

the importance of geographic variation within song types, as well as my hypothesis that similarity in the opening motifs might facilitate interspecific territoriality (Stiles 1983).

Consisting as they do of pure-toned, unmodulated, long (0.3 sec or more) whistles, the songs of the two Costa Rican species of *Microcerculus* seem ideally suited for transmission in an obstruction-filled habitat like tropical forest understory (Morton 1975, *Am. Nat.* 109:17–33). Other understory wrens (e.g., *Henicorhina*, *Cyphorhinus*) sing songs of comparable tone quality, as do the other two recognized species of *Microcerculus*, *bambla* and *ustulatus* (cf. Hardy 1978). The songs of the latter two species have a very different temporal structure, however, with the whistles becoming progressively shorter and more rapid (in *ustulatus*, but not in *bambla*, the song finishes as an up- or down-slurred glissando). Of the wide selection of wren songs presented by Hardy (1978), that of *Cyphorhinus aradus* is most comparable in tone quality to those of *Microcerculus*, but is very different structurally: a low, burbling phrase is interspersed with the clear whistles, which themselves are given in a seemingly random order quite unlike the patterned utterances of *Microcerculus* spp. Thus, although song tends to confirm that the species of *Microcerculus* form a natural unit, it is scarcely helpful in establishing the relationship of this unit to the other genera of wrens.

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Cowbird nest selection.—The Brown-headed Cowbird (*Molothrus ater*) is well known for its brood parasitic habit (Friedmann et al., *Smith Contrib. Zool.* 235, 1977). The large number of recorded hosts testifies to the variety of situations encountered by egg-laying females. Since cowbird nesting activities are not centered on their own nests, the manner of host selection is an important factor in determining reproductive success of individual females. How, then, do cowbirds select host nests?

If all potential host nests are at equal risk (same probability) of being parasitized, and since cowbird parasitism is a “rare” event, the distribution of 0, 1, 2, 3, . . . cowbird eggs per nest will approximate successive terms of a Poisson series. Preston (*Ecology* 29:115–116, 1948) tested for such a distribution and found no good statistical fit; however, within the sample of parasitized nests, the distribution of cowbird eggs after the first egg did fit the Poisson distribution that was generated. He concluded that the first cowbird egg in a nest was placed nonrandomly and subsequent, additional eggs were randomly distributed among the already parasitized nests. Mayfield (*Condor* 67:257–263, 1965) looked at similar data and felt that host nests with one cowbird egg were under represented in the sample. Since some hosts may immediately abandon their nests after the first cowbird egg appears, these abandoned nests become difficult to locate. By adding 10–15% to the number of nests with one cowbird egg, he produced a close fit to Poisson distributions. Mayfield (1965) concluded that cowbirds distribute eggs randomly among available host nests. Elliott (*Auk* 94:590–

TABLE I
 FIT OF COWBIRD EGG DISTRIBUTION TO AN EXPECTED RANDOM DISTRIBUTION; SEE MAYFIELD (1965) OR ORIGINAL PAPERS FOR DETAILED DISTRIBUTION OF COWBIRD EGGS; FIT IS COMPARED WITH A POISSON DISTRIBUTION CALCULATED USING THE METHODS DESCRIBED IN THE TEXT

Study and source	Total nests S	Nests not found $U(0)$	Nests found, not parasitized $F(0)$	Cowbird eggs E	Parasitized nests $T - F(0)$	Fit to Poisson			
						χ^2	df	P	
A. Studies which fit a Poisson distribution									
20 Michigan hosts (Berger, Wilson Bull. 63:26-34, 1951*)	500	349.8	38.2	204	112	1.358	3.10	3	$P > 0.5$
Ovenbird (<i>Seiurus aurocapillus</i> ; Hann, Wilson Bull. 49:145-237, 1937*)	42	17.0	3.0	40	22	1.600	2.42	2	$P > 0.1$
Kentucky Warbler (<i>Oporornis formosus</i> ; Jacobs, Auk 55: 260-262, 1938*)	134	16.7	56.3	80	61	0.682	0.97	1	$P > 0.1$
Song Sparrow (<i>Melospiza melodia</i> ; Nice, Trans. Linn. Soc. N.Y. 4, 1937*)	223	51.8	73.2	129	98	0.754	2.57	1	$P > 0.1$
14 Pennsylvania hosts (Norris, Wilson Bull. 59:83-103, 1947*)	237	121.3	42.7	108	73	0.933	0.62	1	$P > 0.1$
Field Sparrow (<i>Spizella pusilla</i> ; Walkinshaw, in Bent, U.S. Natl. Mus. Bull. 237, pt. 2, 1968*)	664	287.9	194.1	234	182	0.622	2.41	1	$P > 0.1$
Eastern Phoebe (<i>Sayornis phoebe</i> ; Klaas, Occ. Pap. Mus. Nat. Hist., Univ. Kansas, 41, 1975)	377	210.6	85.4	115	81	0.691	0.68	2	$P > 0.5$
13 Kansas hosts (Hill, Wilson Bull. 88:555-565, 1976)	520	232.0	177.0	144	111	0.500	1.78	1	$P > 0.1$

