

REJECTION OF COWBIRD EGGS BY CRISSAL THRASHERS

DEBORAH M. FINCH¹

Rocky Mountain Forest and Range Experiment Station, Forestry Sciences Laboratory,
Arizona State University, Tempe, Arizona 85281 USA

ABSTRACT.—Although the "dwarf" race of the Brown-headed Cowbird (*Molothrus ater obscurus*) is sympatric with the Crissal Thrasher (*Toxostoma dorsale*) in the lower Colorado River valley, I observed no parasitism in 15 thrasher nests. To determine whether or not the absence of cowbird eggs was caused by egg rejection, I experimentally parasitized nine thrasher nests. Cowbird eggs were ejected by thrashers at all experimental nests. To test the prediction that ejection or absence of cowbird eggs reduces nesting mortality, I compared thrasher nesting success to that of a sympatric acceptor, the Abert's Towhee (*Pipilo aberti*). Daily nesting success (\hat{s}) of the Crissal Thrasher was 0.985 during the incubation period, which was significantly higher than clutch \hat{s} of either nonparasitized ($\hat{s} = 0.955$) or parasitized ($\hat{s} = 0.911$) Abert's Towhees. A higher predation rate accounted for the difference ($P < 0.05$) between clutch \hat{s} of nonparasitized towhees and thrashers, but harassment and ejection of towhee eggs by cowbirds explained the much greater difference ($P \leq 0.001$) between clutch \hat{s} of parasitized towhees and thrashers. Ejection behavior by the Crissal Thrasher may either be a preadaptation or an evolved response to repeated cowbird parasitism. Received 31 August 1981, accepted 16 March 1982.

At least 216 avian species have been recorded as victims of brood parasitism by the Brown-headed Cowbird (*Molothrus ater*) (Friedmann et al. 1977). As brood parasitism seriously damages the reproductive success of hosts (Mayfield 1977), it would be advantageous for victimized species to evolve defenses against parasitism (Rothstein 1975a). Egg ejection is one of the most efficient methods of defense; yet, based on experimental tests of 43 species, only 7 species are known to eject cowbird eggs regularly (Rothstein 1975a, 1976a,b, 1977). Because many cowbird eggs may be ejected by hosts before observers detect them, several cases of parasitism probably go unnoticed. Species reported to be rarely or never parasitized may be either (1) rejecters or (2) accepters that are seldom parasitized. Species shown experimentally to be rejecters may be subject naturally to cowbird parasitism that ranges from none to moderately high.

In this paper, I report on the response of the Crissal Thrasher (*Toxostoma dorsale*) to eggs of

the "dwarf" race of the Brown-headed Cowbird (*M. a. obscurus*). The study was conducted on the Colorado River Indian Reservation, about 10 km north of Ehrenberg, Arizona. Cowbirds are abundant in this arid region (Anderson and Ohmart 1976), which is dominated by honey mesquite (*Prosopis glandulosa*), but there were thought to be only three potentially suitable hosts: the Black-tailed Gnatcatcher (*Poliophtila melanura*), which is heavily parasitized (Kathleen Conine pers. comm.); the Abert's Towhee (*Pipilo aberti*), which is moderately parasitized (Finch 1981); and the Crissal Thrasher, for which I had observed no parasitism in 15 nests. To determine whether or not the absence of cowbird eggs may be caused by ejection of cowbird eggs by Crissal Thrashers, I experimented with nine thrasher nests. Because instances of acceptance are rarely documented for ejecter species, I compared thrasher nesting success to that of an accepter, the Abert's Towhee, to test the prediction that ejection behavior reduces nesting mortality.

The honey mesquite habitat of the lower Colorado River contains six other common passerine species (Anderson and Ohmart 1976) that are not suitable hosts because they (1) usually reject cowbird eggs [Northern Oriole (*Icterus galbula bullockii*), Rothstein (1977)], or (2) nest before cowbirds begin breeding in May

¹ Present address: Rocky Mountain Forest and Range Experiment Station, Forest, Range and Watershed Laboratory, 222 South 22nd Street, Laramie, Wyoming 82070 USA.

