	Louisiana Waterthrush	Observed	25	20	7	3	0	55	43	0.90
		Calculated	25.0	20.0	7.6	2.0	0.4			
Hann	Ovenbird	Observed	10	8	2	2	0	22	18	0.85
		Calculated	9.7	7.9	3.2	0.9	0.2			
Jacobs	Kentucky Warbler	Observed	44	15	2	0	0	61	19	0.70
		Calculated	44.7	13.9	2.2	0.2	0			
Mayfield	Kirtland Warbler	Observed	36	29	9	1	0	75	50	0.50
		Calculated	38.5	25.7	8.6	1.9	0.3			
Nice	Song Sparrow	Observed	69	26	3	0	0	98	32	0.40
		Calculated	70.7	23.1	3.8	0.4	0			
Norris	14 Pennsylvania hosts	Observed	45	21	7	0	0	73	35	0.65
		Calculated	45.2	21.7	5.2	0.8	0			
Southern	Red-eyed Vireo	Observed	41	21	6	3	4	75	61	0.02
		Calculated	33.3	27.1	11.0	3.0	0.7			
Walkinshaw	Field Sparrow	Observed	135	42	5	0	0	182	52	0.50
		Calculated	136.8	39.1	5.6	0.5	0			

[1] See table 1 for explanation.

hosts that may be quite dissimilar. For example, I am puzzled to know how to regard a group containing a substantial number of nests of the Catbird (*Dumetella carolinensis*). Ordinarily the Catbird removes the cowbird's egg from its nest so promptly that the human observer is unlikely to record the event; hence, data on cowbird eggs in Catbird nests will not give a true picture of events unless the observer is in constant attendance. Perhaps other species also have defenses against the cowbird, as yet not understood, that alter the number of cowbird eggs we find.

Nevertheless, it is noteworthy that both of these groupings of assorted hosts show distributions of cowbird eggs roughly similar to those of the several species studied individually, some of which do not appear in the two groups. The data of Norris (1947) particularly follows the typical pattern. Presumably this is because most of his species behave toward the cowbird somewhat like the other species presented here independently, but it may be pertinent also that his group was restricted in size, location, and time—14 species in a 90-acre tract during two successive nesting seasons. It is surprising that some tendency to randomness in the distribution of cowbird eggs is still apparent when data on the nests of several hosts are lumped together, although the cowbird seems to exercise considerable selectivity in its choice of hosts, parasitizing some species much more frequently than others in the same region at the same time.

The Louisiana Waterthrush does not appear in table 1, because Friedmann's summary did not indicate how many of these nests did not have cowbird eggs. For Jacob's data on the Kentucky Warbler, I have used a later and more extensive report (1938) than that examined by Preston.

TABLE 3

DISTRIBUTION OF COWBIRD EGGS IN ADJUSTED SAMPLES

Observer	Host		Cowbird eggs per nest 0	1	2	3	4 or more	No. nests	No. cow-bird eggs	P[1]
Mayfield	Kirtland Warbler	Adjusted observations	62	57	29	9	1	158	146	0.90
		Calculated	62.7	57.9	26.8	8.3	2.2			
Walkinshaw	Field Sparrow	Adjusted observations	482	201	42	5	0	730	300	0.90
		Calculated	484.0	198.9	40.9	5.6	0.6			

[1] See table 1 for explanation.

In five of the eight examples in table 1—Ovenbird, Kentucky Warbler, Kirtland Warbler, Song Sparrow, and Red-eyed Vireo—the observed distribution of cowbird eggs appears reasonably close to a random distribution; indeed, in the Kentucky Warbler, the fit is nearly perfect. The most conspicuous deviations from randomness have in each instance too many nests with no cowbird eggs and too few nests with one cowbird egg.

Eight of the nine examples in table 2 show that the placement of subsequent eggs after the first in each nest is often astonishingly close to a random distribution.

To explain this puzzling state of affairs, Preston (1948) suggested that the cowbird's placement of the first egg in each nest was "deliberate," whereas the placement of subsequent eggs was random. That is, he attributed the difference to a conscious action on the part of the cowbird. In my consideration of the issue with the Kirtland Warbler, I suggested that these circumstances might have come about because no cowbirds were present at the sites of some nests when they were being built, and these nests, from the viewpoint of the cowbird, were outside the sample; that is, some nests were not exposed to the cowbird. And when I made calculations based on the assumption that the cowbird's sample of available nests was somewhat smaller than mine, I calculated a chance distribution somewhat closer to actuality than before, but not close enough to satisfy me.

Discussion of table 3.—I now propose with some logical basis another hypothesis that appears to bring the calculations and the actualities into almost perfect agreement for some studies. I suggest that cowbirds lay their eggs in nests of some hosts at random, and the apparent deviations from randomness are actually sampling errors that have arisen from our not finding all host nests at the very start. Since the principal defense of most small songbirds against the cowbird is desertion of the nest, and since a nest deserted early in its existence is less likely to be found by the human observer than a nest that lasts longer, we are less likely to find a nest with one cowbird egg than a nest with none or with two or more eggs. The nest with no cowbird eggs is more likely to endure because it has been spared this gross molestation. A nest with two or more cowbird eggs already has demonstrated a longer life than a nest which was deserted immediately after receiving one cowbird egg; perhaps also it has demonstrated that its owner has some tolerance of this kind of molestation. In short, if we fail to include some nests abandoned as soon as they have been parasitized, we will introduce a bias into our sample by lowering the count in the one-cowbird-egg category.

