A COMPARATIVE STUDY OF COWBIRD PARASITISM IN YELLOW-HEADED BLACKBIRDS AND RED-WINGED BLACKBIRDS

CATHERINE P. ORTEGA AND ALEXANDER CRUZ

Environmental, Population and Organismic Biology Department, University of Colorado, Boulder, Colorado 80309-0334 USA

ABSTRACT.—We compared Yellow-headed Blackbirds (*Xanthocephalus xanthocephalus*) and Red-winged Blackbirds (*Agelaius phoeniceus*) to determine possible explanations for the lack of Brown-headed Cowbird (*Molothrus ater*) parasitism on Yellow-heads. Twenty-three cowbird eggs were cross-fostered from Red-winged Blackbird nests to Yellow-headed Blackbird nests. Eleven of the cross-fostered cowbird eggs hatched, and seven fledged. Of the four that hatched but failed to fledge, three disappeared and one starved as did all except one of its Yellow-headed Blackbird siblings. Of the 12 cowbird eggs that did not hatch, 8 were preyed upon and 4 were inviable. Cowbirds grew at the same rate in Yellow-headed and Red-winged blackbird nests. Differences in breeding characteristics between Yellow-headed and Red-winged blackbirds may help explain the lack of cowbird parasitism of Yellow-headed Blackbird nests. For Yellow-headed Blackbirds the breeding season had an earlier peak of nest initiation, the abandonment rate of active nests was dramatically higher at the end of the season, and nestlings were more heavily parasitized with mites than were Red-winged Blackbird nestlings. *Received 18 December 1990, accepted 4 July 1990.*

AVIAN brood parasitism is a reproductive strategy where parasitic birds lay their eggs in nests of other birds and depend on their hosts to incubate the eggs and raise their offspring. In this dynamic parasite-host relationship, there are constraints upon the parasite, antiparasite defenses by the host, and counter adaptations by the parasite (Payne 1977). Parasites may be constrained by the host's breeding season, egg size, incubation period, diet, acceptance of the parasitic egg and nestling, host growth rate, and postfledging (foster) parental care (Friedmann 1963, Payne 1977). Antiparasite defense mechanisms commonly employed by hosts are aggression toward intruding parasites (Robertson and Norman 1976) and rejection of parasitic eggs through ejection, damage, desertion, or building a new nest floor over the parasitized clutch (Rothstein 1975a, b).

The marsh-nesting Yellow-headed Blackbird (*Xanthocephalus xanthocephalus;* hereafter Yellow-head) is a locally abundant bird in western North America. Its colonial breeding habits provide an opportunity to experiment on large numbers of individuals. Brown-headed Cowbird (*Molothrus ater*) parasitism on Yellow-heads appears to be only "accidental" (Friedmann et al. 1977, Ortega and Cruz 1988), yet Yellow-heads accept cowbird eggs (Ortega and Cruz 1988). The relationship between cowbirds and Yellow-heads is of particular interest because Yellow-heads can readily be compared with the related Red-winged Blackbird (*Agelaius phoeniceus;* hereafter Red-wing). Red-wings also nest in marshes and have similar breeding biology, and they are parasitized frequently by cowbirds (Hergenrader 1962, Friedmann et al. 1977, Ortega and Cruz 1988).

Although extensive egg manipulation experiments have been performed on species that reject parasitic eggs (Victoria 1972; Rothstein 1974, 1976, 1977, 1982; Finch 1982; Cruz and Wiley 1989), and some cowbird mount experiments have been performed on species with low or zero rates of parasitism (Folkers 1982), most studies of brood parasitism have focused on species that commonly serve as hosts. Our purpose was to investigate possible explanations for the lack of cowbird parasitism on Yellow-heads. We attempted to experimentally test two hypotheses: first, that Yellow-heads are above the upper size limit of successful hosts (i.e. the host siblings may outcompete cowbird nestlings for food), and second, that there is an aggressive behavioral response by Yellow-heads which deters cowbirds.

