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DIFFERENTIAL REPRODUCTIVE SUCCESS OF BROWN-HEADED COWBIRDS WITH NORTHERN CARDINALS AND THREE OTHER HOSTS[1]

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Abstract. To understand low production of Brown-headed Cowbirds (*Molothrus ater ater*) by a large host, Northern Cardinal (*Cardinalis cardinalis*), we compared that production with that of three small hosts: Song Sparrow (*Melospiza melodia*), Chipping Sparrow (*Spizella passerina*), and Yellow Warbler (*Dendroica petechia*).

Cowbirds were present in only 11 of 63 broods fledged by cardinals but in 62 of 93 broods fledged by other hosts ($P < 0.001$). Notably, neither the frequency of parasitized nests nor the number of cowbird eggs per parasitized nest varied significantly among the hosts.

Unusual features of cardinals as hosts accounted for the low production of cowbirds by cardinals. First, cardinal eggs were about 50% larger than cowbird eggs. Many cowbird eggs, as well as cardinal eggs, disappeared from nests, which remained active. Second, the incubation period of cardinals was short, only about 10 h longer than for cowbird eggs. Third, cardinal clutches were small (mode = 3 eggs). Many cowbird eggs were laid after incubation had begun. These features combined to produce great differences in body masses of young cardinals and cowbirds, even when cowbirds hatched first. Differences were accentuated when cowbirds hatched after cardinals. Competition in mixed broods often resulted in underweight cowbirds, which usually died before or soon after fledging. Cowbirds reared without cardinal nestmates grew well and usually fledged and survived well. Finally, interbrood intervals were much longer for cardinals than for Song and Chipping Sparrows. Cardinals had the lowest number of successful broods per host-pair. Cowbirds thrived when reared by cardinals in broods with only one or no cardinal nestmates. We suggest that host brood-reduction enables cowbirds to exploit large hosts, particularly when the host-incubation period is short.

Key words: Cowbird reproductive success; cowbird/host laying synchrony; nesting mortality; Brown-headed Cowbird Molothrus ater ater; *Northern Cardinal* Cardinalis cardinalis; *Chipping Sparrow* Spizella passerina; *Song Sparrow* Melodia melospiza; *Yellow Warbler* Dendroica petechia; *Gray Catbird* Dumetella carolinensis.

INTRODUCTION

Much has been written about the effect of the Brown-headed Cowbird (*Molothrus ater*), a brood parasite, upon the success of its hosts, but rather less about the details of its reproductive success with different hosts. Passerine species vary greatly in their tolerance of parasitism (Rothstein 1975). For example, Gray Catbirds (*Dumetella carolinensis*) are intolerant, although often parasitized (Scott 1977), and rarely rear cowbirds (Friedmann and Kiff 1985). In contrast, tolerant species such as Red-eyed Vireos (*Vireo olivaceus*) (Southern 1958) may rear many cowbirds (unless otherwise stated, cowbird refers to *M. ater ater*).

Most hosts are smaller and lay smaller eggs than cowbirds. In nests of tolerant hosts, young cowbirds usually thrive, often to the detriment of their smaller nestmates (Mayfield 1965, Graham 1989). There are, however, tolerant large hosts whose eggs are appreciably larger than cowbird eggs, including Eastern Meadowlarks (*Sturnella magna*), Red-winged Blackbirds (*Agelaius phoeniceus*), and Northern Cardinals (*Cardinalis cardinalis*) (hereafter, cardinal). Nestling cowbirds might be expected to do poorly in competition with larger foster-siblings, but, apparently, this does not always occur. Nestling cowbirds grow well together with nestling Red-winged Blackbirds (Weatherhead 1989, Ortega and Cruz 1991). On the contrary, we have noted that cowbirds often did not survive well, either as nestlings or fledglings, when reared with young car-

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TABLE 1. Number of successful broods including cowbirds from clutches begun by three hosts[a] during the cowbird laying season. Percentages in brackets.

	Pairs	Number of broods			Total broods
		None	One	Two	Per pair
Northern Cardinal	71	21 (30)	37 (52)	13 (18)	0.89
Song Sparrow	42	7 (17)	25 (60)	10 (24)	1.07
Chipping Sparrow	27	1 (4)	18 (17)	8 (30)	1.26
		$G = 10.4$; df = 4; $P < 0.05$			

[a] Yellow Warbler omitted because of small sample; no warbler was known to be successfully double-brooded.

dinals. At London, Ontario, between 1955 and 1961, about 80% of Northern Cardinal nests found during the cowbird laying season were parasitized (Scott 1963), yet few cowbirds fledged and fewer survived for more than a few days (Lemon 1957; Scott, unpubl.).

Was this low production characteristic not only of cardinals, but also of the local assemblage of species containing cardinals? To answer this question, we estimated the annual production of fledgling cowbirds by three other locally common accepter species: Song Sparrow (*Melospiza melodia*), Chipping Sparrow (*Spizella passerina*), and Yellow Warbler (*Dendroica petechia*).

First, we present data on reproductive variables of hosts and cowbirds that affect variation in parasitism. Second, annual production of cowbirds by Northern Cardinals and the three aforementioned species indicates that cardinals are relatively poor hosts. Third, we analyze in detail the success of cowbird eggs and nestlings in cardinal nests. Fourth, we suggest some factors that contribute particularly to the failure of cowbirds to succeed with cardinals. Finally, we discuss the conditions under which cowbirds are reared by large hosts.

METHODS

This study is based on data collected mostly between 1955 and 1968 from more than 700 cardinal nests, including about 230 parasitized nests, that were observed on the campus of the University of Western Ontario, London, Ontario, and some contiguous areas (maps in Darley et al. 1971). Data on cardinals before 1962 were based on birds, usually color-marked, whose nests were normally visited daily to mark cardinal and cowbird eggs for identification and to determine such variables as clutch size, incubation, nestling periods, incidence of parasitism, hatching success, and so on. From 1963 onwards, visits were not made daily but only periodically to determine hatching times, appropriate times for banding, and dates of fledging. A triple-beam balance, modified for field use, or Pesola scales were used to weigh eggs and nestlings.

HOST AND COWBIRD PRODUCTION

We observed a total of 49 breeding pairs of cardinals from 1955 to 1961. For most pairs, the complete annual nesting history and cowbird production were determined.

To examine cowbird production by other passerines, in 1962 and 1963 we trapped and color-banded at least one member of each of 22 pairs of cardinals, 42 pairs of Song Sparrows, 27 pairs of Chipping Sparrows, and 9 pairs of Yellow Warblers. Also, we watched six pairs of Yellow Warblers in years after 1963. To determine the number of broods and cowbirds produced by these birds we visited each pair of cardinals, Song Sparrows, and Chipping Sparrows weekly until we observed a brood (Table 1). Yellow warblers were visited less regularly. Once the presence or absence of a fledgling cowbird in a brood had been ascertained, we did not visit this host pair for another month, this being the minimum interval before another brood could be produced, barring overlapping nests. As our visits were not daily, we could have missed broods or fledglings that died soon after fledging.

