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THE YOUNG COWBIRD: AVERAGE OR OPTIMAL NESTLING?

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ABSTRACT.—We studied whether the young of the Brown-headed Cowbird are more successful than those of nonparasitic passerines when raised by other species. Eggs and nestlings of seven species were placed in Barn Swallow and House Sparrow nests, and the hatching success and nestling survival rates compared. The hatching success was high for all species in both host species' nests. In the Barn Swallow nest, the nestlings of four of the five nonparasitic species did as well as the cowbird nestlings. On the other hand, the three foreign species placed in the House Sparrow nest, including the cowbird, all failed to survive through the nestling stage. In addition, a Red-winged Blackbird, a catbird, and a cowbird were observed immediately after departing from their Barn Swallow host nests; only the cowbird elicited feedings from its host parents. Thus the young cowbird fared no better than the other species as a nestling. Although cowbirds can be reared by their most frequent host species, they may not be particularly successful with some of their less common hosts. They may be especially successful as a fledgling, a hypothesis that awaits further investigation.

The young of many avian brood parasites possess striking adaptations to their unusual rearing situations. The eggs, nestling appearance and mouth markings of several parasitic widowbirds (*Vidua* spp.), for example, are almost indistinguishable from each species' respective host (Nicolai 1974). In addition, the begging postures and vocalizations of each widowbird species match those of its host species. Newborn cuckoos (*Cuculus* spp.) of parasitic species eject the eggs or other nestlings from the nest by maneuvering them onto their slightly concave back and pushing them out. A newly hatched Lesser Honeyguide (*Indicator minor*) has a mandibular hook with which it attacks and kills its nestmates (Skutch 1976).

The Brown-headed Cowbird (*Molothrus ater*) is known to use more host species than any other brood parasite: its eggs have been found in the nests of 217 species and young cowbirds have been reared by 139 species (Friedmann et al. 1977). Do developing cowbirds possess some special adaptations that allow them to be raised by such a diversity of species? Friedmann (1929) suggested that the short incubation period and rapid nestling growth of cowbirds are adaptations to the parasitic habit, but subsequent investigations indicate that these characteristics are in line with those found in many nonparasitic avian species (Nice 1937, 1939, Norris 1947, Ricklefs 1968). Indeed, Nice (1939) stated that "there appears to be no conclusive evidence that the young cowbird shows any such [parasitic] adaptation." If this is the case, the requirements of any developing passerine may be so general that virtually any species can be reared by any other. This proposition seems unlikely considering the complex and dynamic nature of avian parent-offspring relationships (e.g., Muller and Smith 1978) but it remains to be tested thoroughly.

The chief purpose of our study was to determine if young cowbirds survive at a higher rate than nonparasitic passerine nestlings that are reared by parents of another species. Our method was to cross-foster the eggs (and occasionally nestlings) of several species into other species' nests and to compare egg and nestling survival rates. We predicted that if the young cowbirds were more versatile than the nonparasitic species' young in their ability to be reared by foster parents, they would survive at higher rates than the nonparasitic young. We also observed several fledglings immediately after leaving the nest in order to ascertain their ability to induce their foster parents to feed them.

METHODS

LOCATION

The study was carried out within a 25-km radius of Cornell University campus in Ithaca, New York, in

TABLE 1. Incubation period,[a] nestling period,[a] and criterion age for nestling survival of each experimental parasite species.

Species	Incubation period (days)[b]	Nestling period (days)	Criterion age (days)[c]
Barn Swallow	14–16 (4)	17–24	10
House Sparrow	11–14 (3)	15	8
Brown-headed Cowbird	11–12 (3)	10	6
Red-winged Blackbird	10–12 (3)	10–11	6
Bank Swallow	12–16 (4)	19	10
Eastern Phoebe	14–16 (4)	15–17	9
Gray Catbird	12–13 (3)	10	6

[a] From Harrison (1978).
[b] Parentheses contain the time in days considered one-quarter the incubation period.
[c] Minimum age that had to be attained by nestling in order to qualify for "nestling survival" category.

1974 and 1977. Eggs and nestlings were cross-fostered in June and July, and nests were checked and fledglings observed until mid-August.

