COWBIRD-HOST RELATIONSHIPS

Daniel S. McGeen

This is the third in a continuing series of reports on the Brown-headed Cowbird (*Molothrus ater*) and its host relationships. The first (McGeen and McGeen, 1968) reported on numbers of cowbirds and their eggs laid in Yellow Warbler (*Dendroica petechia*), Song Sparrow (*Melospiza melodia*), and Traill's Flycatcher (*Empidonax traillii*) nests. A colony of 50 pairs of Yellow Warblers was the main interest. They were nesting in 55 acres of old pasture in early stages of succession and low wet thicket bordering a canal connecting Cass and Otter Lakes in Waterford Township, just west of Pontiac, Oakland County, Michigan. In 1950 five female cowbirds were believed to be in the area from actual counts and the circumstantial evidence of egg types, measurements, and laying dates. Data were obtained on clutches and on acreage and hosts covered by apparent single females. Some females appeared to specialize on certain host species, others did not.

The second (McGeen, 1971) reported the effect on cowbird success of proper timing with respect to the host's laying (synchronization) and the effect of multiple cowbird eggs in parasitized nests as opposed to single cowbird eggs found with no other cowbird egg or young present. Proper timing was apparently easily achieved with the Song Sparrow host, but not with the Yellow Warbler. Multiple eggs (twos, threes) were accepted routinely by the Song Sparrow, rarely by the Warbler.

With the Song Sparrow host the cowbird apparently achieved good synchronization and a good success even with a high multiple egg frequency, with the warbler it did not. Apparently these two species differ widely in their reactions to parasitism and therefore in their value to the parasite. This report continues on the use of the multiple cowbird eggs as indicators of the cowbird relationships with these two hosts.

Cowbird Density, Pressure, Success, and Host Losses

It might logically be expected that increased parasite densities not only would give a greater frequency of nests parasitized (incidence) but also a greater frequency of multiple eggs (intensity of parasitism). Analyzing several studies for these factors (Table 1) shows the correlation coefficient to be both positive and high as expected (0.96).

As incidence (percent of nests parasitized) and intensity of parasitism (percent of multiple eggs in relation to total cowbird eggs laid) are both factors dependent upon and reflecting cowbird density, perhaps they can be combined into a useful mean, a single "cowbird pressure index" for correlation with host losses to cowbirds or with parasite and host successes.

TABLE 1
COWBIRD DENSITY AND MULTIPLE EGGS

Cowbird females per 100 pairs of hosts	Percent of multiple eggs	Hosts	Source
6.25	26	Field Sparrow	Walkinshaw (1949)
10	28	Yellow Warbler	This work, 1950 season
17.9[1]	49	Song Sparrow	Nice (1937)
17	57	Song Sparrow	This work
25	75	Ovenbird	Hann (1937)

[1] Based on the number of nests found and followed and containing among them the cowbird eggs.

Figures on several species nesting at Otter Lake in 1950 demonstrate through such a mean index that, with one exception, open nest fledging success increases as pressures decrease (Table 2). The exception apparently points up a difference in relative host susceptibilities to the cowbird intruders. As the Song Sparrow under similar environmental conditions attained approximately the same egg success as the Yellow Warbler at twice the parasite pressure, it may be only half as vulnerable to cowbird losses.

If Yellow Warbler fledging success is listed with accompanying parasite pressure (Table 3), an inverse correlation coefficient may be demonstrated, $r = -0.98$. The loss attributed to the cowbirds is also included for reference. The correlation between cowbird pressure and host losses to them is a positive one, $r = 0.6$.

NONSPECIFIC OR UNIVERSAL LOSSES

Warbler success plus losses to parasites totalled about 60 percent of production (Table 3). If these data are typical, then without parasitism one might expect about this success figure, provided other nonparasitic losses are normal. This gives an insight on a possibly most important constant, namely that universal (i.e. nonspecific) losses acting on open nesting host and parasite alike, may skim off approximately the top 40 percent of pro-

TABLE 2
OPEN NEST SUCCESS AT OTTER LAKE, 1950

Species	Total eggs	Successful eggs fledging young (%)	Cowbird pressure[1]
Song Sparrow	41	41	64
Yellow Warbler	270	42.6	28
Traill's Flycatcher	29	58	10
Goldfinch	36	77	0

[1] Pressure throughout this paper is the mean of the incidence (percent of nests parasitized) and the intensity of parasitism as measured by the percent frequency of multiple cowbird eggs (all others than the singles) with respect to total cowbird eggs laid. See Tables 4, 8, 9 for examples, columns 3, 6, and 9.

TABLE 3
YELLOW WARBLER/COWBIRD RELATIONSHIPS

Total warbler eggs	Successful (fledged)		Loss attributed to cowbirds		Cowbird	Expected success without cowbirds[1]		
No.	No.	%	No.	%	pressure	No.	%	Season
46	27	58.8	2	4.3	3.9[2]	29	63	1948
152	62	41	26	17.3	28.5	88	58.3	1949
270	115	42.6	51	19	28	166	61.6	1950
18	11	61	0	0	0	11	61	1951 and 1952[3]
486	215		79			294	60.5	Five seasons

[1] Observed success plus loss to cowbirds.
[2] Effective pressure (removed an accepted egg).
[3] Boston, Massachusetts area.

duction on any well-sampled population in normal or balanced habitat where the system is operating in a steady state of equilibrium.