Our method of estimation in 1962 and 1963 was much less precise than in 1955 to 1961. In the latter years we noted that some cowbirds died soon after fledging. Such events would have been missed in 1962 and 1963. Thus, to make our data from the two sets of years more comparable, we consider only cowbirds that were seen two or more days after fledging as a measure of production per host-pair. Thus, we could have underestimated, but not overestimated, the number of cowbirds produced.

TABLE 2. Apparent interval (days) between fledging and laying of the first egg of the next observed nest or brood.

	Days			
	0–20	21–24	>24	Median
Chipping Sparrow	10	1	0	11
Song Sparrow	9	0	2	14
Cardinal	6	1	15	28

INTERBROOD INTERVALS AND NUMBER OF BROODS

Interspecific variation in interbrood intervals can influence the number of broods produced by different species during the period when they are vulnerable to parasitism. An interbrood interval separates the date of fledging from the date of laying of the first egg in the next nest. It should not be confused with the five or six days following nest failure that precede laying in a replacement nest.

We estimated interbrood intervals from the dates of the first observations of two successive broods of a pair or, if known, the onset of laying in the succeeding nest. Fledgling age and by extrapolation the onset of laying, could usually be estimated from size or the behavior of fledglings. For example, fledglings with stubby tails no longer than a few millimeters, are no older than about a week post-fledging. Fledglings with half-grown tails are about two weeks post-fledging, judged by the rate of growth of juvenile rectrices of cardinals (Jarosch 1976). To estimate the date of the beginning of the clutch, we subtracted the approximate length of the nesting cycle, about 24 days, from the estimated date of fledging. As these estimates were imprecise, we grouped the interbrood intervals into two discontinuous groups: 0–20 days and more than 24 days (Table 2).

OTHER REPRODUCTIVE VARIABLES OF HOSTS AND COWBIRDS

Reproductive success of cowbirds among different host species depends upon the interplay of many factors. First, the proportion of nests that are parasitized (incidence) and the number of cowbird eggs per parasitized nest (intensity of parasitism) set the basis of cowbird production. At this point, several factors bearing on the amount of interspecific competition within a nest come into play including the egg or hatchling masses of cowbird and host, or the synchrony of hatching of the two species, which depends upon the two incubation periods. These may overlap depending on the degree of synchrony of egg-laying of host and cowbird, which in turn depends in part upon the clutch size of the host and the day on which incubation begins. Success of cowbirds also depends on variations in the length of the breeding season of the host, and the length of the interbrood interval. Finally, variation in nest size and nest site may influence survival rates of nests and their broods.

In Table 3 we list values for several reproductive variables: egg and hatchling mass, clutch size, and incubation time. We provide original data for egg and hatchling mass and incubation period for cowbirds and cardinals. Information on the other hosts was derived from Nice (1937) for Song Sparrows, from Walkinshaw (1944, 1952) for Chipping Sparrows, and Schrantz (1943) for Yellow Warblers. Peck and James (1987) contain modal clutch-sizes and descriptions of nests and nest sites.

We used egg mass as well as hatchling mass, as values of the former are more likely to be

TABLE 3. Mean values of some relevant variables of Brown-headed Cowbirds and four hosts[a]; sample sizes in brackets.

Species	Adult	Mass (g) egg	Hatchling	Incubation time (d)	Modal clutch-size
Brown-headed Cowbird	40 (♀), 51 (♂)	3.2 (10)[b]	2.3 (9)	11.9 (12)[c]	
Northern Cardinal	43	4.9 (16)	3.5 (10)	12.3 (16)	3
Song Sparrow	22	2.3 (44)	1.8	12.6 (32)	5
Chipping Sparrow	12	1.6 (24)	1.3	11.9 (9)	4
Yellow Warbler	9	1.5 (12)	1.3	11.3 (7)	4

[a] Data on Brown-headed Cowbirds and Northern Cardinals from Scott (unpubl.), except adult cowbird body-masses are from Ankney and Scott (1980). Other body-masses from Dunning (1993). Egg and hatchling-masses and incubation time on other species are from Nice (1937), Schrantz (1943) and Walkinshaw (1944 and 1952). Other modal clutch-sizes are from Peck and James (1987).
[b] Cowbird eggs from cardinal nests.
[c] Incubation time based on cowbird eggs laid on morning of cardinal-clutch completion or later.

TABLE 4. Numbers and percentages of cowbird eggs laid on successive days of the prelaying, laying, and incubation periods of four hosts at London, Ontario.

Species	Prelaying	Days in laying and incubation periods					
		1	2	3	4	5	6 and later
Northern Cardinal	20 (14)	13 (9)	44 (31)	35 (25)	17 (12)	7 (5)	6 (4)
Gray Catbird	3 (12)	4 (15)	10 (38)	6 (23)	2 (8)	1 (4)	0 (0)
Song Sparrow	1 (4)	2 (8)	7 (28)	6 (24)	1 (4)	2 (8)	6 (24)
Yellow Warbler	40 (62)	6[a] (9)	9[a] (14)	3 (5)	2 (3)	0 (0)	5 (8)

[a] Includes 4 eggs laid on days 1 or 2; in Table, two eggs assigned to each day.

accurate and more readily available in the literature. Incubation times for cowbird eggs were obtained from eggs laid in cardinal nests on the morning of the last cardinal egg or later. Incubation times for cardinals were measured from the hour of laying of the final egg (ca. 06:30) to its hatching.

To understand cowbird reproductive success, the degree of synchrony in daily laying between cowbird and host should be known. Cowbird eggs laid after host incubation has begun may hatch after host eggs have hatched. We have much data on cowbird/cardinal synchrony in laying, but rather little on the other three hosts, one of which, the Yellow Warbler, is unusual in its response to cowbird laying. To make our sample more representative of cowbird/host synchrony in our study area we use original data on cowbird/Gray Catbird egg-laying synchrony. We present in Table 4 the number of cowbird eggs laid on each day of the nesting cycle. Because of the nest failures throughout the cycle, the data presented numerically give disproportionate weight to the early days of the cycle, but this bias is not great (Nolan 1978:382).

SUCCESS OF COWBIRDS IN CARDINAL NESTS

We analyzed reproductive success of cowbirds in cardinal nests but could not do so for the other hosts as adequate data were lacking. For cardinals we have three samples. One, comprising 148 cowbird eggs found on the day of laying, measures success between laying and fledging (Table 7). The second describes the fates of cowbird nestlings between hatching and fledging and compares them with cardinal nestmates (Table 9). This sample includes the nestlings from the first sample and augments them with observations on nestlings hatched from eggs that, unlike those in the first sample, had not been observed on the day of laying. Because the sample was small, we added four birds that had been removed from nests in another study (Smith 1969). In each case, we could reasonably have predicted that these nestlings, because of their size, would have either fledged or perished in the absence of nest failure and our interference. Finally, we enumerate the frequencies of broods of different combinations of cowbird and cardinal nestlings. In doing so, we assumed that the brood composition when found had not changed since hatching (Table 8). The sample comprised 105 parasitized nests; 75% were found before hatching. Some bias may have been introduced by using nests found containing only one or two large nestlings. In such nests ($n = 8$) smaller nestlings, particularly cowbirds, might have disappeared. Cardinal nestlings rarely starve to death. Only eight of 195 cardinal nestlings disappeared from successful nests. Values are presented as means ± SE.