SUBJECTS

We selected host species according to several considerations: they had to be locally abundant, not subject to heavy predation, and they had to accept foreign eggs placed in their nest. Although we also wanted to use a species commonly parasitized by the cowbird, the above criteria were met by only two species, both of which are not normally victimized by the cowbird—the Barn Swallow (*Hirundo rustica*) and the House Sparrow (*Passer domesticus*).

Species used as experimental parasites were the Red-winged Blackbird (*Agelaius phoeniceus*) and the cowbird (placed in both host species' nests), the Barn Swallow (into the House Sparrow nests), and the Gray Catbird (*Dumetella carolinensis*), Eastern Phoebe (*Sayornis phoebe*), Bank Swallow (*Riparia riparia*), and the House Sparrow (into the Barn Swallow nests). The term "experimental parasite" refers to any egg or nestling placed in the nest of another species. The species in whose nest they were placed, either a Barn Swallow or a House Sparrow nest, is referred to as the "host." In addition to these experiments, we switched Barn Swallow eggs into other Barn Swallow nests, and House Sparrow eggs into other House Sparrow nests in an effort to determine the effects of the cross-fostering technique on hatching success and nestling survival.

All of the eggs and nestlings were collected in the field, except for the cowbird eggs, which were taken from a group of captive cowbirds. The cowbird eggs were incubated by Canaries (*Serinus canaria*) for 9 to 10 days and hatched one to two days after being placed in the host nest.

PROCEDURE

An egg was removed from each nest found and candled to determine the stage of incubation. In no case was our estimate of the incubation stage off by more than one quarter of the incubation period. The absolute value in days of one-quarter of the incubation period differed among the species (Table 1). The location, contents, and approximate stage of incubation of all nests were recorded.

A total of 180 eggs were cross-fostered into Barn Swallow and House Sparrow nests in 1974 and 1977. Five cowbird eggs placed in House Sparrow nests during the summer of 1973 were also included, making a total of 185 eggs switched. In addition, 34 nestlings less than three days old and three four-day old nestlings were placed in host nests, for a total of 222 crosses. Nestlings were cross-fostered when a nest was found containing young nestlings and appropriate host nests were available, or when the age of a previously candled clutch was misjudged and the eggs hatched before the cross was made.

Each experimental parasite and conspecific control egg was matched to a host nest in such a way that the egg was expected to hatch before the host clutch. In only 16 of 222 crosses were the host young older than the bird placed in the nest.

Once an egg was matched to a host, the cross was not carried out until late in the experimental parasite or conspecific control egg's incubation period. Of the eggs crossed, 4 were switched in the first quarter of their incubation period, 14 in the second quarter, 28 in the third quarter, and 139 in the last quarter. We tried to switch eggs or nestlings that were not too far out of synchrony with the stage of incubation of the host clutch, so that the cross-fostered young did not hatch extremely early in the host's incubation period. Of 208 egg and nestling crosses for which information on both the host and parasite hatch dates were known, 16 host clutches were one to four days older than the cross-fostered egg or nestling, 29 parasites hatched the same day as the host clutch, 76 parasites were one to four days older than the host, 53 parasites were five to eight days older, and 33 were nine to 13 days older than the host young.

Eggs and nestlings were taken from their own nest and transported to their host nest in small vials filled with cotton. No eggs or nestlings were kept out of a nest for more than two hours, and most crosses were completed in less than one-half hour. Each host clutch was parasitized with only one egg, although we tested subsequent clutches at the same nest.

After completing the cross, we visited each nest at least once, and none more than three times. At each nest check, we recorded the status of the fostered egg or nestling as either present (with estimated age), or absent. We also noted the state of the host young at the time of the last check for 100 of the nests.

Nests were checked until 1) the switched egg was judged to have failed to hatch, 2) the fostered egg or nestling was gone, 3) some catastrophe had befallen the nest, such as predation, desertion, or nest destruction, or 4) the parasite nestling had survived to its criterion age for successful passage through the nestling stage.

The disappearance of the contents of the nest was attributed to predation. Desertion was indicated by a cold clutch and the absence of an incubating female at the nest. The criterion for nestling survival was half the nestling period, the age in days depending upon the nestling period of each species (Table 1).