The steady state is defined by Odum (1971: 57) as a system in a dynamic equilibrium; inflows balance outflows of material and energy. The rate of production by green plant producers is in equilibrium with the supply or rate of inflow of the minimum limiting constituents, i.e. the law of minimum is applying. All food chains and energy transfers above this producing level base are geared to this steady-state energy flow and transfer. The organisms with which we are dealing are, for the most part, first-level carnivores feeding directly on the insect herbivores during the breeding season for most of (Song Sparrow) or all (Yellow Warbler) of their energy requirements. As the insect herbivores are rarely resource (food) limited, it is often the climatic factor, the presence of cold, wet periods or protracted hot, dry ones, which are both connected with depressions in insect reproduction and availability, that is limiting to these avian carnivores. Even with these and other element-caused perturbations (storms, etc.) that may depress success in one part of a season, compensatory higher-than-mean successes in other parts of the season often, in fact usually, level the total season's success out to a steady-state mean. Hence adequate samplings over one or more total breeding seasons are needed to bring forth these relations. It follows that the mean harvest by the universal hazards in terms of percent of the total reproduction attempts (eggs) of these open nesters may also be expected to reach an equilibrium.

As the 40 percent universal loss/60 percent fledging success (in the absence of cowbirds) pattern assumes the steady state, what evidence shows this actually existed at Otter Lake during the periods of study? Except for a minor flood in 1949 that affected only briefly a small amount of habitat and but one Song Sparrow nest, no major perturbations in the steady state were apparent, and no repressive human interferences were present, other than the minimal impact of the observer. Also no successional changes of visibly great importance were evident in the two comparatively short periods of the study. All of these conditions would apply to both the warbler and sparrow observations. Numbers involved based upon adult counts and nest finds for hosts, and on adult counts and egg finds, separated as to types from presumably different female cowbirds, were: 42 pairs of Yellow Warblers (there may have been a few more), 22 pairs of Song Sparrows, and 4^+ cowbird females in 1949; 50 pairs of warblers, 25 pairs of sparrows, and 5 cowbird females in 1950; and 50 pairs of warblers, 20 pairs of sparrows, and 5 cowbird females in 1953. Time limitations allowed only half the field work in 1950, so again a few more sparrows may have been present. These population figures reflect the stability of the system and also help justify the assumption of a steady state when the 40 percent universal loss/60 percent fledging success pattern is present.

Hann's (1937) Ovenbird (*Seiurus aurocapillus*) fledging success of 43 percent plus loss to cowbirds of 18 percent also supports the approximate 60 percent area of expected success without parasitism in open nesting passerines. His area, being a climax forest, was also apparently free from major perturbations in the steady state, and no important disturbing human factors were evident. Lawrence's (1953) fledging success of 60 percent on a well-sampled but nonparasitized population of Red-eyed Vireos (*Vireo olivaceus*) also supports this view. Apparently when the nests of open nesting passerines are sampled adequately, sooner or later a loss to universal hazards of approximately 40 percent of the total eggs laid is disclosed. This then may be the steady-state level for this part of the energy flow of the ecosystem of which the host and parasite, if present, are a part. The cowbird eggs and subsequent nestlings are subject to these same universal hazards as the host eggs and nestlings in all categories, as well as being subjected to those hazards peculiar to parasitism, such as nonsynchronization and nonacceptance (being covered, ejected, or deserted by the host). Thus both host and cowbird successes and losses to this interaction between parasite and host must be applied to and studied with respect to the preexisting steady-state matrix already delineated by reasonably convincing, but at this time necessarily limited, supporting data. These 40 percent universal loss and 60 percent open nest host fledging success figures when cowbirds are not present may then be used as best estimates until proved otherwise.

This knowledge may help plot a theoretical poor host reaction pattern to parasitism. If at zero cowbird pressure 60 percent host fledging success results under adequate sampling, therefore steady-state conditions, then at complete saturation pressure of 100 (every nest parasitized with at least two and often more cowbird eggs per nest) we might logically expect under these extreme conditions of competition with the larger parasites that with

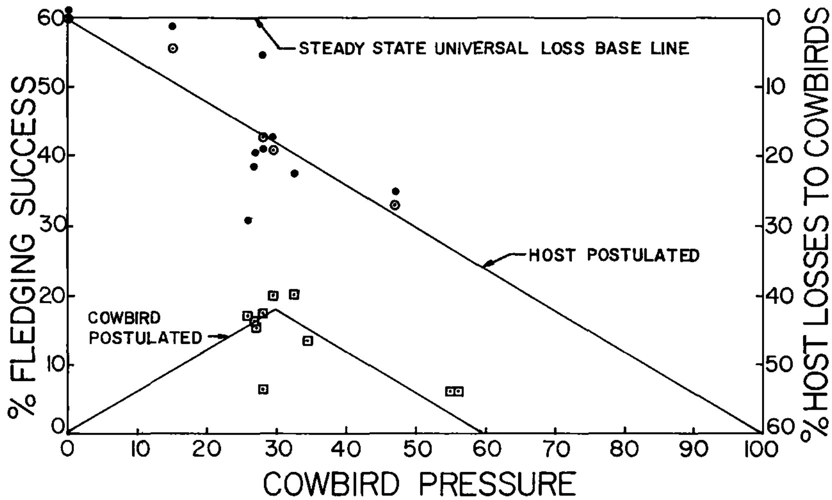

Figure 1. Yellow Warbler postulated (under steady-state conditions, universal losses just 40 percent) and observed losses to cowbirds (○). Also Yellow Warbler postulated and observed success (●), and cowbird postulated and observed success (□) in percent of total eggs laid under varying cowbird pressures (see text and Table 4).

intolerant and susceptible small host species, no host success would be possible. Connecting these two extreme success points (60 and 0) at the respective extreme pressure areas of 0 and 100 should give us the theoretical poor host reaction line to parasitism; below it lies the host fledging success, above it to the 60 percent steady-state base line lie the losses to the cowbirds, both in percent of total eggs laid (Figure 1).

