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BROOD PARASITISM OF THE ABERT'S TOWHEE: TIMING, FREQUENCY, AND EFFECTS

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ABSTRACT.—The effects of brood parasitism by the dwarf race of the Brown-headed Cowbird (*Molothrus ater obscurus*) on the nesting success of the Abert's Towhee (*Pipilo aberti*) in the lower Colorado River valley were studied. The frequency of cowbird parasitism varied significantly with time of season. The laying season of cowbirds paralleled that of migratory songbirds, but began a month later than that of the sedentary Abert's Towhee. After an influx of breeding cowbirds, 44% of towhee nests were parasitized. Egg ejection by adult cowbirds caused towhee clutches to decline significantly from a laying average of 2.9 eggs to 1.7 eggs at hatching. The probability of nesting success declined from 0.278, before cowbirds arrived on the breeding grounds, to 0.046 for all parasitized nests. The lack of a significant difference between daily mortality rates of nonparasitized nests before and after cowbirds started breeding indicated that the reduced success of late towhee nests was primarily due to cowbird parasitism. The success of cowbird eggs in towhee nests was also low, suggesting that towhees may not be favorable hosts.

Aridland birds in the southwestern United States have been recorded as hosts of the Brown-headed Cowbird (*Molothrus ater*) only rarely (Friedmann 1963, Friedmann et al. 1977). The dwarf race of the Brown-headed Cowbird (*M. a. obscurus*) is abundant in desert riparian regions of the Southwest (Phillips et al. 1964), and its presence in the Colorado River valley was reported as early as 1886 (Grinnell 1909, 1914). Because the host avifauna in honey mesquite habitat of the lower Colorado River is depauperate compared to other North American regions (Finch 1982), rates of cowbird parasitism could conceivably be high enough to severely damage the reproductive success of the few available hosts. This study describes cowbird parasitism of the Abert's Towhee (*Pipilo aberti*), a desert riparian species endemic to the Southwest (Phillips et al. 1964) and abundant along the lower Colorado River (Anderson and Ohmart 1976a, Meents et al. 1981). Although the Abert's Towhee has been reported as an occasional cowbird host (Friedmann 1963, Friedmann et al. 1977), I know of no information on the timing, extent, or effects of brood parasitism. This study documents (1) seasonal variation in the rate of cowbird parasitism of Abert's Towhees, (2) seasonal variation in towhee nesting success, and (3) effects of ejection of towhee eggs by cowbird adults.

METHODS

This study was conducted in the lower Colorado River valley during the summer of 1979 and the spring and summer of 1980. In May 1979, I established a gridded study plot of 20 ha in honey mesquite (*Prosopis glandulosa*) habitat 10 km north of Ehrenberg, Arizona on the Colorado River Indian Reservation. Plants associated with honey mesquite in my study area were the exotic salt cedar (*Tamarix chinensis*), willow (*Salix gooddingii*), saltbush (*Atriplex lentiformis*), inkweed (*Suaeda torreyana*), arrowweed (*Tesseria sericia*), and mistletoe (*Phoradendron californicum*), a parasite of honey mesquite. The vegetation and avifauna were described in detail by Anderson and Ohmart (1976b, 1977) and Grinnell (1914).

I spent approximately 15 hours each week from January to July 1980 searching for Abert's Towhee nests on or near the study plot. An effort was made to standardize hours spent in search effort in order to sample the breeding population each month without bias. I inspected nests and took notes between 10:00 and 12:00 every second or third day. Desertion due to human disturbance was not important. Only one nonparasitized nest was deserted, and the extended incubation period (over 14 days) at that nest suggested that the eggs were not viable.