We watched three individual young immediately after they left their Barn Swallow nest. The birds were a Red-winged Blackbird, a catbird, and a cowbird, all

of which were placed in the host nest as eggs. A blind was set up at least one day before the expected departure of the parasite young so that the swallow foster parents could become accustomed to it. We were careful not to influence the departure of the experimental fledglings from the nest. The young were watched until nightfall and, in the cases of the cowbird and the catbird, for several hours the next morning. Their begging behavior and vocalizations were recorded in conjunction with the presence and behavior of their foster parents.

In order to determine if the cowbird did significantly better in hatching success or nestling survival than any other experimental parasite species placed in a given host nest, a Fischer Exact Probability Test was performed on each experimental parasite/cowbird pair.

RESULTS

EGG STAGE

Eggs not included in hatching analysis. We were unable to learn if 26 of the switched eggs hatched. Five nests were robbed before the first visit and nine were deserted or destroyed. We used eggs from seven nests that were cold when they were found; the eggs probably were dead before they were cross-fostered. In five cases, the fate of the switched egg was unknown, as these nests were not visited until the expected fledge date; the absence of the young bird could not be explained with certainty. Thus, 159 cross-fostered eggs provided data for the calculation of hatching success.

Hatching success. The overall hatching rate for the experiment was 87% (Table 2), individual species ranging from 75% to 100% in House Sparrow nests, and from 83% to 100% in the Barn Swallow nests. The conspecific control crosses had hatching rates of 86% for the Barn Swallow and 83% for the House Sparrow. No significant differences were found ($P < .05$) in the hatching success of the cowbird relative to that of the other experimental species in either host nest.

TABLE 2. Hatching success of the experimental parasite and control cross species for each host species.

Parasite species	Total number of eggs cross-fostered	Number of eggs hatched	Hatching success
Host: Barn Swallow			
Brown-headed Cowbird	24	20	83%
Red-winged Blackbird	22	20	91%
House Sparrow	19	17	89%
Gray Catbird	11	10	91%
Eastern Phoebe	14	13	93%
Bank Swallow	1	1	100%
Barn Swallow control	28	24	86%
Barn Swallow host subtotal	119	105	88%
Host: House Sparrow			
Brown-headed Cowbird	7	6	86%
Red-winged Blackbird	8	6	75%
Barn Swallow	7	7	100%
House Sparrow control	18	15	83%
House Sparrow host subtotal	40	34	85%
Total	159	139	87%

NESTLING STAGE

Nestlings not included in survival analysis. The two sources of information about nestling survival were cross-fostered eggs that hatched in the host nests, and young placed in the host nests as nestlings. Of the 139 nestlings that hatched in the host nests, 10 provided no data on nestling survival. The fate of seven nestlings was ambiguous, as at the first check the nestling was present but had not reached criterion age, and the next visit was on the date of expected departure, so the nestling's absence could have been due to either death or fledging. Two other nests were robbed and one nest fell after the eggs had hatched.

Of the 37 nestlings cross-fostered after hatching, seven yielded no data. Five were taken by predators, one nest was destroyed, and one nest was deserted.

Combining of nestling data. Before pooling these sources of data, we first had to determine that the two manipulations did not differentially affect nestling survival. Of 129 informative nestlings that hatched in host nests, 63% survived to the criterion age of one-half their nestling period. Of the 30 informative nestlings that hatched before being placed in host nests, 40% survived to criterion age. Although this suggests that the latter were less successful than the former, an examination of the survival of the cross-fostered nestlings by species reveals that this was not the case (Table 3). Ten of the cross-fostered nestling failures were four Red-winged Blackbird and six Barn Swallow nestlings placed in the House Sparrow nests, which corresponds to the failure of all 11 nestlings of these two species that hatched in the House Sparrow nests. Conversely, 88% of the House Sparrow nestlings placed in the Barn Swallow nest survived, as compared to a survival rate of 76% of nestlings which hatched in the host Barn Swallow nest. In addition, the one phoebe (in a Barn Swallow nest) and two House Sparrow (in House Sparrow nests) nestlings placed in the host nest all survived. Also, the failure of seven out of eight

TABLE 3. Survival of the experimental and control nestlings for each host species.