STUDY AREA AND METHODS

We investigated Red-winged and Yellow-headed blackbird nests from 1985 through 1986 in nine cattail (*Typha latifolia* and *T. angustifolia*) marshes and two flooded willow (*Salix* sp.) stands in Boulder County, Colorado. All study sites were surrounded by open fields, primarily pastoral and agricultural. The two willow stands and four marshes were on the shores of Boulder Reservoir (approximately 103 surface hectares at low water level). Within the breeding season, the water fluctuated as much as 1 m; the low point occurred during the nest-building phase. Two sites were along the periphery of small ponds (both approximately 1.2 surface ha). No Yellow-heads nested in the above sites, whereas Red-wings nested in all. Both Yellow-heads and Red-wings nested in three additional marshes. One of these marshes (Walden Ponds) is a reclaimed gravel pit (9.3 surface ha) and was surrounded by a patchy distribution of cottonwoods (*Populus sargentii*) and willows as well as weedy fields. Approximately 100 Yellow-heads and 30 Red-wings nested during both 1985 and 1986 in this marsh. Two of the three marshes (Olive east and Olive south, approximately 1.6 and 4 surface ha), divided by a small road, supported at least 800 nesting Yellow-heads and 50 Red-wings in 1986. These two marshes, studied only in 1986, were surrounded by weedy fields and agricultural land.

Red-wing and Yellow-head nests were found and identified with individually numbered tags. We visited each nest every 1–3 days and recorded nest contents. Nestlings were marked individually by color-coding their tarsi with permanent ink. They were weighed and measured at each visit.

Experimental parasitism.—We cross-fostered 23 cowbird eggs from Red-wing nests to 23 Yellow-head nests during the egg-laying stage and early incubation. Eggs transferred between nests were, to the best of our knowledge, the same age within a day or two of the host eggs.

Measuring eggs and nestlings.—Eggs were weighed to the nearest 0.1 g on a 10-g Pesola spring scale. Egg width and length were measured to the nearest 0.01 mm with a Mitutoyo metal dial caliper. In 1986, nestlings were weighed to the nearest 0.1 g on 10-g, 50-g, and 100-g Pesola spring scales. We measured to the nearest 0.01 mm tarsus length, culmen length, width of bill at loral feathering (gape width), and length of ninth primary, according to Baldwin et al. (1931).

Breeding season analysis.—For visual display, the breeding season (1 May to 30 July) was divided arbitrarily into 1-week periods. For statistical analysis, each day was considered as a category. To calculate the number of nests initiated, we used only nests with known date of initiation (i.e. nests that were found during the egg-laying stage or that we followed through to the hatching stage and could estimate dates of initiation). Nest initiation was considered the date of the first egg laid. For the analysis of number of active nests, we included all nests that were followed for at least two 1-week periods (two visits or more), whether or not we knew the initiation date.

Aggression experiments.—To test aggression toward intruders at nest sites, we placed models 1 m from Yellow-head and Red-wing nests for 5 min. Only birds in the phases of egg laying or early incubation were tested. Models were birds mounted in a lifelike perching position, presented on poles, slightly above and facing the nest. At each nest tested, we used an adult female cowbird and a control model that was either an adult White-crowned Sparrow (*Zonotrichia leucophrys*) or an immature Western Meadowlark (*Sturnella neglecta*). These species were selected because both occurred in the surrounding area; therefore, blackbirds may have been as familiar with them as they were with cowbirds. The controls were considered appropriate because they posed relatively little competition for food and nesting resources.

For half the experiments, cowbirds were used first; and for the remainder, control models were used first. We allowed 10 min between cowbird and control tests. Observations were made as far away as possible, usually >40 m. In a few cases, however, we observed the test birds from as close as 20 m because of the density and height of the cattails. Both blackbird species were initially disturbed by our approach and left their nest sites, but most returned quickly after we left the immediate nest vicinity. We did not use a blind. In all cases, the test bird returned to the nest site within the 5-min period. Because colonial nesting may aid in providing defense against brood parasites, our observations included all birds responding to the mount.