RESULTS

REPRODUCTIVE VARIABLES OF COWBIRDS AND HOSTS

Laying seasons. Cowbirds begin laying at London in late April, about a week later than the beginning of cardinal laying, about the same time as Song Sparrows, and about three weeks before Chipping Sparrows and Yellow Warblers, and cease laying by mid-July. Their laying season encompasses that of Yellow Warblers but ends well before those of the two sparrows and cardinals (Scott, unpubl.).

Number of broods. Cardinals and the two sparrows were frequently successfully double-brooded, unlike Yellow Warblers which seemed to be only single-brooded (Table 1). The number of broods per pair varied significantly ($P < 0.05$) among the double-brooded species. Cardinals produced the least number of broods per pair and Chipping Sparrows the most.

All second broods ($n = 13$) of cardinals fledged

from clutches initiated when the rate of parasitism had begun to decline in early July and which terminated by mid-July. Five of these broods were seen before August but the remainder did not appear until early August. Thus, the latter could only have been produced from clutches laid when cowbirds had almost ceased laying. In contrast, 15 of 18 second broods of Chipping and Song Sparrows were seen before August. They came from clutches in late June or early July when cowbirds were still laying regularly. This proportion (15:3) is significantly greater than that (5:8) for cardinals ($G = 6.8$; $P < 0.01$). Thus relatively fewer second broods of cardinals were likely to be parasitized than were those of the sparrows.

Interbrood intervals and nest survival rates. Differences in brood frequency could arise from a combination of interspecific differences in interbrood intervals or survival rates of nests. The apparent interbrood interval was much shorter for Chipping Sparrows and Song Sparrows than for cardinals (Table 2). Significantly more intervals for sparrows (pooled values) fell between zero and 20 days whereas cardinal intervals usually exceeded 24 days (19:2 for sparrows vs. 6:15 for cardinals, $G = 16.9$; $P < 0.001$).

Survival rates of nests varied among the hosts. Using the Mayfield method of analysis (Mayfield 1975), we determined that the daily rate of nest loss for cardinals (May and June only) during incubation and brooding was 87 losses during 1,355 days of observation, a rate of 0.064 nest losses per day. Similar determinations showed daily rates of nest loss of 7/157 (0.045) for Chipping Sparrows, 15/379 (0.040) for Song Sparrows, and 4/180 (0.022) for Yellow Warblers. The combined rate of loss of nests of these species was 26/716 (0.036), significantly lower than that of cardinal nests ($G = 7.5$; $P < 0.01$).

Interspecific variation in masses of adults, eggs, and hatchlings. Cowbirds are strongly sexually dimorphic in body mass; adult females weigh 40 g, about 20% less than adult males (Table 3). Both sexes are much heavier than adult Song Sparrows, Chipping Sparrows, and Yellow Warblers. On the other hand, female cowbirds but not males are lighter than cardinals (43 g). Notably, adult cowbird body masses of the sexes bracket those of adult cardinals, but egg and hatchling masses of cowbirds (3.18 ± 0.15 g; 2.34 ± 0.06 g) are about one-third less than those of cardinals (4.88 ± 0.07 g; 3.55 ± 0.11 g). Large cowbird eggs (4.0 g or more) are heavier than small cardinal eggs (3.7 g). Cowbird egg-mass is about twice that of Chipping Sparrows and Yellow Warblers but only about 30% greater than that of Song Sparrows. The range of egg mass of cowbirds probably overlaps that of large Song Sparrow eggs.

Clutch size. Modal clutch sizes vary from three for cardinals, four for Chipping Sparrows and Yellow Warblers, to five for Song Sparrows (Table 3). As these species lay daily, the lengths of laying periods vary interspecifically. Thus, the opportunity for cowbirds to closely synchronize their laying with their hosts is least in cardinal nests and most in nests of Song Sparrows, provided that the schedule of cowbird laying does not vary from host to host.

Incubation period. The incubation period of cowbird eggs is shorter than that of Song Sparrows and cardinals and about equal to those of the two smallest hosts (Table 3). The mean incubation period of cowbird eggs incubated by cardinals (286.00 h ± 4.54 h) was significantly shorter than the 295.26 h ± 3.04 h incubation period of cardinal eggs (one-tailed t-test, $t = 1.77$, $df = 26$, $P < 0.05$).

Synchrony of laying by cowbirds and hosts. Cowbirds parasitized nests most frequently on day 2, followed by day 3, of the laying periods of three hosts, excluding the Yellow Warbler (Table 4). With each host, more than 50% of cowbird eggs were laid on those two days. Clearly, with three hosts, the daily pattern of cowbird laying varied little. Thus, the degree of synchrony varied directly with the clutch size. That is, as cardinals had the smallest clutch-size, relatively more cowbird eggs were laid asynchronously in cardinal nests after incubation of the entire clutch had begun than in the nests of the other three hosts. Cowbirds, however, usually failed to synchronize their laying with that of Yellow Warblers because of the behavior of the host. Forty of 65 cowbird eggs were laid before day 1 of the Yellow Warbler laying period; most nests parasitized then were deserted. Of the remaining 25 eggs, 15 were laid on days 1 and 2 pooled, 5 on days 3 and 4, and the remainder after day 5.

SUCCESS OF COWBIRDS WITH DIFFERENT HOSTS

The proportion of cardinal broods containing cowbird fledglings was 10/44 in 1955 to 1961 (Table 5). It varied from 0/7 in 1960 to 5/6 in 1961. In each other year, only one successful

TABLE 5. Proportion of successful broods with fledgling cowbirds seen with presumed hosts: Northern Cardinal, Song Sparrow, Chipping Sparrow, and Yellow Warbler[a].

	Number of pairs	Proportion of broods with cowbirds	Annual production of cowbirds per host-pair
Northern Cardinal			
1955–1961	49	10/44 (12)[b]	0.18
1962–1963	22	1/19 (1)	
Song Sparrow			
1962–1963	42	29/45 (31)	0.74
Chipping Sparrow			
1962–1963	27	23/34 (24)	0.89
Yellow Warbler			
1962–1987	15	10/14 (10)	0.67

[a] Based on broods estimated to have been initiated within the cowbird laying season (ca. 20 Apr. to ca. 20 July). Only broods with cowbirds more than two days post-fledging are included.
[b] In brackets, numbers of cowbirds. Some broods had more than one cowbird.

brood contained cowbirds. Thus, we do not regard the low proportion observed in 1962–1963 as being particularly unusual. The difference in the values for 1955–1961 and 1962–1963 is not significant (10:34 vs. 1:18, $G = 2.6$; $P < 0.05$). Accordingly, for further analysis, we pooled the data from the two sets of years.

A pair of cardinals produced about 25% as many fledgling cowbirds as each pair of the other hosts. Only 11 of 63 cardinal broods had cowbirds that were seen later than two days following fledging, in contrast to 62 broods containing cowbirds in 93 broods of the other hosts (11:52 vs. 62:31, $G = 38.7$; $P < 0.001$).