Parasite species	Nestlings hatched in host nest		Nestlings crossed into host nest		Nestling survival
	Total number of nestlings hatched	Number of nestlings survived	Total number of nestlings cross-fostered	Number of nestlings survived	
Host: Barn Swallow					
Brown-headed Cowbird	18	12	—	—	67%
Red-winged Blackbird	17	10	—	—	59%
House Sparrow	17	13	9	8	81%
Gray Catbird	10	6	—	—	60%
Eastern Phoebe	12	10	1	1	85%
Bank Swallow	1	1	8	1	22%
Barn Swallow control	22	20	—	—	91%
Barn Swallow host subtotal	97	72	18	10	72%
Host: House Sparrow					
Brown-headed Cowbird	6	0	—	—	0%
Red-winged Blackbird	4	0	4	0	0%
Barn Swallow	7	0	6	0	0%
House Sparrow control	15	9	2	2	65%
House Sparrow host subtotal	32	9	12	2	25%
Total	129	81	30	12	58%

one- to two-day old Bank Swallows cross-fostered into Barn Swallow nests (for which we have no comparable data for nestlings crossed as eggs) was apparently not due to the fact that they were crossed as nestlings; five of the seven nestlings that failed to reach criterion age were alive at seven days of age (five days after the switch), and died subsequently. The failure was thus due to events in the host nest, rather than the switching of the birds as nestlings. Because of this lack of systematic differences between the two sources of nestling survival information, the data were pooled for analysis.

Nestling survival. The nestling survival rates in the Barn Swallow nests for five of the experimental species ranged from 59% for the Red-winged Blackbird to 85% for the phoebe. The sixth experimental parasite, the Bank Swallow, had a nestling survival rate of only 22%. Sixty-seven percent of the cowbirds survived to criterion age, and the Barn Swallow had the expected highest rate of success at 91% (Table 3).

In the House Sparrow nests, by contrast, none of the nestlings of any of the three experimental species lived to criterion age. Nineteen of the 27 experimental parasite nestlings died within six days after hatching; the rest died subsequently. All appeared to be losing weight until they disappeared from the nest or were found dead. In order to determine if older nestlings would do better, we put three four-day old blackbird nestlings in House Sparrow nests and weighed them daily. One died by day 7, and the other two lost weight until they died on day 9. Necropsies disclosed atrophied musculature although the stomach and gizzard were full of insect and seed matter, indicating that the nestlings had been fed by their foster parents. Unlike the experimental parasites, the House Sparrow conspecific control crosses had a relatively high survival rate of 65%.

Only the Bank Swallow had significantly lower nestling survival ($P < .05$) than the cowbird in the Barn Swallow nest. There were no significant differences (at the $P < .05$ level) in survival between the cowbird and the two experimental parasites in the House Sparrow nest, as all three species died.

Asynchrony of hatching between parasite and host species. We examined the relative ages of the parasite nestling and the host brood in order to determine if the discrepancy affected the survival of the parasite. We analyzed 150 cases, measuring the age of the host brood from the hatching date of the oldest young. In 14 cases, the cross was made such that the host clutch was one to four days more advanced than the individual placed in the nest, owing to either a miscalculation of the age of the candled egg or the unavailability of a host clutch at the appropriate stage. Four of the parasite nestlings survived, an observed survival rate of 29%. The expected nestling survival rate (see legend, Table 4, for formula) for this sample was 71%. Thus, the observed sur-

TABLE 4. Parasite nestling survival in relation to the degree of hatching asynchrony of the parasite and the host clutch.

	Total number of crosses	Nestlings survived	Observed nestling survival	Expected nestling survival[a]
Parasite 1–4 days younger than host brood	14	4	29%	71%
Parasite same age as host brood	18	9	50%	49%
Parasite 1–4 days older than host brood	49	31	63%	55%
Parasite 5–8 days older than host brood	43	27	63%	59%
Parasite 9–13 days older than host brood	26	17	65%	65%

[a] $SR_e = \Sigma nr/N$ where SR_e is the expected survival rate for each sample, n is the number of crosses from each parasite-host condition in the sample, r is the overall nestling survival rate for that parasite host condition, and N is the total number of crosses in the sample.

vival rate was 42% lower than that expected in a random sample of that species composition. The same procedure was carried out for the samples of nestlings that were the same age as the host young, one to four days older than the host young, five to eight days older, and nine to 13 days older than the host young. The survival rates for these four samples did not differ greatly from their expected values, the largest discrepancy being 8% (Table 4).