We classified observed behaviors in order of increasing aggressiveness as follows: 0 was normal behavior about the nest, with no visible or audible response directed toward the mount; 1, distracted behavior without alarm calls or other vocalizations; 2, fly-by investigation; 3, close investigation (within 1 m) without alarm calls or other vocalizations; 4, distracted behavior with alarm calls or other vocalizations directed toward the mount; 5, skulking or hovering near or over the nest and mount; 6, mob (more than one individual) skulking or hovering near or over nest and mount; 7, attacking mount with physical contact; and 8, mob attacking mount with physical contact.

We classified behavior duration as follows: 1 was brief response or response given once; 2, response given repeatedly for up to 1 min; 3, response given repeatedly for 1–2 min; 4, response given repeatedly for 2–3 min; 5, response given repeatedly for 3–4 min; and 6, response given repeatedly for 4–5 min.

We calculated aggressive values of behavioral responses as the sum of the products of behavioral response values and duration of response values (Robertson and Norman 1976).

Statistical analyses.—The two-tailed Mann-Whitney *U*-test was used to test for differences between Yellow-heads and Red-wings in the time lapse from nest construction to egg laying (Zar 1984). Kolmogorov-Smirnov goodness-of-fit test was employed to detect

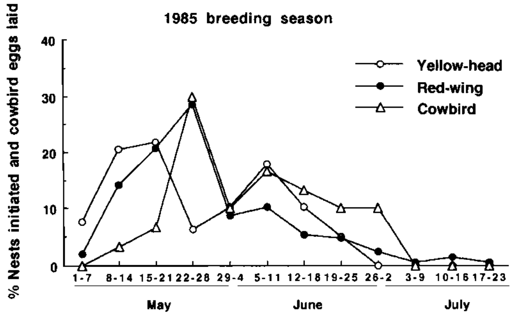

Fig. 1. Percentages of Red-winged and Yellow-headed blackbird nests initiated and Brown-headed Cowbird eggs laid in Red-winged Blackbird nests during 1985 in Boulder County, Colorado.

differences in the breeding season between years within a species and between species within a year. To test whether the proportion of abandoned nests varied as the breeding season progressed, we used analysis of variance to test the significance of the regression. Because proportions do not form a normal distribution (Zar 1984), we submitted the proportions to arcsine transformation. We used G log-likelihood tests with Williams correction to analyze all contingency-table data (e.g. predation rates between Yellow-heads and Red-wings, cowbird eggs that did not hatch between Yellow-heads and Red-wings, and aggression occurrences toward cowbird mounts between Yellow-heads and Red-wings) (Sokal and Rohlf 1981). The binomial distribution was employed to test whether the number of cowbirds fledged (from a group of Yellow-heads that hatched but were not preyed upon) was significantly more than those that did not fledge (Zar 1984). The Kolmogorov-Smirnov test was used to assess normality of growth data (Sokal and Rohlf 1981). We used linear regression to test for the significance of growth slopes before using multiple analysis of variance (MANOVA) to test for differences between growth slopes of cowbird nestlings in Yellow-head and Red-wing nests (Hull and Nie 1981). We used a two-tailed Wilcoxon paired-sample test to detect differences between responses to cowbird models and control models (Zar 1984). Standard deviations are provided for all mean values.

RESULTS

Breeding season.—The length of time that cowbirds could have observed Yellow-headed and Red-winged blackbird nests under construction was the same. The mean time between the beginning of nest construction and first egg laid was 4.23 ± 2.05 days (range: 2–10 days) for Yellow-heads and 4.36 ± 2.14 days (range: 2–11 days) for Red-wings. There was no difference in this time lapse between species ($P = 0.8944$, two-tailed Mann-Whitney test, $U = 871.0$, $z = 0.1327$).