YELLOW WARBLER/COWBIRD RELATIONSHIPS

Plotting available Yellow Warbler data (Table 4) shows a good fit with the theorized pattern for 12 of 15 plot points (Figure 1). Some reasons for nonconformity merit discussion. As cowbird success in part determines host success by being responsible for some of the losses, then if cowbird success is high or low by chance, or for other reasons, host success can be depressed or elevated a reciprocal amount. This recognized deviation I term the cause-effect situation. It is significant that two of the three above deviant host success plot points are from data where known (this work, 1948 season) or suspected (Schrantz, 1943) cowbird egg removal by humans would in this manner account for their slightly elevated positions.

If the host success data are off the pattern because of greater or lesser universal losses than the usual 40 percent, then cowbird success will also be expected to be off by an equal amount and in the same direction, above or below expectation as the host success data indicate. This recognizable situation, assuming adequate sampling, is called henceforth a deviation in the steady state. As the cause-effect deviations are on opposite sides of the expectation line, it will be recalled, the distinction is clear.

If host success data prove to be in the steady state, then with adequate sampling the cowbird success data should also be in this generalized equilibrium situation and therefore reliable for recognizing the correlation between cowbird pressure and cowbird success, as well as the interaction pattern between parasite and host.

Parasite success may theoretically begin and end at zero, rising to a peak at optimum cowbird density and pressure. Beyond this the law of diminishing returns, activated by the feedback of increasing cowbird competition and host intolerance with increasing cowbird interventions and layings, would carry it back to zero at a pressure cutoff point dictated by the susceptibility of the host. At the other end of the pressure scale there can obviously be no cowbird success if no parasite eggs are laid (zero pressure). Also cowbird eggs and subsequent young, if hatched, are subject to all the universal hazards that host eggs and young must survive. But before even qualifying to meet these universal hazards, they must first be accepted by the host. As acceptance is rare if eggs are not synchronized or if they are multiples with this warbler host, then it follows that as nonsynchronization and multiple eggs in one nest are very common events, the probability of success with the few eggs of low pressures is also low, increasing to the optimum only with increased layings and pressures.

Plotting available data for cowbird success against cowbird pressure (Table 4, Figure 1) suggests that cowbird success rises from zero at zero pressure to an optimum of about 18 percent at 30 pressure and then descends parallel to host success to the null point at 60 pressure in accordance with the above theoretical expectations and Allee's principle, which states that a low density may be just as inimical to a species success as a high density.

At this 30 pressure area, it will be noted a matching 18 percent of host production is lost to the cowbird leaving a 42 percent host success if the steady-state condition of 40 percent universal loss exists. Both Nice (1937) and Hann (1937) have noted the fact that open nesting passerine success seems to average to about 43 percent though Nice (1957) believed later data raised this figure by 3 percent.

Six of seven cowbird success plot points fit the above theory well. The seventh (Schrantz, 1943) is probably off expectation because of human interference, as already noted. The sample is small (15 cowbird eggs) and chance can thus be a factor also.

Small deviations from the parasite success pattern are expected in the

TABLE 4
COWBIRD PRESSURES AND COWBIRD-HOST RELATIONSHIPS WITH YELLOW WARBLER

	Nests[1] parasitized		Cowbird eggs						Host eggs					
				Multiple		Successful				Successful		Loss to cowbirds		
Total	No.	%	Total	No.	%	No.	%	Pressure	Total	No.	%	No.	%	Source
13	4	30.7	4	0	0	0[2]	0	15	46	27	58.8	2	4.3	This work, 1948 season
46	15	32.6	17[3]	4	23.5	3[2]	17.6	28	152	62	41	26	17.3	1949 season
108	33	31	40	11	28	8	20	29.5	270	115	42.6	51	19	1950 season
5	0		0	0		0		0	18	11	61	0		1951 and 1952 seasons, Boston, Mass. area
66	24	36.4	28	4	14.3	5[4]	17	26	217	66	31			1953 season
24	8	33	9	2	22.4	0		27.7	63	11	17.4			1954 season
262	84	32	98	21	21.4	16	16.3	26.7	766	292	38.2			Totals, this work
41	12	29.2	15	4	26.7	1[4]	6.7	28	168	91	54.2			Schrantz (1943)
20	9	45	10	2	20	2	20	32.5	75	29	38.5			Batts (1961)
323	105	31.5	123	27	22	19	15.4	27	1,009	412	40.5			Totals, 3 sources
44	18	41	33	24	72	2	6	56						Berger (1951)
11	7		7	0		1								1951 season, Otter Lake[5]
21	12	57	17	9	53	1	6	55						Young[6] (1963)
399	142	35.6	180	60	33.3	25[7]	13.9	34.5						Totals, 5 sources

1 Containing eggs and/or young.
2 Omitting one egg removed.
3 Including two eggs found in fall nest finds.
4 Possible, eggs removed, after acceptance, by me; apparently so by Schrantz.
5 See acknowledgments.
6 By isolation of his own data.
7 Including as successes the two removed in 1948 and 1949, as nests involved were successful.

usually small cowbird sampling and in most cases reasons can be ascribed, but not if host success data are lacking. For instance, the Young (1963) and the Berger (1951) data loci for cowbird success at the two highest pressures are high (Table 4 and Figure 1). Two causes are possible. The first is chance on small samples (17 eggs, Young) or even those considered adequate in statistics (33 eggs, Berger), in which case the host success would be below expectations because of the greater than expectation success of the cowbird and the concomitant greater host losses thereto (the cause-effect situation). The second is deviation in the steady state with lessened predation and other mortality. In this case the unknown data on host success would also be equally above expectations. So it is apparent that without host success data we cannot explain these small, but expected, deviations from the pattern in parasite success.

