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RESPONSES OF FIVE HOST SPECIES TO COWBIRD PARASITISM[1]

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Abstract. Responses of the Red-eyed Vireo (*Vireo olivaceus*), Yellow Warbler (*Dendroica petechia*), Northern Cardinal (*Cardinalis cardinalis*), Chipping Sparrow (*Spizella passerina*), and Song Sparrow (*Melospiza melodia*) to Brown-headed Cowbird (*Molothrus ater*) parasitism were determined from nest records compiled at the Ontario Nest Record Scheme. Nest desertion was the principal mode of rejection of cowbird eggs. The Yellow Warbler also rejected parasite eggs by burying clutches under a second nest bottom. The probability of rejection did not vary during the breeding season or between multiply- and singly-parasitized pairs. Possible stimuli used by hosts to recognize parasitism are discussed.

Key words: Brown-headed Cowbird; parasitism; desertion; Red-eyed Vireo; Yellow Warbler; Northern Cardinal; Chipping Sparrow; Song Sparrow.

INTRODUCTION

The Brown-headed Cowbird (*Molothrus ater*) parasitizes over 50% of the nests in some passerine populations (Elliott 1978, Zimmerman 1983) and is known to reduce reproductive success in many species (Mayfield 1960, Friedmann 1963, Payne 1977, Clark and Robertson 1981, Finch 1983). Because cowbird parasitism usually reduces host nesting success, adaptations that mitigate the effects of parasitism should be selected, if these adaptations are less costly than accepting cowbird eggs (Rothstein 1975, Robertson and Norman 1977). Some species eject cowbird eggs (Rothstein 1975, 1977; Finch 1982) and other species desert parasitized nests (Rothstein 1976, Clark and Robertson 1981). Yellow Warblers (*Dendroica petechia*) bury cowbird eggs under a second nest bottom (Clark and Robertson 1981).

I studied the Red-eyed Vireo (*Vireo olivaceus*), Yellow Warbler, Northern Cardinal (*Cardinalis cardinalis*), Chipping Sparrow (*Spizella passerina*), and Song Sparrow (*Melospiza melodia*) to determine if these species reject cowbird eggs. For each species, I compared nest-desertion rates of parasitized and unparasitized nests. For the Yellow Warbler, I also compared egg-burial rates of parasitized and unparasitized nests.

Hosts may desert parasitized nests because of the presence of cowbird eggs. Alternatively, Rothstein (1975) suggested that hosts may desert parasitized nests because of human disturbance. I examined the tenability of this alternative explanation by comparing human visitation rates at parasitized and unparasitized nests.

Nest desertion and egg burial cause delays of several days (Clark and Robertson 1981) in a pair's effort to reproduce. Clark and Robertson (1981) argued that these delays are more costly late in the breeding season. If this is true, then acceptance rates may be higher late in the breeding season. I evaluated whether acceptance rates were higher late in the breeding season.

The cost of accepting parasite eggs may increase as the number of parasite eggs in the nest increases. Consequently, rejection may be more frequent in multiply-parasitized hosts (≥two cowbird eggs) than in pairs parasitized with a single cowbird egg. I evaluated this possibility for each species.

METHODS

Data on cowbird parasitism and host responses were collected from nesting records compiled in the Ontario Nest Record Scheme housed at the Royal Ontario Museum in Toronto, Ontario. Data were assessed from Ontario locations south of the French River, Lake Nipissing, and Mattawa River line (46°20′N to 45°55′N) where cowbird densities are high (Speirs 1985).

Cards for parasitized and unparasitized nests that were observed during the egg-laying period were examined. Only nests observed over the egg-laying period were assessed, as parasitized nests found later would include only pairs which had accepted parasitism. All parasitized nests were active at the time of parasitism. Nests where

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humans ejected cowbird eggs were not considered.

Host responses were classified into four categories: deserted nest, buried eggs, accepted parasitism, and no parasitism/normal nesting. Pairs were considered to have deserted if nest contents remained intact, but were no longer tended by the hosts. If this happened within 3 days of parasitism, hosts were considered to have deserted in response to parasitism. A host was judged to have buried the eggs if the observer recorded egg burial. Hosts were considered to have accepted parasitism if the pair remained active around the nest for at least 3 days after parasitism occurred. Unparasitized pairs who continued laying or incubating eggs for at least 3 days after discovery were considered to be nesting normally. Nests depredated within 3 days of parasitism or observer discovery were not considered.

All Red-eyed Vireo, Northern Cardinal, and Song Sparrow nests that met these criteria were analyzed. Because of the profusion of Yellow Warbler and Chipping Sparrow records, nest records of these species were sampled that fulfilled the above criteria and resulted in an even distribution of nests throughout the study area. Eighty-five Red-eyed Vireo, 256 Yellow Warbler, 97 Northern Cardinal, 161 Chipping Sparrow, and 139 Song Sparrow records were examined.