The breeding season of Red-wings did not differ between 1985 and 1986 ($P = 0.1106$, maximum $D_i = 37$, Kolmogorov-Smirnov); however, that of the Yellow-head did ($P = 0.0072$, maximum $D_i = 36$, Kolmogorov-Smirnov). The breeding season differed between Yellow-heads and Red-wings in both years (1985: $P = 0.0080$, maximum $D_i = 18$; 1986: $P = 0.0001$, maximum $D_i = 15$; Kolmogorov-Smirnov).

In 1985, Yellow-heads began egg laying in the first week of May. The number of new nests peaked in mid-May and again in the first week of June (Fig. 1). Nest initiation of Red-wings peaked sharply in the fourth week of May, and their season lasted three weeks longer than Yellow-head season. Cowbirds laid only 10% of their eggs in the first 3 weeks of May, whereas Yellow-heads had initiated 50% and Red-wings had initiated 37% of their nests by this time. Cowbirds laid the highest proportion of eggs at the same time Red-wing nest initiation showed the highest peak; they continued to lay at proportions of 10–17% during July as the availability of Red-wing nests declined.

In 1986, initiation of Yellow-head nests peaked sharply in the second week of May, and 69% of Yellow-head nests were initiated by 21 May (Fig. 2). In contrast, only 44% of the Red-wing nests had been initiated by this time, and only 16% of cowbird eggs had been laid by 21 May.

As the Yellow-head breeding season progressed, the possibility of abandonment increased (Fig. 3). In both years, significantly higher proportions of active Yellow-head nests were abandoned as the season progressed and fewer nests were active (1985: $P < 0.001$, ANOVA $F = 28.64$, residual df = 9, $r^2 = 0.761$; 1986: $P < 0.005$, ANOVA $F = 25.019$, residual df = 8, $r^2 = 0.758$). This contrasts with the rate of abandonment of Red-wing nests, which did not increase with their breeding season in either year (1985: $P > 0.50$, ANOVA $F = 0.068$, residual df = 11, $r^2 = 0.068$; 1986: $P > 0.50$, ANOVA $F = 0.391$, residual df = 10, $r^2 = 0.038$).

Predation.—Overall predation was 48.5% for Yellow-heads and 48.3% for Red-wings in the study areas where the two species coexisted. There was no statistical difference between predation rates of Yellow-heads and Red-wings for each of the study sites by year (Table 1).

Parasitism.—Rates of parasitism on Red-wings

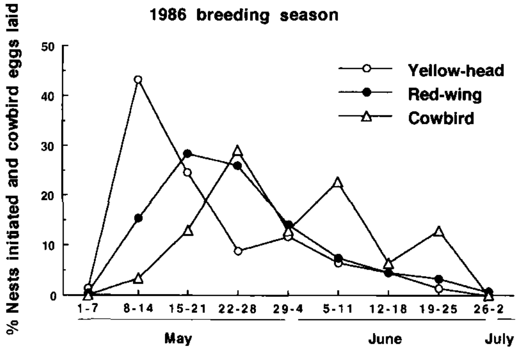

Fig. 2. Percentages of Red-winged and Yellow-headed blackbird nests initiated and Brown-headed Cowbird eggs laid in Red-winged Blackbird nests during 1986 in Boulder County, Colorado.

varied from 0% to 40.9%, depending on year and site. Overall parasitism rates in active Red-wing nests were 7% in 1984, 13% in 1985, and 10% in 1986. Parasitism rates for each site where both Red-wings and Yellow-heads nested are listed in Table 2.

Egg sizes.—The average cowbird egg measured 16.3 ± 0.62 mm by 20.9 ± 1.06 mm (n = 78); the average Yellow-head egg was 18.1 ± 0.57 mm by 26.33 ± 1.16 mm (n = 842); and the average Red-wing egg measured 18.0 ± 0.61 mm by 25.0 ± 1.27 mm (n = 1,614).