[Phainopepla (*Phainopepla nitens*), Anderson and Ohmart (1978)], or (3) build inaccessible domed nests [Cactus Wren (*Campylorhynchus brunneicapillus*), and Verdin (*Auriparus flaviceps*)], or (4) nest in cavities [Ash-throated Flycatcher (*Myiarchus cinerascens*) and Lucy's Warbler (*Vermivora luciae*)]. Of the last four species, only Verdins and Lucy's warblers have been recorded as occasionally serving as hosts (Friedmann 1963, Friedmann et al. 1977)

METHODS

Experimental procedures were similar to those of Rothstein (1975a) except that I parasitized nests with real rather than artificial cowbird eggs and did not remove any thrasher eggs because I wanted clutches intact for computing nesting success. During the dwarf cowbird's breeding season (mid-April through July), I parasitized 3 nests during the thrasher egg-laying period, 4 nests during the first 3 days after clutch completion, and 3 nests late in the incubation stage. One of these nests was experimentally parasitized twice during the incubation stage, and another nest was parasitized twice during the egg-laying stage and once during the incubation stage. Thus, a total of 12 experiments was conducted at nine nests. Each nest was revisited 30–60 min after parasitism except for 2 nests that were observed from 100 m away to determine the form of rejection. At the time of experimental parasitism, thrashers were flushed from 5 nests and were absent at 4 nests. Some nests were parasitized more than once to determine whether or not parental responses to cowbird eggs differed for different nesting stages.

Because captive female cowbirds prefer to lay in nests that contain host eggs smaller than their own (King 1979), I measured the length (L) and breadth (B) of eggs with vernier calipers. One newly laid egg from each of three Crissal Thrasher and 16 Abert's Towhee clutches was weighed on an Ohaus scale accurate to 0.01 g. Ten fresh cowbird eggs were weighed and treated as independent samples of the population. Eggs that are clutchmates do not represent independent samples, so I calculated mean egg weight, length, and breadth for each thrasher and towhee clutch before estimating population means. Estimates of egg weight provide an index of weight advantages at hatching. Initial weights of eggs were estimated from Hoyt's (1979) equation: $Weight = K_w \cdot LB^2$. The weight coefficient (K_w) is a species-specific constant that I calculated from the relationship $K_w = W/LB^2$ (Hoyt 1979), where W is equal to measured fresh weight.

Nesting success was calculated using Mayfield's method based on nest-days of exposure (Mayfield 1961, 1975). The number of nest-days of exposure (EXP) is the period when a known nest is at risk

(Johnson 1979). Daily mortality rate (DMR), probability of survival for one day (s), and probability of survival of broods through incubation and nestling phases of length t days (s^t) were estimated. (Estimates of s are symbolized as \hat{s} .) To obtain a large-sample estimate of the variance (V) of \hat{s} , I used Johnson's (1979) estimator $V(\hat{s}) = (EXP - losses) \times losses / EXP^3$. The square root of this quantity is the estimated standard error of \hat{s} . To test for variation between daily mortality rates (e.g. incubation and nestling phases), I used Johnson's (1979) statistic, herein denoted as $|\hat{s}_2 - \hat{s}_1| [V(\hat{s}_1) + V(\hat{s}_2)]^{1/2}$, where the subscript specifies each group (note that $DMR_1 - DMR_2 = \hat{s}_2 - \hat{s}_1$). If Johnson's statistic is greater than $z_{\alpha/2}$, then the null hypothesis that $\hat{s}_1 = \hat{s}_2$ is rejected.

RESULTS AND DISCUSSION

Cowbird eggs were rejected at all nine thrasher nests (12 rejections), regardless of nesting stage or presence or absence of thrashers at the time of parasitism. On 23 June 1980, I observed a Crissal Thrasher ejecting the cowbird egg I had deposited at 1010 after flushing the incubating parent (sex unknown). At 1011 the thrasher returned, perched on the nest rim, and lifted the cowbird egg up in its bill. The egg either slipped or was dropped over the side of the nest. The thrasher immediately retrieved the cracked egg and carried it out of sight. At 1017 it returned to the nest and resumed incubation. Ejection was also observed at another nest. Ejection is the most common form of rejection behavior by parasitized species (Rothstein 1975a).