Host nestling survival. Data on the effect of the cross-fostered bird on the status of the host young at the time of the last nest check were available for 100 nests. A host clutch was rated a success if half or more of the number of host eggs originally in the nest were alive and at least four days old at the time of the last check. If no host young, or less than half the original number of eggs were alive at the last check, the nest was considered a failure (nests in which the host young had not yet hatched or were less than four days of age were not included in the calculations). Of the 16 nests in which the cross-fostered egg did not hatch, all host clutches were successful. In addition, in the 40 nests in which the cross-fostered individual died, 39 of the host clutches were successful. However, of the 44 nests in which the cross-fostered nestling survived to criterion age, only 31 host clutches were successful (Table 5).

FLEDGLING STAGE

Fledgling's behavior. One blackbird and one catbird were each observed for seven hours immediately after leaving the host Barn Swallow nest, and the cowbird was followed for a total of 9.5 h after fledging. Each fledgling spent most of its time vocalizing. As measured by the proportion of one-minute intervals during which the fledgling was calling, the blackbird called during two-thirds of the observation period, and the catbird and cowbird each vocalized for more

TABLE 5. Success of host clutch[a] in relation to the fate of the cross-fostered bird.

	Fate of the parasite					
	Did not hatch		Died		Survived	
Parasite species	Success[a]	Failure	Success[a]	Failure	Success[a]	Failure
Host: Barn Swallow						
Brown-headed Cowbird	2	0	2	0	2	1
Red-winged Blackbird	1	0	5	1	2	2
House Sparrow	2	0	3	0	6	5
Gray Catbird	1	0	4	0	3	0
Eastern Phoebe	0	0	1	0	9	1
Bank Swallow	0	0	6	0	1	0
Barn Swallow control	4	0	0	0	7	2
Barn Swallow host subtotal	10	0	21	1	30	11
Host: House Sparrow						
Brown-headed Cowbird	1	0	0	0	0	0
Red-winged Blackbird	2	0	6	0	0	0
Barn Swallow	0	0	8	0	0	0
House Sparrow control	3	0	4	0	1	2
House Sparrow host subtotal	6	0	18	0	1	2
Total	16	0	39	1	31	13

[a] Host clutch success measured as survival (to at least 4 days of age) of half or more the number of host eggs originally in the nest.

than 90% of the observation period. The approach of the foster parents often elicited calling from a silent fledgling, or increased the rate of calling in a bird already vocalizing.

The calls and the rate of calling differed among the three fledglings. The blackbird vocalized least, usually at a rate of 15 to 25 calls per minute, with a maximum rate of 35 calls per minute. The catbird called 25 to 50 times per minute (maximum, 60/min) and the cowbird usually called between 40 and 55 times per minute (maximum, 75/min).

When one of the foster parents came near, the fledgling sometimes assumed a begging posture. The Red-winged Blackbird often gaped towards the adult silently, whereas the catbird and the cowbird frequently accompanied their begging with vocalizations.

Foster parents' behavior. The three pairs of Barn Swallow parents appeared to be very nervous and excitable during the observation period. They frequently flew into and out of the area where the fledgling was calling, and occasionally panted (a sign of stress). The parents spent much time oriented towards, perched near, flying by and sometimes circling the fledgling.

Barn Swallows characteristically feed their young while hovering slightly above and facing them. The Barn Swallow foster parents of the catbird hovered near it 18 times, and the blackbird's foster parents hovered 28 times, but on no occasion did these parents attempt to feed the fledgling. In fact, neither of these fledglings was fed by their foster parents during the observation period. The foster parents of the cowbird, in contrast, hovered without attempting to feed it only twice, whereas they hovered while attempting to exchange food 54 times during the observation period. Although many of the attempted exchanges were unsuccessful (e.g., the cowbird dropped the insect), the fledgling swallowed after other exchanges and clearly was fed. The cowbird was first fed 4.5 h after leaving the nest; hovering near the other fledglings first occurred one hour after the blackbird fledged and three hours after the catbird fledged. The hovering behavior appeared identical whether or not an exchange of food with the fledgling was attempted.