This great difference in the production of cowbirds between cardinals and the other hosts cannot be attributed to interspecific differences in incidence or intensity of parasitism, as neither varied significantly among the hosts (Table 6). Incidence varied between 68% and 92% of Yellow Warbler and Chipping Sparrow nests respectively ($G = 4.4$; $P > 0.1$). The number of cowbird eggs in parasitized nests varied between 1.55 and 2.10 eggs in Chipping Sparrow and cardinal nests, respectively ($G = 7.0$, $P > 0.1$). Thus, given similar amounts of parasitism in early incubation, production of cowbirds should not vary much among the hosts. If it does mortality rates of cowbird eggs or nestlings vary among the hosts and/or different hosts produce significantly different numbers of successful broods during the cowbird laying season.

TABLE 7. Fate of 148 cowbird eggs in 76 cardinal nests and 57 cowbird eggs in 20 Yellow Warbler nests[a].

	In nests of	
	Cardinals	Warblers
Causes of death		
Buried in nest	4	20
Nest abandoned before host completed laying	3	27
Removal of complete clutch (predation)	46	2
Removal of single eggs, possibly some by cowbirds	33	0
Desertion after some eggs removed	17	2
Reached hatching time, but did not hatch	9	1
Miscellaneous (laid late, storms, human interference)	16	2
Hatched	20	3

[a] All nests were found before hosts began laying and were followed until fledging or abandonment.

BASES OF COWBIRD SUCCESS OR FAILURE

Survival from laying to fledging. In cardinal nests, cowbird-egg mortality was about 85% (Table 7). Most mortality resulted from egg removal or nest desertion following loss of part of a clutch. Because female cowbirds commonly remove eggs

TABLE 6. Incidence and intensity of parasitism on nests of four species at London, Ontario between 24 April and 2 July[a].

Host	Incidence % (nests)	No. and percentages of nests containing different number of cowbird eggs					$\bar{x}$ number[b]
		0 eggs	1 egg	2 eggs	3 eggs	>3 eggs	
Northern Cardinal	82 (106)	19 (18)	37 (35)	24 (23)	14 (13)	12 (11)	2.10 eggs
Song Sparrow	85 (54)	8 (15)	18 (33)	16 (30)	9 (17)	3 (6)	1.96
Chipping Sparrow	92 (25)[c]	2 (10)	9 (45)	8 (40)	1 (5)	0 (0)	1.55
Yellow Warbler	6 (19)	6 (32)	6 (32)	3 (16)	3 (16)	1 (5)	1.92

[a] Most cowbird laying occurs in this period.
[b] Per parasitized nest.
[c] Includes five parasitized nests whose exact contents were unknown.

TABLE 8. Species composition of broods in 105 parasitized cardinal nests.

	Brood composition: cardinal/cowbird[a]										
	2/0	1/0	0/1	0/2	1/1	1/2	2/1	2/2	3/1	3/2	4/1
Number of broods	19	12	13	6	14	7	17	7	6	2	2

[a] Thirty-one nests that had been parasitized did not hatch any cowbird eggs.

(Scott et al. 1992), normal predation could not always be recognized. Losses of entire clutches were attributed to predation. Cowbirds may have removed some single cowbird eggs on days when cowbirds were laying (there is no strong evidence that cardinals often eject normal cowbird eggs). Often some eggs but not the entire clutch disappeared and the remaining eggs were abandoned. Some such incidents may have been caused by cowbirds, especially at nests that were multiply parasitized. Cowbird-egg removal by cardinals or cowbirds was important accounting for about 25% of egg loss.

Cardinals rarely deserted parasitized nests unless there was obvious interference by cowbirds. Cowbirds often laid before a cardinal laid the first egg of a clutch. Of 18 such nests, only two were abandoned without cardinal laying. In each abandoned nest a cowbird egg had been cracked or broken.

Mortality of cowbird eggs in Yellow Warbler nests was about 95%. The causes of mortality, however, differed greatly from those in cardinal nests. Most cowbird eggs (65%) were buried and/or abandoned, usually before a first host egg was laid. Accordingly predation was less important.

In cardinal nests, 20 cowbird eggs hatched and eight hatchlings fledged. Thus, reproductive success of cowbirds from laying to fledging was 5.4%. In Yellow Warbler nests, three of 57 cowbird eggs hatched; each nestling fledged. Thus, the survival rate from laying to fledging was almost identical, 3/57 = 5.3%, to that in cardinal nests.

Brood composition of parasitized cardinal nests. As a result of differential egg-mortality, the number of nestlings that hatched was not only fewer but often differed in species composition from the original clutch of cardinal and cowbird eggs (Table 8). Thirty percent of broods lacked cowbirds and 20% lacked cardinals. Broods of one cowbird and one or two cardinals were the most common (55%) of all mixed broods. Broods of four or more nestlings, which would be unusual even for parasitized nests, formed the remaining mixed broods.

Cowbird nestling and fledgling mortality. To provide a larger sample of nestlings for analysis, we augmented the preceding sample of 20 nestlings (Table 7) with records of 41 other cowbirds hatched in nests found after laying had begun. There were 61 cowbird and 68 cardinal nestmates (Table 9). Excluding nestlings apparently lost to predators, the proportion of cowbirds (27 of 43) that fledged was significantly lower than the proportion (44 of 49) of cardinals that fledged ($G = 9.8$; $P < 0.005$). There were two groups of nestling cowbirds: one, reared in mixed broods with cardinal nestmates, and one, without any cardinal nestmates, which we designate as monospecific cowbird broods, regardless of whether there were one or two cowbird nestlings. The two groups differed in survival rates, body masses, and duration of nestling life.

TABLE 9. Fate of 61 cowbird nestlings and their 68 cardinal nestmates, and 93 cardinal nestlings in unparasitized nests, observed from the day of hatching.

	Monospecific broods		Mixed broods	
	Cardinals	Cowbirds	Cowbirds	Cardinals
Nestlings	93	22	39	68
Fate of nestlings				
Nest failed	36	10[a]	8	19
Disappeared or died in nest	2	1	15[b]	5
Fledged	55	11[c]	16	44
Fate of fledglings				
Not sought after fledging	22	7	1	9
Not found two days after fledging	2	0	7	1
Survived beyond two days	31	5[d]	7	34

[a] Two nestmates disappeared one and three days after hatching; they seem to have been taken by a predator before remaining eggs were taken on the fourth day.

[b] Two nestlings, much underweight, 9 and 11 g, at 4 or 5 days of age were collected; assumed that they would have died of starvation.

[c] Two nestlings, 27 g each and about 8 days old collected; assumed that they would have fledged.

[d] One cowbird was reared with another cowbird and a cardinal; these last two were taken by a predator on day 9 of the nestling period. Thus, the surviving cowbird became a solitary fledgling without post-fledging competition.

TABLE 10. Length (days) of nestling life of 70 cardinals and 23 cowbirds reared by cardinals.

Fledged between	Cardinals alone		Mixed broods[a]		Cowbirds alone
	Solitary nestling	Two or more nestlings	Cardinals	Cowbirds	
7 and 9 d	1	1	0	0	0
8 and 9 d	2	5	5	0	0
8 and 10 d	1	13	3	0	0
9 and 10 d	2	8	14	7	3[b]
9 and 11 d	0	5	3	0	0
10 and 11 d	1	3	3	7	2
11 and 12 d	0	0	0	2	0
11 and 13 d	0	0	0	0	1
12 and 13 d	0	0	0	0	1

[a] Includes a mixed brood of two cardinals and one cowbird described by Laskey (1944).
[b] Collected on tenth day of nesting life.