Cross-fostering success.—All of the 23 cowbird eggs cross-fostered into Yellow-head nests were accepted; 11 hatched and 7 fledged. Of the 4 that did hatch but failed to fledge, 3 were preyed upon, and 1 died of starvation, as did all but one of its foster Yellow-head siblings. Of the 8 cowbirds that hatched but were not preyed upon, significantly more (7) cowbirds fledged than did not (binomial distribution, $P = 0.03125$). Of the 12 cowbird eggs which did not hatch, 8 (66.7%) were preyed upon, and 4 (33.3%) remained intact but did not hatch. Of all cowbird eggs cross-fostered into Yellow-head nests, 17.4% (4/23) were inviable; this is similar to the 14.9% (10/67) of cowbird eggs in Red-wing nests that did not hatch ($P > 0.75$, $G_{adj} = 0.074$).

Cowbird nestling growth.—Growth curve slopes for all measurements were significant. Cowbirds raised by Red-wings and by Yellow-heads were similar with respect to growth slopes of

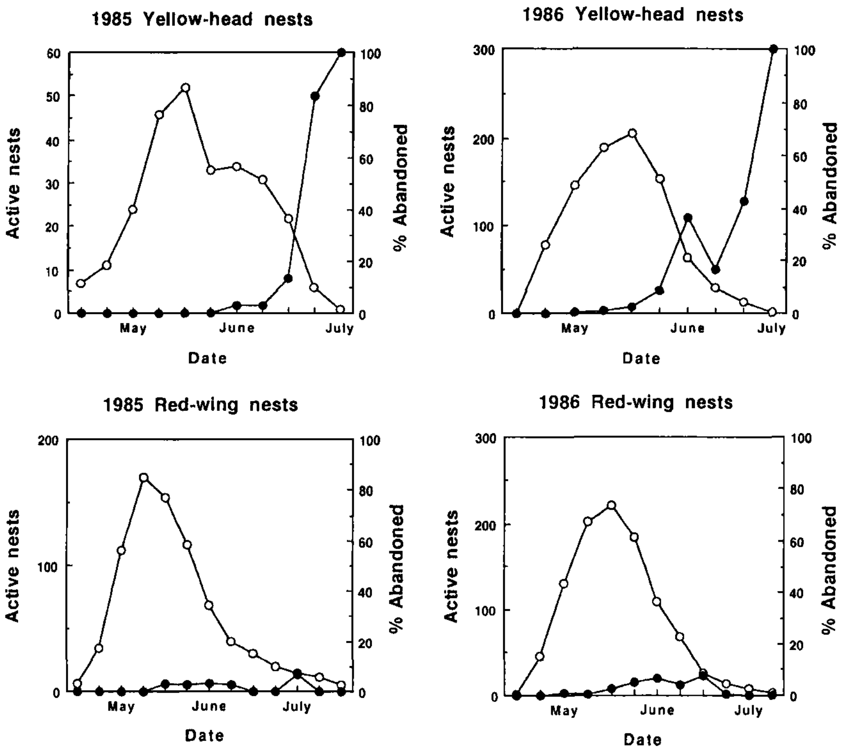

Fig. 3. Number of Yellow-headed and Red-winged blackbird nests active (O) and percent abandoned (●) in Boulder County, Colorado, 1985–1986.

TABLE 1. Number (and percentage) of Yellow-headed Blackbird (YHB) and Red-winged Blackbird (RWB) nests preyed upon at sites where Yellow-headed and Red-winged blackbirds coexisted, Boulder County, Colorado.