Mayfield's (1961, 1975) method was used to calculate daily and total probabilities of nesting success. Because this technique uses only information from the period during which a nest was under observation, it avoids bias introduced by finding nests at different stages of development. The daily mortality rate (DMR) for a given nest stage was estimated by dividing the number of nests that failed by the total number of days all nests were under obser-

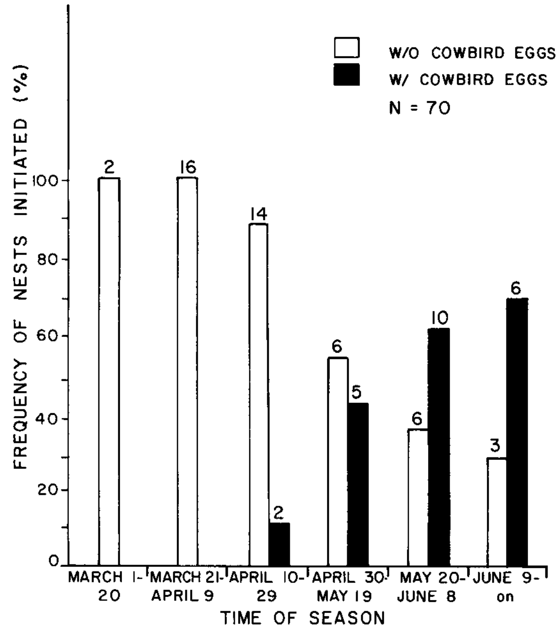

FIGURE 1. Frequency of cowbird parasitism in relation to time of breeding of Abert's Towhees. Number of nests is given above each column.

vation. The probability of survival for one day ($\hat{s}$) was equal to 1 − DMR. The probability of survival through incubation or nestling phases was equal to $\hat{s}^t$ where the exponent t was the development time of embryos (14 days) or nestlings (12 days). To compute the probability of partial losses, Mayfield's formula based on egg or nestling days of exposure was used. The success probability of nest contents for the entire nesting cycle was equal to the product of all $\hat{s}^t$ values times the hatching rate (HR), which was the number of eggs hatched divided by the number of eggs laid. Nests were visited frequently so I used Mayfield's midpoint assumption (see Johnson 1979 for definition). A large-sample estimate of the variance (V) of estimated $\hat{s}$ was obtained by using Johnson's (1979) equation $V(\hat{s}) = EXP^3/(EXP - \text{losses})$, where EXP is the number of nest-days of exposure (Mayfield 1961, 1975) on which a known nest risks failure. The square root of $V(\hat{s})$ is the estimated standard error of $\hat{s}$. To test for variation between DMR's of parasitized and nonparasitized nests before and after cowbirds arrived in the lower Colorado River valley, I used Johnson's (1979) statistic 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 $> z_{\alpha/2}$ then the null hypothesis that $\hat{s}_1 = \hat{s}_2$ (or $DMR_1 = DMR_2$) is rejected. To determine if nesting failure had a constant probability, I divided the breeding season into six periods of 20 days each and calculated total $\hat{s}^t$ for each period.

A G-test of independence was used to determine if the frequency of cowbird parasitism was dependent on time of season. To determine if egg ejection by cowbird adults increased losses from towhee nests, mean clutch size of parasitized and nonparasitized nests at the beginning of incubation (i.e., before any losses) was determined and contrasted with mean clutch size at hatching. I used one- and two-tailed t-tests for paired and unpaired observations in order to test for differences between: (1) initial clutch sizes of parasitized and nonparasitized nests, (2) initial and hatching clutch sizes of parasitized or nonparasitized nests, and (3) hatching clutch sizes of parasitized and nonparasitized nests.

RESULTS

Abert's Towhees in the lower Colorado River valley bred from mid-March until July (Finch 1981a). The first towhee clutch that I found to be parasitized was started (first egg laid) on 22 April and parasitized on 24 April. A total of 22 of 69 towhee clutches (32%) were parasitized. Of these, 14 nests (64%) had one cowbird egg, 5 nests (23%) had two cowbird eggs, and 3 nests (14%) had three cowbird eggs. In addition, one cowbird laid an egg in an inactive towhee nest. Cowbirds began arriving in the study area as early as March but did not start laying until late April. Because cowbirds began breeding more than a month later than towhees, 19 early nests (28% of 69) escaped parasitism. Thus, 44% of the 50 towhee nests initiated during the cowbird's breeding activity were parasitized.