Proportionately more cowbirds fledged from monospecific broods than from mixed broods (11:1 vs. 16:15, $G = 6.9$; $P < 0.01$). The fledging rates of monospecific broods of cowbirds and cardinals were virtually identical (11:1 vs. 55:2, $G = 0.5$; $P > 0.05$). However, the rate of fledging of cowbirds from mixed broods was significantly lower than that of cardinals (16:15 vs. 44:5, $G = 14.7$; $P < 0.001$).

Relatively more cowbird fledglings from monospecific broods survived than from mixed broods, but the difference was not significant (5:0 vs. 7:7, $P = 0.14$, Fisher's exact test). Cowbirds survived less well than cardinals in mixed broods (7:7 vs. 34:1, $P = 0.006$, Fisher's exact test).

Cowbird nestling and fledgling masses. Nestling cowbirds, close to fledging, varied greatly in body mass from about 21 to 35 g. Body masses of nestlings from mixed broods of cardinals were lightest. They differed significantly at $P < 0.1$ from those of monospecific broods reared by cardinals ($\bar{x} = 24.79$ g $\pm$ 1.40 $n = 8$ vs. $\bar{x} = 28.00$ g $\pm$ 0.85 $n = 8$, $t = 1.83$, df = 14). This comparison does not consider the numerous disappearances of underweight cowbirds from mixed broods of cardinals. The difference in body masses was even greater between cowbirds from mixed broods of cardinals and those reared by other hosts ($\bar{x} = 28.67$ g $\pm$ 0.92 $n = 13$, $t = 2.94$, df = 19, $P < 0.01$). The body masses of monospecific broods of cowbirds reared by cardinals did not differ significantly from those reared by other hosts ($t = 0.60$, df = 19, $P > 0.50$).

We failed to determine the sex of cowbird nestlings until alerted to the possibility that cowbird nestlings might show sexual differences in growth rates, as do nestling Red-winged Blackbirds (Williams 1940). Thereafter, we collected three nestling cowbirds from monospecific broods in cardinal nests and 11 nestling cowbirds from nests of other hosts. These nestlings were eight or nine days old and gonads could be easily recognized by autopsy. Males were significantly heavier than females (7 males: $\bar{x} = 31.11 \pm 0.83$ g; 7 females: $\bar{x} = 26.10 \pm 0.84$ g, $t = 4.26$, d = 12, $P < 0.005$). We do not know if sexual dimorphism affected survival of nestling cowbirds in mixed broods of cardinals.

Effect of laying and hatching synchrony. The shorter incubation periods of cowbirds relative to those of cardinals when coupled with synchronous laying of cowbird and cardinals ensured that these cowbird eggs hatched first. In nine synchronized cases, where the dates of laying and hatching were known, each cowbird egg hatched before any of 19 cardinal eggs (two-tailed binomial test; $P < 0.004$). On the other hand, all cowbird eggs ($n = 6$) known to have been laid after clutch completion hatched after hatching of cardinal eggs.

The rate of fledging of cowbirds in successful cardinal nests depended on synchrony of hatching with cardinal eggs. Eight of 12 cowbirds fledged from eggs that hatched before or with cardinal eggs. Only one of nine cowbirds fledged from eggs that hatched later than cardinal eggs (8:4 vs. 1:8, $P = 0.038$, Fisher's exact test).

The success of cowbirds that hatched first or synchronously in mixed broods was related to the number of cardinal nestmates. No cowbirds ($n = 4$) survived in broods containing three cardinals. Three died in the nest (9, 20, and ca. 20 g) and one (20 g) was not seen after fledging. In broods containing one or two cardinals, seven of eight cowbirds fledged; four survived for at least two days. The eighth, which was not underweight (24 g), disappeared from the nest when it was six-days-old.

Cowbirds that hatched late grew slowly. Four appeared abnormally small when they disappeared in the first four days after hatching. Ages and weights near death of four others were 3 d (2 g), 5 d (11 g), 8 d (14 g), and 9 d (9 g). The ninth bird that fledged and survived was in a nest of a female cardinal that laid exceptionally small eggs.

Length of nestling period of cowbird and cardinals. Cowbirds typically fledged later than cardinal nestmates (Table 10). In mixed broods,

most cowbirds (9 of 16) did not fledge until they were at least ten-days-old in contrast to cardinals, most of which (22 of 25, excluding three that fledged between 9 and 11 days) fledged before that age (7:9 vs. 22:3, $G = 9.3$; $P < 0.005$). On the other hand, solitary cowbirds spent longer in the nest than cowbirds in mixed broods. All four undisturbed solitary cowbirds remained between ten and 13 days in nests unlike many from mixed broods, but the difference in ratios (4:0 vs. 9:7) is not significant ($P = 0.15$, Fisher's one-tailed exact test). However, three solitary cowbirds collected on their tenth day, if undisturbed, could have remained longer in the nest and thus, increased the proportion that remained as nestlings for more than ten days.

DISCUSSION

Cardinals, per pair, produced annually significantly fewer fledgling cowbirds than any of the other three hosts studied, despite similar amounts of parasitism among the hosts. Therefore, cardinals were not ideal hosts for cowbirds.

INTERSPECIFIC COMPETITION IN CARDINAL NESTS

Cardinals were suitable hosts when rearing solitary cowbirds, which attained body masses characteristic of cowbird nestlings recorded in many studies of hosts, ranging from much smaller to much larger than female cowbirds (Friedmann 1929, Herrick 1935, Nice 1937, Norris 1947, Weatherhead 1989, Ortega and Cruz 1991). In those studies, body masses of about 30 g seemed typical of many cowbirds at fledgling, similar to most body-masses of cowbirds reared here by Song Sparrows, Chipping Sparrows, and Yellow Warblers. That is, there was no apparent difference in body masses of fledging cowbirds reared alone by cardinals and those reared by other hosts. The sex of many nestling cowbirds was not determined. Thus, the interpretation of fledgling body-masses is difficult because of the apparent existence of sexual dimorphism in body masses. But Weatherhead (1989) found no significant sexual dimorphism in body masses of seven-day-old cowbird nestlings. The nestling life of solitary cowbirds reared by cardinals was usually ten or more days, a period commonly reported by the authors cited above. This agrees with the duration of nestling life reported for many North American icterines (Bent 1958).

Cardinals were often unsuitable hosts when cowbirds were part of a mixed brood. Then, cowbirds did not always grow well and weighed less than cowbirds reared alone. Death of underweight cowbirds occurred in mixed broods throughout nestling life, and apparently into the first few days after fledging. Possibly, cowbirds fledged prematurely when cardinals fledged, as solitary cowbirds fledged at an older age. Thus, cowbirds from mixed broods may be underweight, unable to fly well, and be at unusual risk of predation. Woodward and Woodward (1979) noted that eight of 21 fledgling cowbirds disappeared within two days of fledging. Even some cowbirds that hatched before cardinal nest-mates did not gain weight normally and apparently suffered from intrabrood competition. Some cowbird nestling deaths, apart from losses to predators, occurred in large mixed broods, despite prior hatching and close synchronization of laying.