		Number (%) of nests preyed upon			
Study site	Year	YHB	RWB	G_{adj}	P
Walden Ponds	1985	39/71 (54.9)	8/12 (66.7)	1.362	$P > 0.10$
Walden Ponds	1986	42/77 (54.5)	11/18 (61.1)	0.250	$P > 0.50$
Olive—east	1986	45/91 (49.5)	3/5 (60.0)	0.193	$P > 0.50$
Olive—south	1986	4/29 (13.8)	6/23 (26.0)	1.179	$P > 0.10$

weight, tarsus length, culmen length, gape width, and length of ninth primary (Table 3).

Aggression experiments.—The mean aggressive response values by Yellow-heads were 5.25 ± 11.71 (range: 0–40) toward the cowbird model and 7.25 ± 10.23 (range: 6–34) toward the control. There was no difference in Yellow-head response toward cowbirds and controls ($P >$ 0.20, two-tailed Wilcoxon paired-sample, $T- =$ 42, $T+ = 27$, $n = 12$). There were only two cases (16.7% of 12 tests) of Yellow-head aggression toward cowbird models. In both cases, the model was attacked physically. In both cases, however, the same individuals also attacked the control model. This strongly contrasts with Red-wing response toward cowbird models. The mean aggressive response values of Red-wings were 23.47 ± 13.18 (range: 0–48) toward the cowbird model and 6.05 ± 10.48 (range: 0–36) toward the control. Of 19 experiments, Red-wings made physical contact with 10 cowbird models (52.6% of 19 tests) and hovered over or otherwise threatened 7 (36.8% of 19 tests) others, whereas the control models were only struck twice ($P < 0.001$, two-tailed Wilcoxon paired-sample, $T- = 3.5$, $T+ = 149.5$). Red-wings were significantly more aggressive than Yellow-heads ($P < 0.001$, $G_{adj} = 16.844$, df = 1, G log-likelihood test with Williams correction). Red-wings displayed aggressive behavior in 17 (89.5%) of 19 tests, whereas Yellow-heads displayed aggressive behavior in only 2 (16.7%) of 12 tests.

TABLE 2. Number (and percentage) of Red-winged Blackbirds parasitized by Brown-headed Cowbirds at sites where Red-winged and Yellow-headed blackbirds coexisted, Boulder County, Colorado. Number of nests include some which could not be followed up.

Study site	Year	Number (%) of nests parasitized
Walden Ponds	1985	9/22 (40.9)
Walden Ponds	1986	4/20 (20.0)
Olive—east	1986	2/8 (25.0)
Olive—south	1986	3/28 (10.7)

DISCUSSION

Host size–growth rate of cowbirds.—As stated in Hypothesis 1, Yellow-heads are above the upper size limit of successful hosts, and, nestling cowbirds cannot compete with Yellow-head foster siblings. Although our sample size is small, the results demonstrate that, of those cowbirds hatched but not preyed upon, a significant proportion of cowbirds fledged. Therefore, this hypothesis is not supported by our cross-fostering experiments.

Most hosts to the Brown-headed Cowbird are approximately the same size or smaller than the cowbird, although birds slightly larger—such as Red-wings and Brewer's Blackbirds (*Euphagus cyanocephalus*)—also are important hosts in some areas (Friedmann et al. 1977, Weatherhead 1989). Even though Yellow-head nestlings were larger than Red-wing nestlings (pers. obs.), cowbirds grew as well in Yellow-head nests as they did in Red-wing nests. Cowbird growth rates in nests of both blackbird species were similar to rates in nests of smaller hosts (Marvil and Cruz 1989).

Female Yellow-heads typically fledge at 12 days, male Yellow-heads fledge at 12.5 days (Richter 1983, pers. obs.), and most cowbirds in Yellow-head nests fledged at 12 days. This is a day or two later than cowbirds fledge in nests of some other hosts, such as Solitary Vireos (*Vireo solitarius;* Marvil and Cruz 1989), Red-winged Blackbirds (pers. obs.), Kirtland's Warblers (*Dendroica kirtlandii;* Mayfield 1960), Prairie Warblers (*D. discolor;* Nolan 1978), and Song Sparrows (*Melospiza melodia;* Smith 1981). Cowbirds raised by Yellow-heads in our study appeared to be capable of fledging at 10 days of age.