The slight deviation of the Batts (1961) data is apparently a "cause-effect" situation, as is the larger deviation in the Schrantz data. A small sampling of 15 cowbird eggs is here involved (Schrantz) and the large percentagewise deviation represents only one cowbird egg success off expectation and possibility without getting into fractions of eggs or fledglings. Actually no data on cowbird success were given, and probable observer interference is suspected. As this one egg was accepted and had a chance for success without interference, I so designated it.

Testing the observed host and parasite success and the loss to cowbird data with that expected according to the pattern, by means of the 2×2 χ^2 test for goodness of fit, confirms what seems evident from the figures. Only one of the 12 tests shows a significant difference between postulated patterns and observed data (Tables 5 and 6). As already noted exceptions are expected and readily explainable. Of 9 active Yellow Warbler nests found (Kammeraad, 1966), 5 were parasitized with 6 cowbird eggs, 2 of them multiples, 4 singles. At the pressure of 44.3 that these data give, 34.6 percent of 26 total host eggs fledged young and a 7-egg 27 percent loss to cowbird removal was noted. These add to 61.6 percent of egg production and the χ^2 test shows no significant difference between expected and observed data ($P = 1$ for host success and $P = 1$ for both summed). In 1964 he observed 67 percent fledging success in 6 unparasitized nests containing 29 eggs, and again no significant difference from expectation ($P = 0.60$). These data are not in Table 4 nor have they been plotted on Figure 1, but loss to cowbird removal observed in the 1966 report is tested in Table 6, and also shows no significant difference from expectation ($P = 0.90$).

The fit of these data to these theoretical patterns at varying cowbird pressures supports the 60 percent area of success with no parasitism and the approximate 40 percent universal loss, for if these losses were not about 40 percent there would be no fit. So too does the summing of host success and

TABLE 5

OBSERVED AND EXPECTED SUCCESS OF YELLOW WARBLER AND COWBIRD

	Yellow Warbler eggs					Cowbird eggs				
		Successful = Fledged					Successful = Fledged			
Year	Total	Observed	Expected	χ^2	P[1]	Total	Observed	Expected	χ^2	P[1]
1948	46	27	23	1.91	0.10					
1949	152	62	65	2.86	0.05	17	3	3		
1950	270	115	114	0.660	0.40	40	8	7	0.476	0.40
				Total 1949 and 1950[2]		57	11	10	0.313	0.50
1951 and 1952	18	11	11	0						
Batts (1961)	75	29	30	0.557	0.40	10	2	2		
Schrantz (1943)	168	91	72	8.83	0.001	15	1	3		
Berger (1951)						33	2	1		
Young (1963)						17	1	1		
		Total of Berger, Young, Schrantz, and Batts[2]				75	6	7	0.158	0.60

[1] P, approximate value of the significance probability for the χ^2 goodness of fit test. Probability of 0.05 or larger is taken to indicate adequate fit.
[2] Totalled data necessary to comply with stipulation that expected number must be 5 or over.

TABLE 6
LOSS TO COWBIRDS, OBSERVED AND EXPECTED, YELLOW WARBLER HOST

Year	Host eggs Total	Loss to cowbirds		χ^2	P[1]
		Observed	Expected		
1948	46	2	4		
1949	152	26	26		
Total[2]	198	28	30	0.158	0.60
1950	270	51	47	0.413	0.50
1966[3]	26	7	6	0.163	0.90

[1] See Table 5.
[2] 1948 data for expectation is below test's minimum of 5.
[3] Kammeraad, see text.

losses to cowbirds, which add up to this 60 percent area of host production. The χ^2 test reveals no significant difference from expectations in all five cases (Table 7).

Note too that if each unit of cowbird success up to the optimum in poor hosts is gained at the expense of the corresponding unit of host success according to this pattern, then data supplying these two factors (host and cowbird success) but lacking observations on losses to cowbirds, may also reinforce the estimate that about 60 percent host success is usual without cowbirds and about 40 percent is the usual loss to universal or nonspecific hazards on well-sampled populations in the steady state.

The Schrantz and Batts Yellow Warbler and cowbird data support these contentions; possible 6.7 percent cowbird success, 54.2 percent host success for the former; 20 percent cowbird and 38.5 percent host success for the

TABLE 7
YELLOW WARBLER FLEDGING SUCCESS PLUS LOSSES TO COWBIRDS COMPARED WITH EXPECTED FREQUENCY OF 60 PERCENT OF PRODUCTION IN STEADY STATE

Year	Total eggs	Observed success + loss to cowbirds	Expected (60 percent of total)	χ^2	P[1]
1948	46	29	28	0.913	0.30
1949	152	88	91	1.136	0.25
1950	270	166	162	1.137	0.25
1951 and 1952	18	11	11	—	—
Totals	486	294	292	0.368	0.50
Batts (1961)	75	44[2]	45	0.056	0.80
Schrantz (1943)	168	102[2]	100	0.099	0.70

[1] See Table 5.
[2] Same, but using Yellow Warbler success plus observed cowbird success (which equals the missing host loss to cowbirds up to optimum 30 pressure) for observed frequency.