Elsewhere I have discussed more fully how nests that endure longer are more likely to be found and how we may be misled by assuming that nests we find are representative of all nests (Mayfield, 1961).

To test the hypothesis, I will use two of the studies in table 1 where the fit of the observed to the calculated distribution is poorest. Here I will assume that a certain number of one-cowbird-egg nests existed but escaped attention because of early desertion; then I will increase the number of nests, the number of cowbird eggs, and the number of one-cowbird-egg nests in accord with this assumption, arriving at an adjusted sample and using it for recalculation and comparison. The chosen examples are the Kirtland Warbler and the Field Sparrow. Although the data for the Kirtland Warbler fall within the realm of an adequate fit with the calculations, they are borderline. There are two other sets of data in table 1 that do not fit the calculated values, but I reject them because these groups in my judgment are too heterogeneous and contain too many unknowns to provide a logical basis for this type of treatment. That is, nearly half of Berger's (1951) group is made up of nests of the Catbird, Redwinged Blackbird (*Agelaius phoeniceus*), and American Goldfinch (*Spinus tristis*); and a fourth of Norris's (1947) group is made up of nests of the Catbird and Brown Thrasher (*Toxostoma rufum*). All of these are species that have excellent defenses against the cowbird other than desertion, and to treat the groups containing them as though desertion were a major contaminating influence in the data would appear to be a dubious procedure. Such uniform treatment of the groups might be inappropriate for other members also, for reasons that are not yet fully understood.

In the case of the Kirtland Warbler, I shall assume arbitrarily that an additional 15 per cent of the sample (21 nests) actually received one cowbird egg early in their existence and were abandoned before we were able to find them. If so, the actual sample should be increased by 21 in each of the following categories: total nests, total cowbird eggs, and number of nests with one cowbird egg.

It is not unreasonable to believe that such a number of short-lived nests escaped discovery, especially since not all of the sample was drawn from areas receiving daily attention. It may be argued, of course, that not all of the nests deserted during the egg-laying period were parasitized. While this may be true, the cowbird is certainly a major cause of early desertion and conceivably a more frequent cause than we realize. Since I have no basis for guessing how many early desertions are caused by factors other than the cowbird and wish to simplify this issue to the utmost in testing the hypothesis here, I have made the adjustment on this one basis alone.

Similarly, in the case of the Field Sparrow, I have assumed arbitrarily that 10 per cent of the nests (66 in number) escaped discovery because they were abandoned early after receiving one cowbird egg. Obviously, the adjustment needed will vary from study to study according to the behavior of the birds and the conditions of observation. A smaller adjustment in the second of these two examples may be rationalized because a large part of Walkinshaw's unpublished data were gathered by continuous attention to a study area near his home.

For these two studies, the new presumed actual distributions of cowbird eggs and the distributions expected by chance are shown in table 3. The application of the chi-square test for goodness-of-fit confirms what is apparent to the eye, namely that the adjusted observations now fit the calculations more closely than before. Thus, it appears that if we could have found all the nests of these two hosts at the very start, we might have found the cowbird eggs placed among them with almost the random impartiality of a roulette wheel.

There are other interesting aspects of tables 1 and 2 that I have not discussed because they seemed extraneous to my main line of inquiry. It is apparent the Red-eyed Vireo is least typical of the individual species reported. It is the only species for which the observed distribution of subsequent eggs did not fit the calculated pattern as well as the distribution of all eggs. But this species was different in other ways too. The ratio of parasitized nests, 72 per cent of the nests, is phenomenally high. A lag of two to four days between the completion of the nest and the laying of the first egg by this host causes the first cowbird egg to be laid ahead of the Red-eyed Vireo's first egg more often than is customary among other hosts (Norris, 1947:92).

It is notable also in Southern's (1958) study of the Red-eyed Vireo and Berger's (1951) group of 20 hosts that there are more nests with four or more cowbird eggs than expected by chance. In Berger's (*op. cit.*) study the instances occurred in nests of the Red-eyed Vireo, Indigo Bunting (*Passerina cyanea*), and Song Sparrow. Elsewhere Friedmann (1963:12–13) has listed instances of as many as eight or more cowbird eggs in a nest. Of course, nests with many cowbird eggs are more likely than ordinary nests to find their way into the published record. Such extremes would occur very rarely by chance alone. It is possible that abnormally large deposits of cowbird eggs could be caused by a local and temporary shortage of suitable host nests, or that several female cowbirds might be prompted occasionally to lay in "dump nests" for unknown reasons. Also it is obvious that one aberrant female cowbird could overload two or three nests in a sample and distort the distribution at the end where the figures are small.

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SUMMARY

The Brown-headed Cowbird lays one egg in about 60 per cent of hosts' nests but sometimes lays two or more eggs in a nest. Nine studies of host species were examined, and in five of these the distribution of cowbird eggs was nearly random as shown by comparison with a Poisson series. In eight studies, the distribution of subsequent cowbird eggs after the first in each nest was nearly random. I propose the hypothesis that the appearance of nonrandomness in some studies is a result of a sampling error caused by the human observer's failure to find some nests abandoned early in existence because of the deposit of a cowbird egg. If the data from studies of the Kirtland Warbler and Field Sparrow are adjusted in accordance with this hypothesis, there is then a close fit between the presumed actual distribution and that predicted from a random placement of cowbird eggs.

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