In summary, all three fledglings were persistent yet different in their begging. Only the cowbird was able to elicit feeding from its Barn Swallow foster parents.

DISCUSSION

EGG STAGE

The hatching success of all the species cross-fostered into both the Barn Swallow and the House Sparrow host nests was quite high. The cowbird eggs, however, did not do significantly better than those of the other foreign species placed in either host species' nest. Thus, although the pattern and conditions of incubation differed somewhat among the species studied, as among passerines in general, these differences did not significantly affect hatching.

When given the advantage of hatching before the host young, nonparasitic young appeared to fare as well as the cowbird through the egg stage. However, the crosses were made late in the incubation period, and avian embryos may be more susceptible to variations in the pattern of incubation during early development. Although our data do not suggest that the cowbird has any special adaptations allowing it to be successfully incubated by so many species, further work on this subject would be useful.

The hatching success of the conspecific control crosses corresponds well with hatching rates reported for normal clutches of these species (Seel 1968, Snapp 1976). Thus, the cross-fostering technique appeared to cause little or no decrease in hatching success.

NESTLING STAGE

The nestling survival rates for the conspecific control crosses correspond well to those reported for normal broods (Seel 1970, Snapp 1976), indicating that the viability of the nestlings was not affected by the manipulation.

It was practical to record nestling mortality for only the first half of the nestling stage (criterion age). Studies of normal broods suggest that the major cause of death in the second half of the nestling period is starvation, reflecting the adequacy of the food supply available to the female (Robertson 1973, Caccamise 1976). As the earlier-hatching experimental parasite could easily outcompete the host young and was often the only nestling left in the nest, the Barn Swallow hosts probably had no difficulty in providing the parasite with sufficient food. Unless there were incompatibilities between the Barn Swallow and the experimental parasite that did not appear until the second half of the nestling stage, which seems unlikely, survival to criterion age provides a

reasonable measure of the cowbird's nestling survival rate relative to the other species studied.

The cowbird nestling was successfully reared by the Barn Swallow, as were four of the other five foreign species placed in the Barn Swallow nest. On the other hand, neither the cowbird, the Barn Swallow, nor the Red-winged Blackbird survived in the House Sparrow nest. This suggests that cowbirds are no better equipped to cope with parent-young incompatibilities than are nonparasitic species.

It is interesting to note that the Bank Swallow was the least successful of the six species cross-fostered into the Barn Swallow nest although it was the closest relative. One might expect that these species would have had the most similar developmental requirements. Differences in their ecology and the microenvironment of their nests, however, may have led to incompatibilities in the parent-young interaction. The Bank Swallow nests in holes whereas the Barn Swallow does not. The behavior and communication between parents and nestlings are probably quite different in these two situations.

The failure of the three fostered species to be reared by the House Sparrow presents a more dramatic demonstration of the inability of some avian young to be reared by a different species. Although Friedmann (1963) reported two observations of House Sparrow adults feeding cowbird fledglings, the survival rate from the nest of this rare host species appears to be low. We speculate that the nutritional requirements of the fostered young were not met. The loss of weight and muscular atrophy of the two blackbird nestlings transferred at four days of age, despite their full stomachs, argue that the diet was insufficient. However, 19 of the 27 nestlings died within six days posthatching. Data from four studies on House Sparrows, compiled by Summers-Smith (1963), show that 70–100% of the food brought to the nestlings during the first six days is animal matter, compared to only 33–50% for the remainder of the nestling period. Thus, the high rate of mortality during the early part of the nestling period suggests that there may be other incompatibilities besides nutrition between the House Sparrow parents and the cross-fostered young.

If the House Sparrow diet is insufficient to rear cowbirds, this implies that some species that are commonly parasitized cannot raise nestling cowbirds. For example, the Purple Finch (*Carpodacus purpureus*) and the American Goldfinch (*Carduelis tristis*) are host species that feed their young regurgitated plant seeds. The Cedar Waxwing (*Bombycilla cedrorum*) feeds its young a partly frugivorous diet; although it usually ejects cowbird eggs, over 50 cases of parasitism of this species are known (Friedmann et al. 1977). Field studies of cowbird parasitism of the American Goldfinch (Middleton 1977) and Cedar Waxwing (Rothstein 1976) support the contention that the cowbird nestling cannot survive on a diet of seeds or fruit.