TABLE 3. Linear regression equations ($Y = a + bx$)[a] of Brown-headed Cowbird nestling growth (1–13 days old) raised by Red-winged Blackbirds (RWB) and Yellow-headed Blackbirds (YHB), Boulder County, Colorado, 1986. Regression equations are based on measurements of 11 Brown-headed Cowbirds raised by Yellow-headed Blackbirds and 9 raised by Red-winged Blackbirds.

Measurement	Raised by RWB	Raised by YHB	P^b	F
Weight (g)	$y = 2.481x + 0.487$	$y = 2.401x + 1.275$	0.779	0.079
Tarsus length (mm)	$y = 1.881x + 6.443$	$y = 1.631x + 6.864$	0.143	2.196
Culmen length (mm)	$y = 0.641x + 4.821$	$y = 0.632x + 4.673$	0.895	0.018
Gape width (mm)	$y = 0.335x + 9.950$	$y = 0.411x + 9.548$	0.398	0.723
Ninth primary length (mm)	$y = 3.633x - 7.191$	$y = 3.740x - 5.706$	0.699	0.150

[a] Slopes of all linear regression equations were significant at $P < 0.0001$.
[b] Probability of comparison between growth slopes using MANOVA.

Host defenses.—We suggested in Hypothesis 2 that there is a behavioral response by Yellow-heads which discourages cowbird parasitism.

There are two broad host defenses that may actively deter an intruding nest parasite; the potential host may practice nest guarding or reject the parasitic egg after it has been laid. Aggression toward intruding cowbirds is one method of avoiding parasitism through nest guarding; another is refusal to leave the nest (Hobson and Sealy 1989). Robertson and Norman (1976) predicted that species commonly used as hosts by cowbirds are generally more aggressive toward cowbirds than species that are not parasitized. According to this prediction, Red-wings should be aggressive toward cowbirds, and Yellow-heads should not. Indeed, we found Red-wings to be selectively aggressive toward the cowbird models and Yellow-heads to be nonaggressive toward both the cowbird and control models. Only one Yellow-head refused to leave her nest during experiments with cowbird mounts; three Yellow-heads sat on their nests during experiments with controls. No Red-wings sat tight on their nests during experiments. The two Yellow-head aggression events involved individuals who were generally aggressive and who did not appear to differentiate between the cowbird mount and control. On several occasions, however, we observed Yellow-heads supplant cowbirds on foraging grounds.

We recognize certain problems with aggression experiments and the interpretation of the results. Some are unavoidable. Aggression may alert cowbirds to the location of available nests and may also serve as an indicator that the potential host may offer aggressive protection from predators. Likewise, lack of aggression at the nest site may also serve as an avoidance strategy if aggressive behavior would reveal the nest location (Smith 1981). In addition, some hosts or potential hosts may require more stimuli to elicit aggressive behavior than a simple stuffed bird. The test bird may respond quite differently to a live bird. Although we observed little Yellow-head aggression, their larger size could pose a serious threat of injury to cowbirds caught in the act of egg laying. Nevertheless, our aggression model experiments did not support the hypothesis that Yellow-heads discourage parasitism through aggressive behavior. Aggression experiments also do not account for birds that refuse to leave their nests in the presence of the parasite, which may be an effective avoidance strategy.

Breeding season.—Relative to the Red-wing, a smaller proportion of Yellow-head nests were in a stage suitable for parasitism during the peak cowbird egg-laying period. Because all data for number of cowbird eggs laid were collected from Red-wing nests and our activity coincided with the Red-wing breeding season, this may not have reflected accurately the timing of cowbird reproductive activity in Boulder County. Marvil and Cruz (1989) also found that the rate of cowbird parasitism on Solitary Vireos in Boulder County increased after the peak of vireo egg laying (in the last week of May and first week of June). Others have also found that the peak of parasitism occurred after the peak of host nest initiation (Furrer 1974, Rothstein pers. comm.).