TABLE 1
CONTINUED

Study and source	Total nests S	Nests not found $C(O)$	Nests found, not parasitized $F(O)$	Cowbird eggs E	Parasitized nests $T - F(O)$	c	χ^2	Fit to Poisson	
								df	P
24 midwest hosts (Lowther, Bird-Banding 48:358-369, 1977)									
	466	289.7	98.3	111	78	0.630	2.17	1	$P > 0.1$
Prairie Warbler (<i>Dendroica discolor</i> ; Nolan, Orn. Monogr. 26, 1978)									
	336	-2.1	256.8	104	92	0.300	1.97	1	$P > 0.1$
Pooled studies	3499	516.4	930.6	1270	910	0.690	1.33	3	$P > 0.5$
Heterogeneity χ^2							17.36	11	$P = 0.1$
B. Studies which do not fit a Poisson distribution									
3 Kansas hosts (Elliott 1977)									
	72	-5.5	24.5	144	53	1.857	29.64	3	$P < 0.01$
Kirtland Warbler (Mayfield 1960*)									
	137	-18.2	80.2	125	75	0.806	12.21	2	$P < 0.001$
Red-eyed Vireo (Southern 1958*)									
	104	-28.8	57.8	136	75	1.024	12.90	2	$P < 0.001$
Red-winged Blackbird (Linz and Bolin 1982)									
	258	43.5	105.5	182	109	0.848	9.27	2	$P < 0.01$

* Studies used in Mayfield (1965).

593, 1977) felt Mayfield's (1965) correction introduced other uncontrolled biases and he supported Preston's (1948) earlier interpretation.

My approach to examining cowbird egg distribution considers a different sort of bias in the data. I consider parasitism of host nests by female Brown-headed Cowbirds to be a 2-step process: (1) a successful search for a host nest and, (2) selection of the nest from among those nests that have already been found by the cowbird. A nest with a cowbird egg is known to have been found by a cowbird; nests without cowbird eggs either may be known to cowbirds but not selected to be parasitized or may have remained undetected from nest-searching cowbirds.

Of a sample of nests, let the total number of nests, S , be the sum of the series,

$$S = N(0) + N(1) + N(2) + N(3) + \dots = \sum_{i=0}^j N(i),$$

where $N(i)$ is the number of host nests with $i = 0, 1, \dots, j$ cowbird eggs. Those nests without cowbird eggs, $N(0)$, are of two types:

$U(0)$ = those nests remaining unknown to cowbirds and therefore not exposed to risk of parasitism and, properly, not to be included in the sample (Mayfield, *The Kirtland's Warbler*, Cranbrook Inst. Sci., Bull. 40, 1960:155; 1965:260); and

$F(0)$ = those nests which had been found by cowbirds but not parasitized.

Randomness of cowbird egg distribution ought to be tested using the series,

$$T = F(0) + N(1) + N(2) + N(3) + \dots,$$

where T is the total number of nests found by cowbirds. The value of $F(0)$, however, is difficult to know. The Poisson expansion provides a means to overcome this problem. Individual terms of a Poisson series can be expressed as

$$N(i) = c^i T e^{-c} / i!$$

for $i = 0, 1, 2, \dots, j$ cowbird eggs/nest, and where c = mean number of cowbird eggs/nest for those nests found by cowbirds, e = base of natural logarithms, and $N(i)$ and T as defined above. The ratio of successive terms can be used to provide estimated values of c and T . Using the ratio $N(2)/N(1)$ gives,

$$N(2)/N(1) = (c^2 N e^{-c} / 2!) / (c N e^{-c} / 1!) = c/2.$$

This equation leads to the equality $c = 2[N(2)/N(1)]$. If the total number of cowbird eggs in the sample is E , and since $c = E/T$ also, T can be found as $T = E/c$. (Because both c and T are derived from the data, an additional 2 degrees of freedom are lost in χ^2 goodness-of-fit testing to the Poisson distribution that is generated. One then uses $m - 3$ (or $j - 2$, j as used above) degrees of freedom where m = number of categories of nests with different numbers of cowbird eggs.)