SYNCHRONY OF COWBIRD AND HOST LAYING

Reports on synchronization of egg laying of Brown-headed Cowbirds and hosts are few: Hann (1937), Mayfield (1960), Klaas (1975), Nolan (1978), Clark and Robertson (1981), Sealy (1992), Wolf (1987), and Marvil and Cruz (1989). These studies and ours show that most cowbird eggs were laid during the prelaying and laying periods of the hosts. For most species, other than the Yellow Warbler, fewer than 30% of cowbird eggs were laid during the days ending with the laying of the first host egg (day 1). In Yellow Warbler nests, 70% of cowbird eggs were laid before any warbler egg had been laid. Peak rates of deposition in other hosts occurred on days 2 and 3 of the laying period of the host. The daily rate of deposition declined after day 3 of the laying period, regardless of the host's clutch size. Thus, for most hosts the peak days of cowbird deposition occurred after the host had begun to lay and was less likely to desert but before incubation by the host has begun in earnest. As a passerine often begins incubation with her penultimate or even earlier egg (Mayfield 1960), cowbird eggs laid early will undergo incubation earlier than cowbird eggs laid later. Thus, the advantage of an early start to incubation could offset the greater probability of survival to hatching if laid later. This is particularly significant in the interaction between cowbirds and cardinals because the clutch size of cardinals is most commonly three.

Cardinals begin some incubation with the first egg (Scott and Lemon, unpubl.). Consequently, cowbird eggs laid on day 3 or later began incubation later than the first eggs of a cardinal clutch. Cowbirds that hatched late were at a great disadvantage. None of five cowbirds, hatched from eggs laid on days 4 or 5, fledged from otherwise successful broods. When cowbird laying was closely synchronized with cardinals, cowbirds hatched first, by as much as 18 h. However, cowbird incubation was only about 10 hours shorter than cardinal incubation. Thus, there is insufficient time for cowbird hatchlings to attain body masses that could match potential competition from a full brood of cardinal nestlings. Some cowbirds, although hatching first, died presumably from starvation induced by interspecific competition.

OTHER FACTORS AFFECTING SUITABILITY OF CARDINAL AS HOST

Loss of cowbird nestlings through starvation and interspecific competition was insufficient to account alone for the low production of cowbirds by cardinals. If all nestling cowbirds that were lost through starvation, either as nestlings or recent fledglings, had survived, production of cowbirds would have only doubled. Apparently therefore, some major factors that did not operate on the small hosts reduced the success of cowbirds.

Removal of cowbird eggs. Cowbird eggs rarely disappear singly from active nests of small accepter hosts (Hann 1937, Hofslund 1957, Mayfield 1960, and Nolan 1978). We found, however, that single cowbird eggs as well as cardinal eggs frequently disappeared during the days when cowbirds were laying in cardinal nests. We do not know, however, whether these eggs were being removed by cowbirds or cardinals or some predator. Mayfield (1960) and Mengel and Jenkinson (1970) suggested that female cowbirds, when confronted by host eggs as large or larger than their own, may err in their selection of an egg for removal. Rothstein (1971) found no ejection of artificial cowbird eggs by cardinals in seven tests but later (1975) reported one ejection in seven tests. Burhans (pers. comm.) found that cardinals ejected white-painted cowbird eggs in seven of 15 tests. Regardless of the cause of removal, these cowbird egg-losses are a distinctive feature of the interaction between cowbirds and cardinals. This removal accounts for the absence of any cowbird eggs at hatching from nests that had been parasitized.

Rate of brood production. Cardinals produced far fewer successful broods with cowbirds than the three smaller hosts, although all hosts were heavily parasitized. This lower production by cardinals arose from variation in three factors: 1) lengths of interbrood intervals, 2) rates of nest survival, 3) rates of survival of cowbird eggs.

Interbrood intervals of cardinals were about twice as long as those for the two sparrows. Yellow Warblers apparently did not attempt more than one successful brood. Our values agree closely with interbrood intervals reported elsewhere for cardinals, Song, and Chipping Sparrows: 20 days for cardinals (Kinser 1973: 171), for Song Sparrows 10 days (Nice 1937) and 11 days (Smith and Roff 1981, Table 2), and 9 days for Chipping Sparrows (Keller 1979). Scott and Lemon (unpubl.), searching deliberately for cardinal nests, determined that intervals following 30 broods fledged before 1 July were 17 days for broods of one and 32 days for broods of two or more nestlings.

The rate of nest survival to fledging was lower for cardinals than for each of the other three hosts studied, which agrees with estimates of rates of predation on nests of these species (Martin 1993). Martin showed that bush or shrub-nesting species were often more vulnerable to predation than ground-nesting species, contrary to widespread belief. He found that the percentages of nests lost to predators in forest and shrub/grassland habitats for the hosts studied by us were for cardinals (54.7 and 53.3 in two studies), Chipping Sparrows (41.2), Song Sparrow (36.5), and Yellow Warbler (34.2). Three of these species are shrub or bush nesters but Song Sparrows usually nest on the ground or close to it (Peck and James 1987, pers. obs.). Our estimate of daily mortality rates of cardinal nests was about 0.064 losses per day, almost identical with the daily mortality rate of 0.062 reported by Filliater et al. (1994). J.N.M. Smith (pers. comm.) noted that daily nest-failure rates of Song Sparrows varied annually from 0.015 to 0.045, similar to our estimate of 0.040.

Estimates of cowbird-egg survival in the nests of the four hosts did not agree completely with estimates of cowbird fledglings seen with the four hosts. Five percent of cowbird eggs survived to fledging in our samples of cowbird eggs from nests of cardinals and Yellow Warblers. Yet Yellow Warblers produced significantly more cow-

bird fledglings than cardinals. It seems likely that our sample of Yellow Warbler nests was biased. Most cowbird eggs (41 of 57) were found in early nests in May and usually were buried or deserted before incubation. Clark and Robertson (1981) found that Yellow Warblers did not often accept cowbird eggs in early nests but did so later. Clearly, most cowbird production must come from late Yellow Warbler nests, of which we had an inadequate sample. This sample ($n = 16$) of cowbird eggs, accepted by the host, produced four fledglings, a survival rate of 0.25. By comparison, 170 cowbird eggs found undergoing incubation by cardinals had a survival rate of 0.07. The probability of cowbird egg success was 0.20 (40 eggs) and 0.33 (12 eggs) in Song Sparrow and Chipping Sparrow nests respectively. Song Sparrows rarely desert parasitized nests (Cavalcanti 1981, Smith and Arcese 1994) and high reproductive success of cowbird eggs is to be expected. Values of cowbird-egg success of 0.30 and 0.52 were reported by Young (1963a) and Smith and Arcese (1994) for Song Sparrows. Smith and Arcese (1994: Table 4) studied cowbirds that were smaller than Song Sparrows but Young (1963a) reported on cowbirds which were larger than Song Sparrows. Less is known about cowbird success with Chipping Sparrows. Young (1963a) reported a success rate of 0.17 ($n = 12$ eggs) of cowbirds. As Chipping Sparrows are a widespread host, a comprehensive study of parasitism on this species is needed.