My observations indicate that thrashers eject eggs as soon as they detect them, so I had little opportunity to verify natural parasitism. Host-cowbird interactions are apparently of recent origin (Friedmann 1963), however, and the best current strategy for the cowbird may be to parasitize all nests found, including those of poor hosts (Rothstein 1976b). The Crissal Thrasher may not represent a favorable host choice, even if it were to accept cowbird eggs, because its own eggs are 135% heavier than cowbird eggs (Table 1); hence, cowbird hatchlings would be at a competitive disadvantage because of their smaller size. Another ground-foraging species that shares many features (e.g. distribution, seasonal status, habitat, body coloration, dispersion, and mating system) with the Crissal Thrasher is the Abert's Towhee. Although the Abert's Towhee lays eggs 92% heavier than cowbird eggs (Table 1), 22 of 69 towhee nests

TABLE 1. Initial egg weights of Crissal Thrashers, Abert's Towhees, and Brown-headed Cowbirds.^a

Species	K_w (mg) ^b	Egg length (mm)	Egg width (mm)	Initial egg weight (g)
Crissal Thrasher	0.531 (3:3)	26.53 ± 0.425 (8:21)	19.57 ± 0.138 (8:21)	5.45 ± 0.112 (8:21)
Abert's Towhee	0.537 (16:16)	24.65 ± 0.228 (37:98)	18.30 ± 0.113 (37:98)	4.45 ± 0.076 (37:98)
Brown-headed Cowbird	0.554 (10:10)	19.27 ± 0.109 (15:15)	14.72 ± 0.214 (15:15)	2.32 ± 0.052 (15:15)

^a Numbers in parentheses are number of clutches:number of eggs.

^b See Hoyt (1979).

(32%) in my study area were parasitized (Finch 1981).

Unless predation interferes, towhees are able to raise cowbirds to fledglings if cowbird eggs are laid during the egg-laying stage of the towhee (Finch 1981). A shorter incubation period of 10–11 days (Friedmann 1963) (as opposed to 14 days for Abert's Towhees and Crissal Thrashers) gives cowbirds the headstart in growth necessary to compete successfully with larger hatchling towhees. Rearing patterns should be similar in Crissal Thrashers if they were to accept cowbird eggs, because, like towhees, they begin incubation before the second egg is laid (thus, nestlings hatch asynchronously). In addition, mimids tend to have slower nestling growth rates (Rand 1941, Ricklefs 1968: 425) and lower predation rates (Slack 1976, Reynolds and Rich 1978) than towhees (Finch 1981), which could make them potentially better hosts. Because cowbirds parasitized Abert's Towhees frequently despite larger towhee egg size, the possible discrimination of free-living cowbirds against Crissal Thrashers may be a consequence of rejection behavior rather than the larger size of host eggs (contra King 1979).

The total probability of nesting success of Crissal Thrashers was 0.475 (see Table 2 for \hat{s}^t values). Although the probability of thrasher brood \hat{s} was lower than clutch \hat{s} (Table 3), the difference was not significant (Johnson's statistic = 0.62, $P > 0.50$). The Abert's Towhee, on the other hand, suffered greater losses during the incubation stage, primarily because towhee eggs were frequently removed by cowbirds and nests were sometimes deserted after cowbird harassment (Finch 1981). Brood \hat{s} of Crissal Thrashers did not differ significantly from brood \hat{s} of parasitized or nonparasitized

Abert's Towhees (Table 3). Clutch \hat{s} and egg \hat{s} of Crissal Thrashers differed greatly ($P < 0.001$), however, from clutch \hat{s} and egg \hat{s} of parasitized towhees. Clutch \hat{s} (but not egg \hat{s}) of nonparasitized towhees also differed significantly ($P < 0.05$) from clutch \hat{s} of thrashers, which suggests that predation, the major cause of nesting failure in both species, was higher for towhees. Even though the clutch size of Crissal Thrashers (2.79 eggs, $n = 14$) was not significantly different from that of Abert's Towhees (2.85 eggs, $n = 59$) (t -test = 1.13, $df = 71$, $P > 0.25$), Crissal Thrashers produced 130% more fledglings per nest. [Number of young fledged per nest is equal to average clutch size times total \hat{s}^t . For Crissal Thrashers, this value is $2.79 \cdot 0.475 = 1.33$ young, and for Abert's Towhees, this value is $2.85 \cdot 0.199$ (Finch 1981) = 0.57.]