The low survival rate of parasite nestlings that were one to four days younger than the host brood demonstrates the role of competition in nestling survival. In many passerines, hatching is asynchronous and late-hatching young suffer higher mortality (Ricklefs 1965, Willson 1966, Seel 1970, Hussell 1972, Dyrcz 1974, Howe 1976, Strehl 1978). The female cowbird's tendency to lay in nests that have one or two host eggs (Ficken 1961, Hann 1941, King 1979) can be seen as a behavior insuring that her egg is not laid in a nest in an advanced stage of incubation. In addition, her tendency to use nests containing eggs smaller than her own (King 1979) also provides an advantage in competition with the host young. When the nonparasitic species' nestlings in this study were provided with a similar advantage in another species' nest, they were as successful as the cowbird nestling.

The reduction of host brood success when the parasite nestling survived to criterion age, as opposed to when it did not hatch or died, also demonstrates the impact of competition on nestling survival. The nests were checked only until the cross-fostered nestling reached criterion age, and in some cases the host broods included in our calculation were between four days old and criterion age (eight days for the House Sparrow, ten days for the Barn Swallow). Only those broods in which the parasite survived remained in competition with it. Hence, these host broods probably would have been even less successful if they had been followed to their criterion age. The reduction of host brood success of naturally parasitized nests is well documented, and this study shows that the earlier hatching of nonparasitic species will also reduce the success of the host brood.

It is important that the cowbird did not fare better than other, nonparasitic species placed in a given host nest. Wallace

(1979:124) claimed that "the host may attend to the young (cowbird) parasite in preference to its own young" and that the cowbird is a "supernormal releaser" for parental care. This implies that there is some set of characteristics that are integral to parent-offspring interactions among all passerines, and that the young cowbird has improved these features. Our data, however, suggest that in fact there may not be such a set of universal features. Rather, the young cowbird may be an "average" nestling in the sense that it is moderately successful in its interactions with its most frequent host parents, while it may be a failure with some of its rarer hosts.

Rothstein (1976) has shown that cowbirds do not employ the best reproductive behavior since they sometimes parasitize species that eject cowbird eggs. We suggest further that cowbirds sometimes parasitize species that accept the egg but cannot rear the nestling to independence. Gochfeld (1979) found that the Shiny Cowbird (*Molothrus bonariensis*), which also parasitizes many species, commonly lays in the nest of the Long-tailed Meadowlark (*Sturnella loyca*), although the cowbird apparently cannot be reared to fledging by this host. Thus, occasionally wasting eggs by parasitizing unsuitable hosts appears to be one of the costs of a generalist manner of brood parasitism.

FLEDGLING STAGE

Our most salient finding was that the cowbird fledgling was fed by the Barn Swallows, while the Red-winged Blackbird and Gray Catbird fledglings were not. This suggests that a fledgling that has been raised by another species may be unable to learn the parent-offspring communication system of the foster species. The habit of not feeding fledglings of a different species may have evolved in response to selection pressures other than cowbird parasitism (as the Barn Swallow is not a usual cowbird host). Thus, species that have not evolved specific defenses against cowbird parasitism early in the nesting cycle (Rothstein 1975; e.g., aggression against adult cowbirds to prevent egg laying [Robertson and Norman 1975] or egg ejection [Rothstein 1970]), may still present a potential problem to the young cowbird's survival at the fledgling stage. The extent of this reluctance to feed nonconspecific fledglings among species that the cowbird normally parasitizes will determine the severity of this problem for the cowbird as a species.

The ability of the fledgling cowbird to coax its Barn Swallow foster parents to feed it tempts us to speculate that it does possess adaptations that enable it to deal with a foster parent's reluctance to feed a foreign fledgling. P. Woodward (pers. comm.) suggested that a cowbird's loud and persistent calling may serve this function. Neither the catbird nor the blackbird, however, was fed despite their loud and almost continuous vocalizing. This suggests that if, indeed, a fledgling cowbird does something special, it is more complex and subtle than simply begging more often than the host young. Whether the cowbird fledgling is able to induce feeding from a broader range of species than the young of nonparasitic passerines needs further study.

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