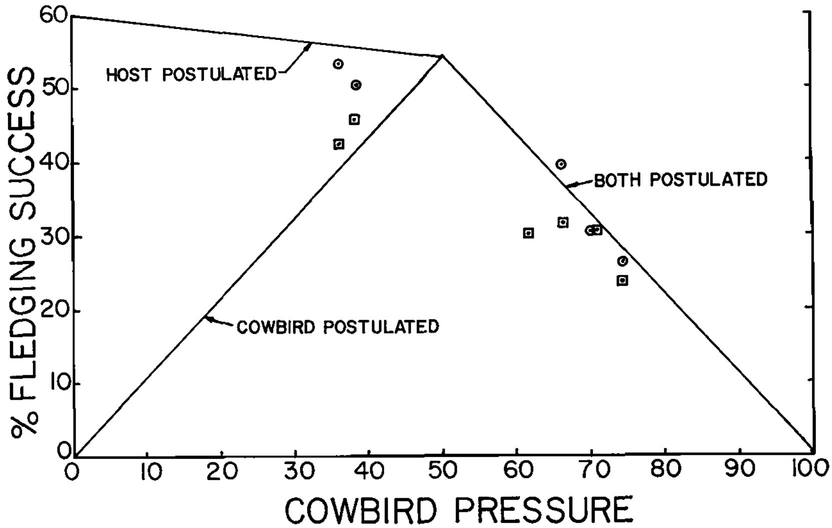

Figure 2. Song Sparrow and cowbird postulated (under steady-state conditions) and observed fledging success (○ = Song Sparrow, □ = cowbird) in percent of total eggs laid under varying cowbird pressures from all extant usable data (see text and Table 8).

latter, both adding to the 60 percent area (Table 4). Again χ^2 reveals no significant difference from expectation (Table 7).

Thus with adequate sampling and the system in a steady state we can expect agreement with these patterns, as apparently cowbird parasitism with this host is a finely balanced homeostatic mechanism that prevents host overpopulation.

Song Sparrow/Cowbird Relationships

My Song Sparrow data from several years, totalling 32 cowbird and 84 host eggs, under a cowbird pressure of 66.4 (derived from 73 percent nests parasitized and 59 percent multiple eggs averaged) show a 31.4 percent cowbird and 39.4 host fledging success (Table 8). These host and cowbird success data are plotted (Figure 2) using a midpoint thereof (because of the cause-effect situation) on the Y axis against pressure on the X axis. We may assume, as now seems evident in the Yellow Warbler, that at 100 or complete saturation pressure no host success is possible even with this larger host. Now connect the two determined points with a straight line and extend it to the 50 pressure area. We may assume that below this 50 pressure area good host success also arises to 60 percent at zero cowbird pressure under steady state as in the Yellow Warbler. Connecting this point, where the above determined success line cuts the 50 pressure line at approximately

TABLE 8

Cowbird Pressure and Cowbird-host Relationship with Song Sparrows

	Nests			Cowbird eggs						Host eggs					
		Parasitized			Multiple		Successful				Successful		Loss to cowbirds		
	Total	No.	%	Total	No.	%	No.	%	Pressure	Total	No.	%	No.	%	Source
Over 50 pressure	46	28	61	68	60	88[1]	16	23.5	74.5	177[2]	46	26			Berger (1951) (subsample) p. 30
	30	22	73.4	32	19	59.4	10	31.4	66.4	84	33	39.4			McGeen, this work
	30	23	77	30	14	46.7	9	30	61.9	127	38	30	18	14.2	Nice (1937) (1935 and 1936 seasons)
	106	73	69	130	93	71.5	35	27	70.3	388	117	30.2			Totals
	13	9		14	12		9								Berger (1951) balance of data from Table 2, p. 28[3]
	119	82	68.4	144	105	73	44	30.6	70.7						Totals
Under 50 pressure	180	66	36.6	83	34	41	27	32.6	38.8	727	270	37.2	23	3.2	Nice (1937) (1930–33 seasons)
	24	8	33	10	4	40	3	30	36.5	103	42	41			Batts (1961)
	204	74	36.4	93	38	41	30	32	38.7	830	312	38			Totals
	27	11		13	4		4								Norris (1947)
	231	85	36.8	106	42	39.5	34	32	38.2						Totals

[1] Assumed from his total sampling.
[2] Using nonparasitized clutch size in the parasitized subsample nests to adjust for cowbird removal.
[3] Total Table 2 data, 59 nests, 37 parasitized; 82 cowbird eggs, 72 multiples, 25 successful at 75.4 pressure.

TABLE 9
SONG SPARROW AND COWBIRD RELATIONSHIPS[1]

	Nests			Cowbird eggs					Pressure %P and %M	Host eggs				
		Parasitized			Multiple		Successful				Successful		Loss to cowbirds	
Year	Total	No.	%	Total	No.	%	No.	%	2	Total	No.	%	No.	%
1930	61	15	24.6	20	10	50	7	35	37.3	236	102	43.2	7	2.9
1931	36	10	27.7	12	4	33.3	2	16.6	30.5	143	65	45.5	2	2.9
1932	50	29	58	36	14	39	16	45.7	48.5	206	76	36.8	9	4.4
1933	33	12	36.4	15	6	40	2	12.3	38.2	142	27	19	5	3.5
1934	13	9	69.2	16[2]	12	75	2[2]	12.5	72.1	52	14	26.2	15	28.9
1935	18	14	77.7	18	8	44.4	4	22.2	61.1	75	22	29.3	12	16
1936	12	9	75	13	7	53.6	5	41.7	64.3	52	17	32.7	9	17.4

[1] Nice (1937) from Tables 20 and 28 and page 150, No. 23. Total host eggs from Table 26, page 141.
[2] Thirteen cowbird eggs collected.