The much higher \hat{s} of incubating thrashers compared to parasitized towhees may be due partly to (1) absence of cowbird parasitism, (2)

TABLE 2. Daily mortality rates (DMR), and probabilities of survival throughout nest period (\hat{s}^t) of 15 broods of Crissal Thrashers.^a

Component	Incubation phase		Nestling phase	
	Clutch ^b	Egg ^b	Brood ^b	Nestling ^b
Losses ^c	2	1	3	2
EXP (days)	129	361	110	282
DMR	0.016	0.003	0.027	0.007
\hat{s}^t ^d	0.804	0.963	0.679	0.905

^a Probability of success for the entire nest period is equal to the product of all \hat{s}^t values times the egg hatching rate (Mayfield 1961, 1975) = 0.475.

^b Brood survival is the probability of at least one host egg or nestling surviving in the nest. Egg or nestling survival accounts for partial losses of the broods.

^c One brood loss is equal to all members of a brood destroyed. One egg loss is equal to a single egg destroyed from a brood that remains active.

^d The exponent t of \hat{s}^t is equal to development time. For Crissal Thrashers, embryo t and nestling t are equal to 14 days.

TABLE 3. Johnson's test comparing probabilities of survival for one day (\hat{s}) of Crissal Thrashers (CT) and nonparasitized (NPAT) and parasitized (PAT) Abert's Towhees.

Species and test	Incubation period		Nestling period	
	Clutch	Egg	Brood	Nestling
Crissal Thrasher \hat{s}	0.985	0.997	0.973	0.993
Nonparasitized Towhee \hat{s}^a	0.955	0.995	0.969	0.994
Parasitized Towhee \hat{s}^a	0.911	0.963	0.938	0.984
Test CT \times NPAT	1.956 ^b	0.538	0.227	0.241
Test CT \times PAT	3.217 ^c	3.663 ^c	0.777	0.555

^a Data are from Finch 1981.

^b $P < 0.05$.

^c $P \leq 0.001$.

nest defense against cowbirds, (3) difficulty of cowbirds in finding unattended nests because of shared incubation by thrasher sexes (nest is only left unattended during thrasher egg-laying period), and/or (4) rejection of cowbird eggs. The last factor may increase clutch and egg \hat{s} by causing the cowbird parent to abandon its parasitic attempt (thus, ending harassment and destruction of host eggs). That mimids defend nests vigorously from intruders (Slack 1976, Robertson and Norman 1976, Scott 1977, Gottfried 1979) may explain the significant difference between clutch \hat{s} of nonparasitized towhees and thrashers.

Although the distribution of Crissal Thrashers overlaps the breeding range of *M. a. obscurus*, this thrasher has never been reported as a cowbird victim (Friedmann et al. 1977: 19). Of nine *Toxostoma* species sympatric in their breeding ranges with the Brown-headed Cowbird, only the Brown Thrasher (*T. rufum*) is known to be parasitized regularly (Rothstein 1975b, Friedmann et al. 1977). Experiments have demonstrated that this species is a rejecter (Rothstein 1975a). Experiments on LeConte's Thrasher (*T. lecontei*) and California Thrasher (*T. redivivum*) show these species to be accepters (Rothstein pers. comm.).