Thus, species differences in interbrood intervals, rates of nest survival, and cowbird-egg success combined to produce differences in the annual frequency of successful parasitized broods, and so could account for differences in cowbird production by different hosts.

COWBIRD SUCCESS WITH OTHER LARGE HOSTS

Incubation periods of large hosts may be much longer than those of brood parasites (Mason and Rothstein 1986, Soler 1992), which could hatch several days before host eggs. The parasites can grow well enough to offset the potential advantage of larger hatchling masses of the host. However, the incubation periods of some large hosts may not be much longer, and parasite nestlings may experience strong competition from host young (Mason 1986, present study).

Red-winged Blackbirds are a common large host of Brown-headed Cowbirds. Unlike cardinals, they are good hosts (Weatherhead 1989), despite being slightly larger than cowbirds. Twenty-seven % of 94 cowbird eggs fledged, a high rate of success compared with most smaller hosts (Young 1963a) and cardinals. Red-winged Blackbird eggs are about 20% smaller than cardinal eggs (4.0 g vs. 4.9 g) and have longer incubation periods than cardinals (Young 1963b). These differences may result in less competition in mixed broods of Red-winged Blackbirds than in mixed broods of cardinals. Cowbirds were most successful in cardinal nests with greatly reduced cardinal broods, but no information was presented by Weatherhead to indicate if clutch and brood reduction was also important in cowbird success in Red-winged Blackbird nests.

Variation in cowbird nestling mortality in relation to brood size and composition, as shown in cardinal nests, helps to explain how cowbirds can survive in nests of large hosts. Egg removal by cowbirds reduces the host clutch, particularly when there is multiple parasitism. Thus, intrabrood competition will be low when the joint brood has been reduced to a number that can be readily fed. Furthermore, a cowbird nestling may receive more food from a large host than from a small host. It should therefore grow faster, as Wiley (1986) argued in the case of nestlings of Shiny Cowbirds (*Molothrus bonariensis*) in nests of a large host, the Greater Antillean Grackle (*Quiscalus niger*).

Much multiple parasitism and decrease in host clutch and brood size occurred in parasitism of two even larger hosts: Brewer's Blackbirds (*Euphagus cyanocephalus*) (Furrer 1974, cited by Friedmann et al. 1977) and Eastern Meadowlarks (Elliott 1978). Egg mass is 4.6 g for the former species and 6.1 g for the latter (Schönwetter 1983). The incidence of parasitism was 55% for Brewer's Blackbirds and 70% for Eastern Meadowlarks. Host-egg reduction was marked in Eastern Meadowlark nests. It must also have been considerable in Brewer's Blackbird nests, as several broods comprised only cowbirds. The success of cowbirds differed strikingly between these hosts. About 33% of cowbird eggs in Brewer's Blackbird nests produced fledglings, but only about 6% of cowbird eggs produced fledglings in Eastern Meadowlark nests. Details of these studies do not permit evaluation of the basis for the differential success of cowbirds, but it seems likely that the difference in egg mass could be important. Meadowlarks, in general, seem to be

unsuitable hosts of cowbirds in North America and in South America (Gochfeld 1979).

Host-brood decrease was clearly implicated in the success of other species of cowbirds in the nests of large hosts. Bronzed Cowbirds (*Molothrus aeneus*) in south Texas multiply parasitized two large hosts and removed or damaged many host eggs (Carter 1986). Fourteen nestling cowbirds fledged from seven nests of these large hosts, which contained only nine host nestlings. Fraga (1985) and Mermoz and Reboreda (1994) also showed that clutch and brood reduction of large hosts allowed fledging of Shiny Cowbirds.

The adaptive basis for egg removal by cowbirds has not been satisfactorily explained (Scott et al. 1992, Sealy 1992). Nevertheless, removal of eggs of large hosts clearly benefits cowbirds and allows them to exploit large hosts. In particular, more host eggs would be lost or damaged if nests were multiply parasitized.

Factors other than host-brood decrease and short incubation periods of cowbirds may enable brood parasites to fledge along with young of large hosts. Recently, Ortega and Cruz (1991) experimented by adding Brown-headed Cowbird eggs to normal unreduced clutches of Yellow-headed Blackbirds (*Xanthocephalus xanthocephalus*), a much larger bird than a cowbird. Despite the increase in clutch size and the pronounced disparity in sizes of host and cowbird nestlings, most (seven of eight) cowbirds fledged. Ortega and Cruz (1992) showed that cowbirds had a relatively larger gape than the host males, which could enable cowbirds to compete successfully with larger host-siblings.

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LITERATURE CITED

ANKNEY, C. D., AND D. M. SCOTT. 1980. Changes in nutrient reserves and diet of breeding Brown-headed Cowbirds. Auk 97:684–696.

BENT, A. C. 1958. Life histories of North American blackbirds, orioles, tanagers, and allies. U.S. Nat. Mus. Bull. 211:1–547.

CARTER, M. D. 1986. The parasitic behavior of the Bronzed Cowbird in south Texas. Condor 88:11–25.

CAVALCANTI, R. B. 1981. Nest desertion: theory and tests of its adaptive significance in birds. Ph.D.diss., McGill Univ., Montreal, Canada.

CLARK, K. L., AND R. J. ROBERTSON. 1981. Cowbird parasitism and evolution of antiparasite strategies in the Yellow Warbler. Wilson Bull. 93:249–258.

DARLEY, J. A., D. M. SCOTT, AND N. K. TAYLOR. 1971. Territorial fidelity of catbirds. Can. J. Zool. 49: 1465–1478.

DUNNING, J. B., JR. 1993. CRC handbook of avian body masses. CRC Press, Boca Raton, FL.

ELLIOTT, P. F. 1978. Cowbird parasitism in the Kansas tallgrass prairie. Auk 95:161–167.

FILLIATER, T. S., R. BREITWISCH, AND P. M. NEALEN. 1994. Predation on Northern Cardinal nests: does choice of nest site matter? Condor 96:761–768.

FRAGA, R. M. 1985. Host-parasite interactions between Chalk-browed Mockingbirds and Shiny Cowbirds. p. 829–844. *In* P. A. Buckley, M. S. Foster, E. S. Morton, R. S. Ridgely, and F. G. Buckley [eds.], Neotropical ornithology. Ornitholog. Monogr. 36. Washington, DC.

FRIEDMANN, H. 1929. The cowbirds. Charles C. Thomas, Springfield, IL.

FRIEDMANN, H., L. K. KIFF, AND S. I. ROTHSTEIN. 1977. A further contribution to knowledge of the host relations of the parasitic cowbirds. Smithson. Contrib. Zool. 235:1–75.

FRIEDMANN, H., AND L. F. KIFF. 1985. The parasitic cowbirds and their hosts. Proc. Western Found. Vert. Zool. 2:226–302.

FURRER, R. K. 1974. Nest site stereotypy and optimal breeding strategy in a population of Brewer's Blackbirds (*Euphagus cyanocephalus*). Ph.D.diss., Univ. of Zürich, Zürich, Switzerland.