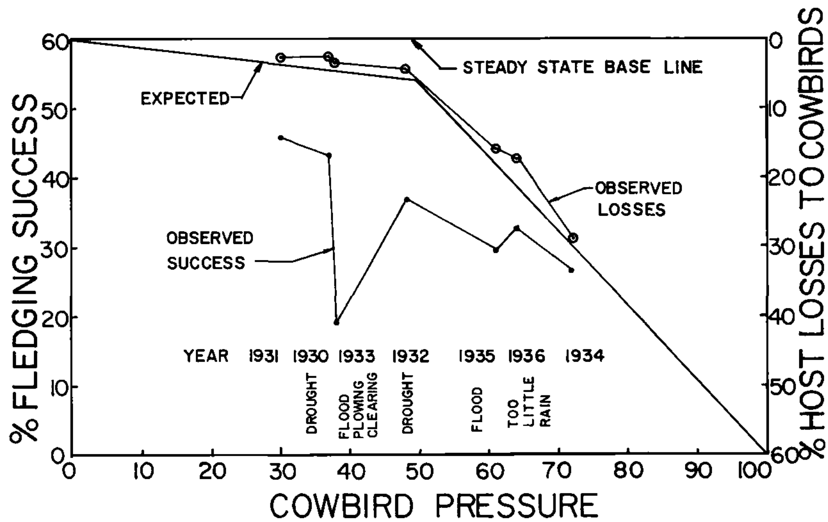

Figure 3. Expected under steady state (this work) and observed Song Sparrow success and losses to cowbirds in percent of total eggs laid at Interpont (Nice, 1937) and cowbird pressure (see text and Table 9). Data in order of increasing pressure, not chronologically. Years and some of the probable factors involved in greater than steady state 40 percent universal losses identified.

54 percent, with the 60 percent host success area of no cowbird pressure thus gives a probable reaction pattern for the Song Sparrow.

Berger's data fit this pattern well, considering cause and effect again, with 26 percent host success and 23.5 percent cowbird success at 74.5 pressure (Table 8, Figure 2). As for the cowbird success line, assuming cowbird success is identical to host success above optimum 50 pressure as seems possible from these meager data, and as no cowbird success is possible at zero pressure, two more points may be connected to complete the cowbird success pattern, namely zero at zero pressure and about 54 percent at 50 pressure.

Just as with the poor host Yellow Warbler, the cowbird success here demonstrates Allee's principle; here also is an optimum pressure, and therefore an optimum density for parasite success. Both below and above this density cowbird success decreases to zero at the extremes of zero and 100 pressure. Exceptions to a fit on these patterns will be expected and can be found. Especially will this be true where samplings are small or obvious deviations from the balanced or steady-state habitat are present from such natural catastrophes as floods or drouth or from human interference.

These latter are true of Nice's Song Sparrow data (1937). She comments (p. 148) "but we know that in reality man is responsible for far more than

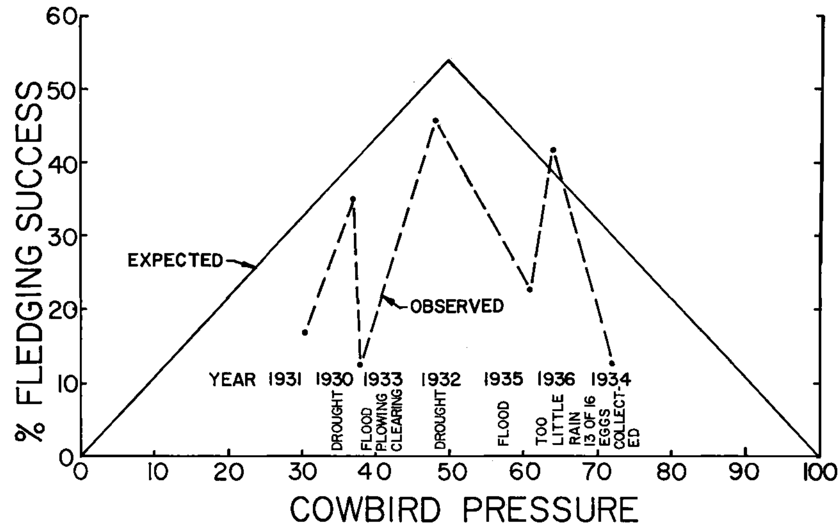

Figure 4. Cowbird success expected under steady state (40 percent universal losses) and observed under existing conditions at Interpont under varying cowbird pressures. Data in order of increasing pressure, not chronologically. Years and some of the probable factors involved in greater than steady state 40 percent universal losses identified as per Nice (1937) (see text and Table 9 here). Men and sampling considerations also involved.

3.7 percent loss. On account of his disturbing activities he should be charged with much of the predator loss (cats, rats, dogs, and in June 1933 Grackles), much of the Cowbird loss, some of the killing of parents, and perhaps even the flood. Indeed, it is only drought, sterile and addled eggs, parental failures and part of the predator and Cowbird damage that cannot ultimately be laid at his door."

Therefore, one cannot expect her host and cowbird success data, as both suffered alike, to fit these steady-state, density-dependent, success pressure patterns (Table 9, Figures 3, 4). Nice made daily and detailed observations of losses to cowbirds (Table 9, column 10), which can be used with the pressure data by counting the losses (at the widely varying pressures her 7-year study revealed) down from the 60 percent steady-state success area as a base line (Figure 3).

The resultant pattern is the first complete one for a good host's losses to cowbirds, thanks to the fortunate wide spread of pressures found on her sampled population during the 7 years of her study. It is the final key to the complete interaction between good host and cowbird, for it verifies the correctness of the pattern from theory and host success data from studies where the steady state apparently existed (Berger, 1951) and this work.

It will be noted her losses are slightly above the line believed to be the true pattern for reasons and supportive data cited and some yet to be revealed. It is interesting therefore to find that even with this high degree of accuracy, Mrs. Nice still realized (1937: 160) that she had been slightly conservative in her assessment of losses to the cowbirds.