My experiments demonstrate that the Crissal Thrasher is a true rejecter species (100% rejection). Its two closest relatives, the LeConte's Thrasher and the California Thrasher (Engles 1940), have been sympatric with cowbirds for less than 50 yr (Lloyd Kiff pers. comm.), whereas Crissal Thrashers and cowbirds have apparently been traditionally sympatric (for historical ranges, see Bendire 1895, Grinnell 1909, Bent 1948), particularly in the lower Colorado River valley (see Grinnell 1914, Dawson 1924, Rothstein et al. 1980: 256). Because the

LeConte's Thrasher and the California Thrasher accept cowbird eggs, these species may not have adapted to the rapid expansion of the western (notably California) range of the Brown-headed Cowbird (for review of range changes, see Rothstein et al. 1980). Rothstein (1975b) reasoned that rejection has no adaptive value until a species is parasitized. The probability of being parasitized in Colorado River mesquite woods is high, because cowbirds are abundant (Anderson and Ohmart 1976) and the number of host species is few. Because the nesting biology of the Crissal Thrasher is somewhat similar to that of the sympatric and frequently parasitized accepter, the Abert's Towhee, the presumption that the Crissal Thrasher is, or formerly was, parasitized seems likely. The Crissal Thrasher may, therefore, have evolved ejection behavior in response to repeated cowbird parasitism. Alternatively, defensive behaviors that were developed to protect the nest from predators, debris, or accidents may have served as preadaptations for egg rejection.

Rothstein (1975a) concluded that six features of rejecters were favorable for the evolution of rejection behavior: (1) eggs distinguishable from cowbird eggs, (2) long history of sympatry with cowbirds, (3) large population size, (4) extreme nest sanitation, (5) large beaks, and (6) large, bulky nests. The Crissal Thrasher displays all of these features. Its eggs are blue and unmarked, unlike the cowbird's speckled eggs, and they are larger (Table 1). Crissal Thrashers have been sympatric with Brown-headed Cowbirds for at least 100 yr. They are common in desert riparian regions of the Southwest and Mexico (Phillips et al. 1964). Extreme nest sanitation is illustrated by the following observation. I placed mothballs under a few nests of

various species in an (unsuccessful) effort to deter predators, and the Crissal Thrasher was the only species observed to lift each mothball up in its bill and carry it far from the nest. The long, decurved bill is capable of carrying objects the size of cowbird eggs and larger. The nests are large, stick structures.

Nevertheless, many parasitized accepters demonstrate these six characteristics also (Rothstein 1975a). For example, some birds with bill sizes similar to the Abert's Towhee are able to eject eggs of larger cowbird subspecies [*M. a. ater* and *M. a. artemisiae* (see Rothstein 1975a and range map Rothstein 1978: 156)]. The ratio of host beak length to width of cowbird eggs is 17.6 mm/116.3 mm = 1.08 for the smallest North American rejecter, the Cedar Waxwing (*Bombycilla cedrorum*) (Rothstein 1975a), whereas the ratio is 17.0 mm ($n = 8$)/14.7 mm (Table 1) = 1.16 for the Abert's Towhee-dwarf cowbird relationship. Thus, the Abert's Towhee should be capable of lifting cowbird eggs or similar-sized objects (e.g. mothballs). Rothstein suggested that one of the more critical factors in the evolution of rejection behavior is nest exposure. Nests that are easily found should be more heavily parasitized. Therefore, species such as the Crissal Thrasher that build large nests have had more selective pressure to evolve host defenses such as ejection of foster eggs.

A cowbird laying an egg in the nest of a rejecter species is making a poor investment unless no other host nest can be found. Natural selection on cowbirds should result in the evolution of a counter response to rejection behavior, i.e. cowbirds should reduce their rate of parasitism of unsuitable host species. Even if cowbirds have not evolved innate host preferences, individuals could learn to become more selective after repeated visits to nests built by hosts that always eject foreign eggs (Rothstein 1976b). Thus, by developing rejection behavior, Crissal Thrashers may ultimately have reduced their probability of being parasitized.

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CORRECTION

Dr. David Johnston has pointed out an inaccuracy in my memorial to Franz Sauer (1982 *Auk* 99: 572). To set the record straight: Franz did not chair the doctoral committees of Charles Collins, Peter Wescott, or Storrs Olson. Dr. Pierce Brodkorb chaired the committees of Collins and Wescott; Olson left Gainesville after one year, earned his M.S. at Florida State University, and his doctorate at Johns Hopkins University.— Oliver L. Austin, Jr.