I used this method to compare cowbird egg distributions reported in several studies (including those used by Mayfield 1965) to Poisson distributions. Most studies showed no significant departure from a Poisson distribution (Table 1). Mayfield's (1965: 260) "most conspicuous deviations from randomness . . . [resulted from] . . . too many nests with no cowbird eggs and too few nests with one cowbird egg." My method assumes some nests were not exposed to parasitism risk and reduces the number of nests with no cowbird eggs. For the 14 studies I examined (Table 1), four cases depart from a Poisson expectation. These studies, with significant departures from randomness, are themselves interesting and relate to the ecology of cowbird-host community interactions. Although the remaining cases seem

to tend towards significance, the pooled data and a heterogeneity χ^2 test (Sokal and Rohlf, Biometry, 2nd ed., W. H. Freeman and Co., San Francisco, California, 1981) do not confirm this tendency. Three exceptions show negative values for $U(0)$ —nests not found—which implies that all nests could be found and were exposed to parasitism risk and that the host community was under heavy cowbird pressure. If cowbird parasitism is not a rare event, the Poisson distribution becomes an inappropriate standard to test for a random distribution. These exceptions are discussed below.

Mayfield's (1965) analysis showed cowbird egg distribution among Kirtland Warbler (*Dendroica kirtlandii*) nests barely demonstrated non-significant departure from a Poisson distribution (Mayfield 1965:Table 1). There is a history of heavy cowbird parasitism on this species, a factor contributing to this warbler's endangered status. Apparently Kirtland Warblers' nests are easily found by cowbirds since few other species are victimized in warbler habitat (Harwood, Audubon 83:99–111, 1981). Most cowbird nest finding is done by sit-and-watch activities (Hann, Wilson Bull. 53:211–221, 1941; Norman and Robertson, Auk 92:610–611, 1975) and Kirtland Warbler habitat provides many places for doing just this (Anderson and Storer, Jack-Pine Warbler 54:105–115, 1976).

Southern (Jack-Pine Warbler 36:105–130, 185–207, 1958) described nest-sites of Red-eyed Vireos (*Vireo olivaceus*) as usually near small clearings in woods. Such a location—at a habitat discontinuity—would be at high risk of cowbird parasitism (Gates and Gysel, Ecology 59:871–883, 1978). Nest location, and perhaps observer interference (J. C. Barlow, pers. comm.), may have aided cowbirds in finding these vireo nests.

Elliott's (1977) prairie community consisted of three primary hosts: Eastern Meadowlark (*Sturnella magna*), Dickcissel (*Spiza americana*), and Grasshopper Sparrow (*Ammodramus savannarum*). Most nests were parasitized more than once and many were visited by two or more cowbirds. Kansas supports high densities of cowbirds (Dolbeer and Stehn, F&WS Spec. Sci. Rept., Wildl. No. 214, 1979) and the low diversity of prairie bird communities means relatively few hosts per breeding female cowbird and a resultant high cowbird pressure on the host community (Zimmerman, Auk 99:292–298, 1982; Bull. Ecol. Soc. Am. 63:102, 1982).

Red-winged Blackbirds (*Agelaius phoeniceus*) studied by Linz and Bolin (Wilson Bull. 94: 93–95, 1982) had more unparasitized nests and fewer one- and two-cowbird egg nests than expected. Colonial red-wings are less often parasitized than upland nesting individuals (Friedmann, U.S. Natl. Mus. Bull. 233, 1963) due, in part, to group defense against cowbirds (Folkers, Kansas Ornithol. Soc. Bull. 33:32–34, 1982; Robertson and Norman, Condor 78: 166–173, 1976). The red-wing population studied by Linz and Bolin (1982) was comprised of birds nesting in cattails along roadside ditches. My analysis suggests that most of these red-wing nests were well defended and under low cowbird pressure (i.e., many nests with no cowbird eggs and few nests with only one cowbird egg). Those nests that were parasitized were parasitized more than once, suggesting that cowbirds were not prevented from visiting them.

Other examples in Table 1 do not show significant departure from a Poisson distribution. This collection of single-host and multi-host studies show a random distribution of cowbird eggs. Female cowbirds are likely opportunists in host selection. Some nests are never exposed to parasitism risk but all others have equal likelihood of being parasitized. Host communities with much cowbird pressure seem exceptions to such a random egg distribution.

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