Besides the losses to humans and natural catastrophe, another reason for success below expectations is already documented by Nice. She notes (1957: 314) that in only one year, 1930, did she make a complete season's census, and that other years would undoubtedly show a greater success if she had. She also mentions (1937: 141–142) the small early season samples of 1933, 1934, and 1935 with their lessened likelihood for success. Also cited is the fact that after an absence of several weeks from her area in late July 1933, nine pairs had young out of the nest from third or fourth attempts. This, if not already incorporated in her data, raises fledgling success that season by 9 percent with the most conservative assessment possible consistent with her data, i.e. 4 eggs per clutch, 2.5 young fledged per successful nest, as in her worst year.

As this study concerns the relative host and cowbird success under varying degrees of parasitic pressure I have plotted four points on Figure 2 as though certain areas were in the steady state, when it is obvious that they were not, in order to make those comparisons valid (Nice, and Batts under 50 pressure data). The former averaged 13 percent lower actual success for host and cowbird and the latter 12 percent, the universal losses being those amounts higher than steady-state expectations. It will be noted, after these necessary corrections are made to clarify relationships, that slight deviations are still apparent, i.e. the cowbird success, being a little off by chance, and a determinator of host success, then shifts the host success in an opposite direction.

The same steady-state deviation in the Nice above 50 pressure success

TABLE 10
Loss to Cowbirds, Data from Nice (1937) Observed and Expected[1]

Year	Total Song Sparrow eggs	Loss to cowbirds: Observed	Loss to cowbirds: Expected[2]	χ^2	P[3]
1930	236	7	12	2.181	0.10
1931	143	2	6	2.787	0.05
1932	206	9	12	0.796	0.30
1933	142	5	7	0.599	0.40
1934	52	15	16	0.914	0.30
1935	75	12	14	0.352	0.50
1936	52	9	11	0.461	0.40

[1] See Table 9 and Figure 3.
[2] On basis of the pattern at the cowbird pressure involved.
[3] See Table 5.

TABLE 11
OBSERVED AND EXPECTED SUCCESS, SONG SPARROW AND COWBIRD DATA FROM NICE (1937)[1]

	Host eggs					Cowbird eggs				
		Successful = Fledged					Successful = Fledged			
Year	Total	Observed	Expected	χ^2	P^2	Total	Observed	Expected	χ^2	P^2
1930	236	102	129	12.45	0.001	20	7	8	0.208	0.50
1931	143	65	80	6.40	0.01	12	2	4[3]	1.5	0.20
1932	206	76	111	24.0	0.001	36	16	19	1.00	0.30
1933	142	27	78	74.0	0.001	15	2	6	4.45	0.025
1934	52	14	16	0.361	0.50	16	2[4]	5	2.62	0.10
1935	75	22	31	4.47	0.025	18	4	7	2.11	0.05
1936	52	22	20	0.325	0.50	13	5	5	0.00	0.995

[1] See Table 9 and Figures 3 and 4 here.
[2] See Table 5.
[3] No correction for fewer than five in expected sample. Summed with 1932 data; total = 48; O.S. = 18, E.S. = 23, $\chi^2 = 2.087$, $P = 0.10$.
[4] Thirteen cowbird eggs collected by Nice.

TABLE 12

SONG SPARROW AND COWBIRD SUCCESS, EXPECTED AND OBSERVED[1]

Host eggs: Total	Host eggs: Successful Observed	Host eggs: Successful Expected	Host eggs: χ^2	Host eggs: P[2]	Cowbird eggs: Total	Cowbird eggs: Successful Observed	Cowbird eggs: Successful Expected	Cowbird eggs: χ^2	Cowbird eggs: P[2]	Source
Over 50 pressure										
177	46	49	0.254	0.60	68	16	19	0.658	0.40	Berger (1951)
84	33	31	0.883	0.40	32	10	12	0.553	0.50	This work
179	58	67	1.925	0.20	47	11	17	3.32	0.05	Nice (1937)
Under 50 pressure										
727	270	402	96.5	<0.0001	83	27	35	3.18	0.05	Nice (1937)
103	42	57	8.84	0.001	10	3	4			Batts (1961)
					13	4	5	0.325	0.50	Norris (1947)
					23	7	9	0.731	0.60	Batts, Norris[3] (combined)

1 See Table 8 and Figure 2.
2 See Table 5, footnote 1.
3 Batts' expected frequency is below test's minimum of five.

data is apparent, but as a need for correction of 11 percent upwards for both host and cowbird is obvious without the confusing complications of two separate expectation lines, plus the "cause-effect" deviations as noted, the correction was not made here. Also this uncorrected sample can be summed along with the Berger and the Pontiac samples to illustrate how the larger the sample, generally the better the fit (overlapping loci closest to expectation line at 70 pressure area, Figure 2).

Again χ^2 tests (Tables 10, 11, 12) reiterate what is already evident from the figures, that no significant lack of agreement exists between postulated and observed data in the majority of cases (22 of 31 tests). Where significant deviations from expectations do occur, they are readily explained by sampling variations or deviations in the steady state caused by natural catastrophe or man (Nice and Batts data).

ACKNOWLEDGMENTS

I wish to thank M. M. Nice and A. J. Berger for their reading and criticism of the manuscript at various stages, W. P. Nickell for his help in banding young, G. M. Sutton for supplying color bands, H. Schick for raising a young cowbird, A. Madden for checking a small series of nests when I was recalled into service in May 1951, C. Frick for drawing the figures, Joanne Johnson for typing the final version, and my wife, Jean, for typing preliminary drafts and for her constant help and encouragement.