Frequency of parasitism was significantly dependent on time of season, increasing over time ($G = 12.082$, $P < 0.01$) (Fig. 1). By the end of the towhee's reproductive period, the rate of parasitism was 67% (Fig. 1). Towhee nesting success (total $\hat{s}^t$) declined from 0.440 before April 9 to 0.144 in June (Table 1). This decline may have been associated with the frequency of cowbird parasitism.

TABLE 1. Probability of nesting success ($\hat{s}^t$) of Abert's Towhees in relation to the percent of nests parasitized for 20-day intervals through the breeding season.

Time of season	Number of nests	Number of nests parasitized[a]	Probability of success
Before April 9	18	0	0.440
April 10–29	16	2 (12.5)	0.291
April 30–May 19	11	5 (45.0)	0.067
May 20–June 8	16	10 (62.5)	0.142
June 9–on	9	6 (67.0)	0.144

[a] Numbers in parentheses are percent of nests parasitized.

TABLE 2. Within-brood losses of parasitized and nonparasitized nests of the host, Abert's Towhee, and the nest parasite, Brown-headed Cowbird.

Status	Number of nests	Total eggs	Total nestlings	Within-brood losses	
				Eggs	Nestlings
Nonparasitized	47	130	67	5 (4%)	3[a] (4%)
Parasitized	22	53	9	17 (32%)	1[b] (11%)
Cowbird	23[c]	33	6	3 (9%)	4[a] (67%)

[a] Losses due to starvation.
[b] Predation by coachwhip.
[c] One cowbird egg laid in inactive nest.

TABLE 3. The effects of cowbird parasitism on mean clutch size of Abert's Towhees.

Status	n	Initial $\bar{x}$ ± SD	Hatching $\bar{x}$ ± SD
Parasitized	12	2.904 ± 0.668	1.667 ± 1.231
Nonparasitized	26	2.960 ± 0.825	2.769 ± 0.863

PARTIAL LOSSES OF EGGS AND NESTLINGS

During the nestling period, partial losses of chicks were low in nonparasitized nests and only slightly higher in parasitized nests (Table 2). Cowbirds lost 9% of their eggs from towhee nests that remained active (Table 2). From the six cowbird eggs that ultimately hatched, four (67%) nestlings disappeared from nests at which there were no nestling towhee losses. Another cowbird nestling was eaten by a snake along with the whole brood of towhees (Finch 1981b), and one cowbird fledged. In one nest, all towhee eggs had been ejected by cowbird adult(s), and the towhee incubated two cowbird eggs only. Cowbirds ejected all towhee eggs at two other nests, but both of these nests were deserted by towhees. A total of four nests were deserted after one to three towhee eggs and in two instances, one cowbird egg, were removed. Another nest was abandoned after two cowbird eggs disappeared, even though the full towhee clutch and one cowbird egg remained.

In order to avoid possible complications introduced by partial predation, I compared mean initial and hatching clutch sizes of undisturbed nests (Table 3). The mean initial clutch sizes of parasitized and nonparasitized nests were not significantly different ($t_{36} = -0.217$, $P > 0.5$), confirming that parasitized clutches were complete before cowbirds laid in them. The mean hatching clutch size of parasitized nests differed significantly, however, from the mean initial clutch size of these same nests ($t_{11} = 3.586$, $P < 0.01$) and from the mean hatching clutch size of nonparasitized nests ($t_{36} = 3.29$, $P < 0.02$). Initial and hatching mean clutch sizes of nonparasitized nests were not significantly different ($t_{25} = 1.188$, $P > 0.2$). Egg ejection by cowbirds caused a significant change in clutch size of parasitized towhees.