To evaluate whether acceptance rates increased late in the breeding season, I compared acceptance rates of nests parasitized before the peak of clutch initiation, with those parasitized after the peak of clutch initiation. The half-month period having the largest number of nests initiated was defined as the peak of clutch initiation. The peak of clutch initiation was 16 to 31 May for the Northern Cardinal and Song Sparrow, and 1 to 15 June for the remaining species. Breeding occurred between 1 May and 31 July for all species.

To compare human visitation rates of parasitized and unparasitized nests, I converted visitation rate values to ranks, and then applied a *t*-test to the ranks. This is equivalent to a Mann-Whitney *U*-test (SAS Institute 1985).

RESULTS

Parasitized nests were deserted more often than unparasitized nests (Table 1) in the Red-eyed Vireo ($\chi^2 = 5.66$, df = 1, $P = 0.02$), Yellow Warbler ($\chi^2 = 30.33$, df = 1, $P < 0.001$), Northern Cardinal ($\chi^2 = 30.52$, df = 1, $P < 0.001$), Chipping Sparrow ($\chi^2 = 34.50$, df = 1, $P < 0.001$), and Song Sparrow ($\chi^2 = 16.41$, df = 1, $P < 0.001$). Desertion rates at parasitized nests ranged from 23% to 52% and from 1% to 12% at unparasitized nests. Yellow Warblers buried parasitized clutches in 50% of parasitized nests, but egg burial was not recorded in 146 unparasitized warbler nests ($\chi^2 = 93.19$, df = 1, $P < 0.001$). Considering both desertion and cowbird egg burial, Yellow Warblers rejected cowbird eggs in 73% of parasitized nests. Cowbird eggs were embedded in the bottom of one Red-eyed Vireo nest, one Northern Cardinal nest, and one Chipping Sparrow nest, and probably resulted from cowbird parasitism of incomplete nests that the host continued building after parasitism. A cowbird egg was broken in one Song Sparrow nest. No instance of cowbird egg ejection was recorded.

TABLE 1. Desertion rates (%) and human visitation rates at parasitized and unparasitized nests.

Species	*n*	% nests deserted	Days between visits ± SD
Red-eyed Vireo			
Parasitized	44	34	3.9 ± 2.2
Unparasitized	41	12	3.3 ± 1.7
Yellow Warbler			
Parasitized	110	23[a]	4.1 ± 2.9
Unparasitized	146	1	4.6 ± 3.1
Northern Cardinal			
Parasitized	27	52	4.1 ± 2.2
Unparasitized	70	4	4.9 ± 2.0
Chipping Sparrow			
Parasitized	100	52	3.4 ± 1.7
Unparasitized	61	7	4.0 ± 1.8
Song Sparrow			
Parasitized	78	27	3.5 ± 2.0
Unparasitized	61	2	3.7 ± 1.7

[a] In addition to desertion, Yellow Warblers buried cowbird eggs in 50% of parasitized nests.

Human visitation rates at parasitized and unparasitized nests (Table 1) were equal in the Red-eyed Vireo ($t = 1.02$, df = 83, $P = 0.31$), Yellow Warbler ($t = 1.85$, df = 254, $P = 0.07$), Northern Cardinal ($t = 1.64$, df = 95, $P = 0.11$), Chipping Sparrow ($t = 1.33$, df = 159, $P = 0.19$), and Song Sparrow ($t = 0.60$, df = 137, $P = 0.55$).

Acceptance rates of nests initiated before vs. after the peak of clutch initiation (Table 2) did not differ for the Red-eyed Vireo ($\chi^2 = 0.01$, df

TABLE 2. Percent acceptance rates (*n*) relative to the peak of clutch initiation, and in singly- vs. multiply-parasitized nests.

Species	% acceptance rate		% acceptance rate	
	Before peak (*n*)	After peak (*n*)	Singly parasitized (*n*)	Multiply[a] parasitized (*n*)
Red-eyed Vireo	62 (16)	64 (28)	58 (24)	70 (20)
Yellow Warbler	25 (28)	28 (82)	28 (86)	25 (24)
Northern Cardinal	25 (8)	52 (19)	44 (25)	50 (2)
Chipping Sparrow	53 (28)	44 (72)	52 (62)	45 (38)
Song Sparrow	72 (48)	70 (30)	71 (38)	73 (40)

[a] Nests with two or more cowbird eggs.

= 1, $P = 0.91$), Yellow Warbler ($\chi^2 = 0.10$, df = 1, $P = 0.75$), Northern Cardinal ($\chi^2 = 1.74$, df = 1, $P = 0.19$), Chipping Sparrow ($\chi^2 = 0.67$, df = 1, $P = 0.41$) and Song Sparrow ($\chi^2 = 0.08$, df = 1, $P = 0.78$).