GOCHFELD, M. 1979. Begging by nestling Shiny Cowbirds: adaptive or maladaptive? Living Bird 17: 41–50.

GRAHAM, D. S. 1989. Rejection, desertion, burial, and the wanton layers. Living Bird Quarterly 8(2): 20–24.

HANN, H. 1937. Life history of the Oven-bird in southern Michigan. Wilson Bull. 49:145–237.

HERRICK, F. H. 1935. Wild birds at home. D. Appleton-Century, New York, NY.

HOFSLUND, P. B. 1957. Cowbird parasitism of the Northern Yellow-throat. Auk 74:42–48.

JAROSCH, C. H. 1976. The early plumages and molts of the Cardinal, *Cardinalis cardinalis*. M.Sc.thesis, Univ. of Western Ontario, London, Canada.

KELLER, M. E. 1979. Breeding behavior and reproductive success of Chipping Sparrows in north-

western Minnesota. M.Sc.thesis, Univ. of North Dakota, Grand Forks, ND.

KINSER, G. W., JR. 1973. Ecology and behavior of the Cardinal, *Richmondena cardinalis* (L)., in southern Indiana. Ph.D.diss., Univ. of Indiana, Bloomington, IN.

KLAAS, E. E. 1975. Cowbird parasitism and nesting success in the Eastern Phoebe. Occas. pap., Mus. Nat. Hist., Univ. Kansas 41:1–18.

LASKEY, A. R. 1944. A study of the Cardinal in Tennessee. Wilson Bull. 56:27–44.

LEMON, R. E. 1957. A study of nesting Cardinals (*Richmondena cardinalis*) at London, Canada. M.Sc.thesis, Univ. of Western Ontario, London, Canada.

MARTIN, T. E. 1993. Nest predation among vegetation layers and habitat types: revising the dogmas. Am. Nat. 141:897–913.

MARVIL, R. E., AND A. CRUZ. 1989. Impact of Brown-headed Cowbird parasitism on the reproductive success of the Solitary Vireo. Auk 106:476–480.

MASON, P. 1986. Brood parasitism in a host generalist, the Shiny Cowbird: I. Auk 103:52–60.

MASON, P. AND S. I. ROTHSTEIN. 1986. Coevolution and avian brood parasitism: cowbird eggs show evolutionary response to host discrimination. Evolution 40:1207–1214.

MAYFIELD, H. 1960. The Kirtland's Warbler. Bull. No. 40, Cranbrook Institute of Science, Bloomfield Hills, MI.

MAYFIELD, H. 1965. The Brown-headed Cowbird, with old and new hosts. Living Bird 4:13–28.

MAYFIELD, H. F. 1975. Suggestions for calculating nest success. Wilson Bull. 87:456–466.

MENGEL, R. M., AND M. A. JENKINSON. 1970. Parasitism by the Brown-headed Cowbird on a Brown Thrasher and a catbird. Wilson Bull. 82:74–78.

MERMOZ, M. E., AND J. C. REBOREDA. 1994. Brood parasitism of the Shiny Cowbird, *Molothrus bonariensis,* on the Brown-and-Yellow Marshbird, *Pseudoleistes virescens.* Condor 96:716–721.

NICE, M. M. 1937. Studies in the life history of the Song Sparrow, Vol. 1. Dover, New York.

NOLAN, V., JR. 1978. The ecology and behavior of the Prairie Warbler *Dendroica discolor.* Ornithol. Monogr. 26. Washington, DC.

NORRIS, R. T. 1947. The cowbirds of Preston Frith. Wilson Bull. 59:83–103.

ORTEGA, C. P., AND A. CRUZ. 1991. A comparative study of cowbird parasitism in Yellow-headed Blackbirds and Red-winged Blackbirds. Auk 108: 16–24.

ORTEGA, C. P., AND A. CRUZ. 1992. Differential growth patterns of nestling Brown-headed Cowbirds and Yellow-headed Blackbirds. Auk 109:368–376.

PECK, G. K., AND R. D. JAMES. 1987. Breeding birds of Ontario: nidiology and distribution, Vol. 2: Passerines. Life Sciences Miscellaneous Publications. Royal Ontario Museum. Toronto.

ROTHSTEIN, S. I. 1971. Observation and experiment in the analysis of interactions between brood parasites and their hosts. Am. Nat. 105:71–74.

ROTHSTEIN, S. I. 1975. An experimental and teleonomic investigation of avian brood parasitism. Condor 77:250–271.

SCHÖNWETTER, M. 1983. Handbuch der Öologie. Akademie Verlag, Berlin.

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

SCOTT, D. M. 1963. Changes in the reproductive activity of the Brown-headed Cowbird within the breeding season. Wilson Bull. 75:123–129.

SCOTT, D. M. 1977. Cowbird parasitism on the Gray Catbird at London, Ontario. Auk 94:18–27.

SCOTT, D. M., P. J. WEATHERHEAD, AND C. D. ANKNEY. 1992. Egg-eating by female Brown-headed Cowbirds. Condor 94:579–584.

SEALY, S. G. 1992. Removal of Yellow Warbler eggs in association with cowbird parasitism. Condor 94:40–54.

SMITH, J. N. M., AND D. A. ROFF. 1980. Temporal spacing of broods, brood size, and parental care in Song Sparrows (*Melospiza melodia*). Can. J. Zool. 58:1007–1015.

SMITH, J. N. M., AND P. ARCESE. 1994. Brown-headed Cowbirds and an island population of Song Sparrows: a 16-year study. Condor 96:916–934.

SMITH, P. C. 1969. Survival and dispersal of juvenal Cardinals. M.Sc.thesis, Univ. Western Ontario, London, Canada.

SOLER, M. 1990. Relationships between the Great Spotted Cuckoo *Clamator glandarius* and its corvid hosts in a recently colonized area. Ornis Scand. 21:212–223.

SOUTHERN, W. E. 1958. Nesting of the Red-eyed Vireo in the Douglas Lake region, Michigan. Jackpine Warbler 36:105–130, 185–207.

WALKINSHAW, L. H. 1944. The Eastern Chipping Sparrow in Michigan. Wilson Bull. 56:193–205.

WALKINSHAW, L. H. 1952. Chipping Sparrow notes. Bird-Banding 23:101–108.

WEATHERHEAD, P. J. 1989. Sex ratios, host-specific reproductive success, and impact of Brown-headed Cowbirds. Auk 106:358–366.

WILEY, J. W. 1986. Growth of Shiny Cowbird and host chicks. Wilson Bull. 98:126–131.

WILLIAMS, J. F. 1940. The sex ratio in nestling Eastern Red-wings. Wilson Bull. 52:267–277.

WOLF, L. 1987. Host-parasite interactions of Brown-headed Cowbirds and Dark-eyed Juncos in Virginia. Wilson Bull. 99:338–350.

WOODWARD, P. W., AND J. C. WOODWARD. 1979. Survival of fledgling Brown-headed Cowbirds. Bird-Banding 50:66–68.

YOUNG, H. 1963a. Breeding success of the cowbird. Wilson Bull. 75:115–122.

YOUNG, H. 1963b. Age-specific mortality in the eggs and nestlings of blackbirds. Auk 80:145–155.