SUCCESS OF PARASITIZED VERSUS NONPARASITIZED NESTS

Use of Mayfield's method (1961, 1975) showed that the total probability of nesting success of towhees before cowbirds began breeding was 0.278; the probability of success of nonparasitized towhees after cowbirds began breeding was 0.307. Daily mortality rates of nonparasitized nests were not significantly different before and after cowbirds arrived on the breeding ground (Tables 4 and 5). The total probability of success of parasitized towhee nests was only 0.046.

Daily mortality rates for different nest stages differed significantly between parasitized and nonparasitized nests (Tables 4 and 5). The incubation stage was most vulnerable to the effects of cowbird parasitism (Tables 4 and 5). Increased mortality of towhee eggs was a result of ejection of host eggs by cowbirds and nest abandonment after egg removal by cowbirds. The nesting success of cowbirds parasitizing towhee nests was also very low (0.044).

DISCUSSION

Because the probability of success of nonparasitized towhee nests did not differ between nestings before and after cowbirds commenced breeding, I conclude that the lower success of late nests was caused by cowbird parasitism. The laying period of cowbirds began in mid-April and paralleled the breeding season of migratory songbirds in the lower Colorado River valley (Anderson and Ohmart 1976a) and also the laying season of cowbirds in central California (Payne 1973). Towhees are resident year-round along the Colorado River (Meents et al. 1981), so they can begin breeding as soon as conditions are favorable. In 1980, conditions were apparently favorable earlier than the traditional breeding period of migratory birds. By breeding more than a month earlier than cowbirds, towhees were successful in producing fledglings.

Cowbirds that laid eggs in towhee nests were no more productive than their hosts. Although Abert's Towhees accepted Brown-headed Cowbird eggs, only one cowbird fledged. One might predict that cowbird nestlings can successfully compete with towhee offspring for parental care because: (1) cowbird parents eject host eggs, and (2) cowbird nestlings have higher growth rates (Ricklefs 1968); but the egg mass of the dwarf race of the Brown-headed Cowbird is 92% less than that of the Abert's Towhee (Finch 1982), and towhees that hatch a

TABLE 4. Daily mortality rates (DMR's) of parasitized and nonparasitized Abert's Towhee broods.[a]

Status	Number of nests	Incubation period		Nestling period	
		Nest	Egg	Nest	Nestling
Nonparasitized					
Before cowbirds	28	0.046 ± 0.014	0.007 ± 0.028	0.028 ± 0.014	0.008 ± 0.010
After cowbirds	19	0.053 ± 0.020	0.000 ± 0.000	0.041 ± 0.274	0.000 ± 0.000
Combined	47	0.047 ± 0.012	0.005 ± 0.002	0.032 ± 0.012	0.006 ± 0.003
Parasitized	22	0.089 ± 0.021	0.037 ± 0.009	0.063 ± 0.043	0.016 ± 0.016

[a] Standard error is included. Nonparasitized status refers to broods present both before and after cowbirds arrived on the breeding grounds.

day or two before cowbirds are more than twice as large as the parasite (e.g., at one nest with one cowbird and one towhee, the five-day old towhee weighed 25.7 g and the three-day old cowbird weighed 4.4 g). During unfavorable feeding conditions, Abert's Towhees may reduce their brood size by selectively feeding larger nestlings. In order to cope with asynchronous hatching (Finch 1981a) and a "brood-reduction strategy" (Ricklefs 1965; Howe 1976, 1978; O'Connor 1978), female cowbirds must find nests before incubation so that ovulation is timed to towhee laying (see also Wiley and Wiley 1980). The only cowbird to fledge was in a nest with no towhee eggs. Most cowbird nestlings disappeared from towhee nests, and I attributed their disappearances to death from starvation (e.g., King 1973).