Acceptance rates of singly- and multiply-parasitized nests (Table 2) did not differ for the Red-eyed Vireo ($\chi^2 = 0.64$, df = 1, $P = 0.42$), Yellow Warbler ($\chi^2 = 0.08$, df = 1, $P = 0.78$), Chipping Sparrow ($\chi^2 = 0.45$, df = 1, $P = 0.50$) and Song Sparrow ($\chi^2 = 0.02$, df = 1, $P = 0.89$). Sample size of multiply-parasitized Northern Cardinal nests was insufficient to permit analysis.

DISCUSSION

Many species experience reduced nesting success when parasitized by the cowbird, including the Red-eyed Vireo (Southern 1958), Yellow Warbler (Clark and Robertson 1981), and Song Sparrow (Smith 1981). Given the selective pressure on hosts, it is reasonable to expect parasitized species to evolve methods of defence against cowbird parasitism. One possible method of defence would be for pairs to desert parasitized clutches. In this study desertion rates were much higher (between 23% and 52%) in parasitized nests than in unparasitized nests (between 1% and 12%). This suggests that desertion is an adaptive response to parasitism. Desertion in response to parasitism has previously been found in the Cedar Waxwing, *Bombycilla cedrorum* (Rothstein 1976), and Yellow Warbler (Clark and Robertson 1981), and suggested for several other species including the Red-eyed Vireo (Southern 1958) and Northern Cardinal (Friedmann 1963).

Another possible method of defence is the burial of cowbird and host eggs under a new nest bottom and the subsequent laying of another clutch. This behavior is practiced by the Yellow Warbler, but not by the other species. Eggs were not buried in unparasitized nests. The frequency of burial (50%), desertion (23%), and acceptance (27%) was very similar to that seen in Clark and Robertson's (1981) study.

Some host species eject cowbird eggs from their nests. Cowbird egg ejection was not detected in this study although it may have occurred. Egg ejection is difficult to detect in naturally parasitized nests because hosts which eject cowbird eggs do so within a few hours of parasitism (Rothstein 1977). However, experimental placement of cowbird eggs in nests of the five host species revealed little or no ejection (Rothstein 1975).

Clark and Robertson (1981) suggested that delays due to renesting become more costly late in the breeding season. They consequently suggested that the rate of acceptance increases late in the breeding season. In this study, acceptance rates did not increase in nests initiated after the peak of clutch initiation. The period after the peak of clutch initiation lasted 1.5 to 2 months for all species studied herein, and delays due to renesting take a maximum of 9 days in the Yellow Warbler (Clark and Robertson 1981). Therefore, most parasitized pairs which nested after the peak of clutch initiation probably had sufficient time to renest.

Nest desertion and egg burial was not more frequent in multiply-parasitized nests. Elliott (1978) also found that rejection rate was no higher in multiply-parasitized nests.

The exact stimulus that hosts respond to before parasite eggs are rejected remains unclear. One possible stimulus is the presence of cowbird egg(s) in a parasitized nest. Alternatively, desertion or egg burial may occur when hosts detect a female cowbird at their nest (Rothstein 1975). Another possibility suggested by Rothstein (1975) is that hosts desert in response to altered clutch sizes created by female cowbirds adding their own egg(s) or removing host egg(s). Rothstein (1975) also suggested that parasitized nests may

be deserted because of disturbance by human observers, but parasitized and unparasitized nests in this study were visited equally often. This suggests that desertion due to human disturbance would occur equally frequently at parasitized and unparasitized nests.

Pairs with complete clutches that subsequently become parasitized may be more likely to accept parasitism than hosts which become parasitized when they have few or none of their own eggs (Rothstein 1976, Clark and Robertson 1981). The relationship between number of host eggs laid when parasitized and acceptance rate may explain an apparent discrepancy in my results and those of Rothstein (1975). Both studies investigated host response to parasitism in the same species, but acceptance rates were much higher in Rothstein's (1975) work. Acceptance rates in this study ranged from 27% to 73%. Acceptance rates in Rothstein (1975) ranged from 66% to 100%. However, Rothstein (pers. comm.) studied only nests which already had at least two host eggs when parasitized. In this study, many nests had less than two eggs when parasitized. The difference in results may have occurred because acceptance of parasitism increases as number of host eggs laid increases.

Another possible explanation for the difference between my results and Rothstein's (1975) involves the precise stimulus which causes host species to desert or bury eggs after being parasitized. If hosts desert or bury eggs because they have discovered a female cowbird at their nest, then little or no desertion should take place if nests are artificially parasitized by a human experimenter (as in Rothstein 1975), but considerable desertion may take place if the parasitism occurs naturally (as in this study).

The Red-eyed Vireo, Yellow Warbler, Northern Cardinal, Chipping Sparrow, and Song Sparrow frequently desert parasitized nests. The Yellow Warbler also frequently buries parasitized clutches. Unlike egg-ejecting species (see Rothstein 1975), however, parasite eggs are also frequently accepted by the studied species. The factors involved in governing whether a parasitized pair will desert, bury, or accept a parasitized clutch require clarification. In general, pairs may accept parasite egg(s) if the cost of a replacement nest and clutch is higher than the cost of acceptance.

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