SUMMARY

Based on data collected near Pontiac, Oakland County, Michigan, and on published material on cowbird-host relationships, steady-state conditions and adequate sampling apparently give about a 60 percent host fledging success and about a 40 percent loss to universal or nonspecific hazards without cowbird brood parasitism. This universal loss of 40 percent is also skimmed off the top of host and cowbird production alike in parasitized nests under similar conditions.

A single pressure index figure dependent upon and reflecting cowbird breeding female density is achieved by averaging two equally important phases of the parasite pressure complex upon the host population, the incidence or percent of nests parasitized and the intensity of parasitism those nests are subject to, as measured by the percent of total cowbird eggs deposited that are laid as multiples (two's, three's, four's) in a nest, as distinguished from the singles. This pressure index, dependent upon and reflecting cowbird density with respect to available hosts, correlates with host losses to cowbirds in a manner consistent with theory.

If sampling is adequate and a steady state exists (the system is in equilibrium), host and cowbird success can also be correlated with cowbird pressures also in a manner consistent with theory. Host data can thus be plotted against this horizontal pressure line (X axis) from two different

aspects, counting up from below on the left (Y axis) for the successes and down from the 60 percent steady-state success base line for losses to cowbirds on the right vertical axis.

In cases where the system is in a steady state of equilibrium and sampling has been adequate, both approaches agree. In cases where sampling is small and/or no equilibrium or steady state exists (as when the habitat has undergone extreme change from weather, or man), the success data cannot be depended upon to furnish a pattern. The losses to parasites then may give the most reliable data, if accurately ascertained. If host success data are off expectation level because of variation in the steady state, then cowbird success data will also be off the expected area in the same direction. A cause-effect deviation can also be recognized to minimize confusion. This is, in essence, recognition of the fact that the cowbird sampling is often small enough to be swayed from success expectation by chance, but being a partial determinator of host success, it then sways host success in an opposite and reciprocal fashion from steady-state expectation.

As pressures are dependent upon and reflect parasite density, these data also determine that cowbird success is density dependent with these two hosts. Its success illustrates Allee's principle, which states a suboptimum density can be as limiting as a supraoptimum density for a species. A definite but differing optimum pressure area for each of these two hosts can be pinpointed, of interest for evolutionary studies.

The Yellow Warbler is a poor host, giving a low maximum fledging success of 18 percent to the cowbird even at a low optimum pressure (30). The Song Sparrow is a good host, giving a higher 42 percent success to the cowbird at 60 pressure, twice the poor host optimum, while a 54 percent maximum success is possible at an optimum pressure of 50. An 18 percent host loss is incurred by both these hosts at these widely different parasite pressures of 30 and 60, demonstrating their differing susceptibilities. These varying susceptibilities control, via feedback in this natural density dependent system, the different successes of the parasites at the various pressures. Host susceptibilities, therefore intolerances honed by evolution, apparently set limits on acceptable cowbird interferences and pressures and therefore densities. Intraspecific competition also depresses cowbird success above optimum density.

Thus two factors apparently determine cowbird fledging success, first choice of host, and second parasite pressure via density with reference to host numbers. Their success can vary from zero at the extremes of pressure (and density) to 18 percent at the optimum with the poor host, Yellow Warbler, and 54 percent at the optimum with the good host, Song Sparrow: but it seemingly averages less than 42 percent with this good host, as they apparently usually level off at a higher than optimum density coinciding with the 60 to 70 pressure area according to later data. The preceding two symmetrical and balanced interaction patterns with parasite optimums at different pressure levels in each, are suggestive evidence, supported by what rigor is inherent in the negatively oriented χ^2 test, that brood parasitism on these two species is apparently a well-regulated homeostatic mechanism.

LITERATURE CITED

BATTS, H. L., JR. 1961. Nesting success of birds on a farm in southern Michigan. Jack-Pine Warbler, 39: 72–83.

BERGER, A. J. 1951. The cowbird and certain host species in Michigan. Wilson Bull., 63: 26–34.

HANN, H. W. 1937. Life history of the Ovenbird in southern Michigan. Wilson Bull., 49: 145–237.

KAMMERAAD, J. W. 1966. Further notes on nesting and survival of Yellow Warblers. Jack-Pine Warbler, 44: 124–129.

LAWRENCE, L. DEK. 1953. Nesting life and behavior of the Red-Eyed Vireo. Canadian Field-Naturalist, 67: 47–77.

MCGEEN, D. S., AND J. J. MCGEEN. 1968. The cowbirds of Otter Lake. Wilson Bull., 80: 84–93.

MCGEEN, D. S. 1971. Factors affecting cowbird success. Jack-Pine Warbler, 49: 53–57.

NICE, M. M. 1937. Studies in the life history of the Song Sparrow, I. Trans. Linnaean Soc. New York, 4.

NICE, M. M. 1957. Nesting success on altricial birds. Auk, 74: 305–321.

NORRIS, R. T. 1947. The cowbirds of Preston Frith. Wilson Bull., 59: 82–103.

ODUM, E. P. 1971. Fundamentals of ecology, third ed. Philadelphia, W. B. Saunders Co.

SCHRANTZ, F. G. 1943. Nest life of the Eastern Yellow Warbler. Auk, 60: 367–387.

WALKINSHAW, L. H. 1949. Twenty five eggs apparently laid by one cowbird. Wilson Bull., 61: 82–85.

YOUNG, H. F. 1963. Breeding success of the cowbird. Wilson Bull., 75: 115–121.

Division of Continuing Education, Oakland University, Rochester, Michigan 48063. Accepted 1 April 1971.