The high incidence of cowbird losses caused by nest desertion and starvation suggest that towhees are unsuitable hosts. However, high rates of predation during the incubation stage severely reduced the sample of clutches that hatched. It is probable that more cowbirds would have fledged if fewer nests were depredated. I observed four instances of towhee adults feeding fledged cowbirds outside of my study area. Also, the cowbird nestling that was eaten by a snake was as large as its towhee "siblings" and was close to fledging at the time of predation. Nonetheless, cowbirds have a high rate of failure. Although towhees do not eject cowbirds eggs from the nest, as do some other hosts (Rothstein 1975, 1976, 1977), thereby fitting Rothstein's (1975) definition of an "accepter," they will abandon nests (after loss of their own eggs through ejection by adult cowbirds). Abandonment of a nest is probably a response to disturbance rather than a direct reaction to the presence of cowbird eggs (Rothstein 1975). The moderately high rate of parasitism of Abert's Towhees may be due to lack of many host alternatives in honey mesquite habitat. Also, Abert's Towhees replace clutches rapidly after nest failure, providing a plentiful supply of clutches that can be readily parasitized by cowbirds. Cowbirds may ultimately be successful because they lay many eggs (Scott and Ankney 1980).

TABLE 5. Tests of hypotheses that daily mortality rates (DMR's) do not differ between (1) nonparasitized nests before and after cowbirds arrive on the breeding grounds, and (2) parasitized and nonparasitized nests.[a]

Comparison	Incubation period		Nestling period	
	Nest	Egg	Nest	Nestling
BEFORE × AFTER[b]	0.295	0.232	0.438	0.164
NONPAR × PAR[b]	1.897[c]	3.533[c]	0.697	0.644

[a] The ratio of the difference between daily mortality rates to its standard error is asymptotically distributed as a standard normal variate (Johnson 1979). Large values of the ratio indicate significant differences between factors.
[b] BEFORE = nonparasitized nests before cowbirds. AFTER = nonparasitized nests after cowbirds. NONPAR = nonparasitized nests before and after cowbirds. PAR = parasitized nests.
[c] $P < 0.057$ for value of 1.897. $P < 0.001$ for value of 3.533.

Abert's Towhees start breeding earlier than migratory birds in the lower Colorado River valley. Heavy cowbird parasitism may be a selection factor for early towhee breeding because the probability of producing fledglings after cowbirds begin laying is very low (though possible). The surest way to avoid parasitism is to breed before cowbirds arrive. The cowbirds' laying season may be adjusted to the breeding of migratory songbirds, which arrive in the Colorado River valley in March and April. By June, many migratory birds, some of which probably serve as cowbird hosts (e.g., Lucy's Warblers, *Vermivora luciae* [Friedmann et al. 1977]), have already left the study area. Cowbirds may adapt to reduced host abundance either by moving into other habitats or by parasitizing more heavily those species that remain in the study area (e.g., Abert's Towhees and Black-tailed Gnatcatchers, *Polioptila melanura* [see Finch 1982]). The increase in the frequency of parasitized towhee nests from 45% in May to 67% in June supports the latter idea. Low nesting success caused by cowbird parasitism and predation combined with the added effects of a declining insect food supply (Cohan et al. 1978), and high air temperatures (Finch 1983) may suffice to explain why the Abert's Towhee did not breed later than July in this study area.

Although the Abert's Towhee is currently abundant, the future for this species should be put in perspective. Its endemism, sedentary habits, preference for a restricted habitat, and role as host to the Brown-headed Cowbird suggest that its survival along the Colorado River could be jeopardized. Desert riparian habitat is steadily diminishing in the southwestern U.S. because of development, agriculture, and recreation (for general review, see Johnson and Jones 1977). Cottonwood and mesquite communities along the lower Colorado have greatly declined in recent years (Ohmart et al. 1977), and have been replaced in many areas by the exotic salt cedar, a habitat that supports fewer birds than native plant communities (Anderson et al. 1977). My study area, in particular, is scheduled for conversion to agricultural fields. Unless destruction of riparian habitat is controlled, the Abert's Towhee along the lower Colorado River may eventually be confined to protected lands such as the Cibola and Havasu National Wildlife Refuges.

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