As the Yellow-head breeding season progressed, the possibility of abandonment increased. This implies that Yellow-heads may require the stimulus of other breeding birds to be successful as do Tri-colored Blackbird (*Agelaius tricolor*; Orians 1960, 1961). Synchrony and timing of the successful breeding season may play a role in the absence of cowbird parasitism in Boulder County. Nevertheless, many Yellow-head nests were available during the cowbird egg-laying period, and because the Brown-headed Cowbird is a generalist, which uses many hosts (Payne 1977), the Yellow-head breeding season should not by itself constrain the cowbird. In addition, the cowbird and Yellow-head seasons may overlap more in other areas and cannot explain the general scarcity of parasitism on Yellow-heads throughout their breeding range.

Predation.—Because there were no differences detected in the rates of nest predation between Yellow-heads and Red-wings, this is not a likely influence on choice of host.

Host egg size.—For hosts to successfully incubate parasite eggs with their own eggs, parasite egg size should not diverge too greatly in either direction from the size of the host eggs (Payne 1977). As evidence from their success as host to the cowbird (Ortega and Cruz 1988), larger Red-wing egg size is not a constraint upon cowbirds. Because Yellow-heads successfully incubated cowbird eggs, Yellow-head egg size is not likely to restrain cowbird parasitism.

Incubation period.—The incubation period for cowbird eggs (10–12 days) is among the shortest for passerines (Friedmann 1929, 1963; Rothstein 1975a; pers. obs.). Most hosts have longer incubation periods, which allows the cowbird to gain an advantage by hatching first and developing faster (Rothstein 1975a). The shorter incubation also provides a longer period in which cowbirds can parasitize nests of most hosts. Parasitism of typical hosts can occur as late as a few days after incubation begins.

Rothstein (pers. comm.) suggested that cowbirds prefer hosts with longer incubation periods than their own. Indeed, Yellow-head incubation is almost as short (12–13 days) as the cowbird's (Fautin 1941, Willson 1966, pers. obs.). However, the Red-wing's incubation period (10–13 days) is similar to the cowbird's (Bent 1958, Wiens 1965, Brown and Goertz 1978, pers. obs.) and slightly shorter than the Yellow-head's. The generally low rates of parasitism on Red-wings (Smith 1943, Berger 1951, Hill 1976, Ortega and Cruz 1988) may reflect a preference for other hosts with longer incubation periods. The success of Red-wings as hosts (Ortega and Cruz 1988) indicated that the short incubation of Yellow-heads, relative to other hosts, does not preclude them as hosts. However, it may serve as one constraint upon the cowbird.

Diet.—The growth rates of cowbird nestlings fed by different host species are similar (Norris 1947), and nutritional constraints are not significant in host selection (Payne 1977). Yellow-heads rely on dragonflies (Odonata) as their primary food resource (Orians and Horn 1969, Orians 1985), which should be adequate for the high-protein diet required by cowbird nestlings. The types of prey items delivered by Red-wings and by Yellow-heads to nestlings and fledglings overlap by 85% (Orians and Horn 1969). Red-wings provide cowbird nestlings an appropriate diet, and because 7 cowbird nestlings fledged from 8 nests that hatched a cowbird but were not preyed upon, we assume that the diet of the Yellow-head probably does not constrain the cowbird.

Other potential influences.—Colonial nesting is another breeding characteristic that may serve as a passive host defense but is not necessarily an adaptation to brood parasitism. Both Yellow-heads and Red-wings are colonial nesters, but Yellow-heads nest in much denser colonies than Red-wings (Orians 1980), which provides a greater possibility of group detection and defense against intruding parasites. One might expect that, if nesting in dense colonies discourages cowbird parasitism, individuals that nest apart from the main colony may be subject to parasitism. Yellow-head colonies at two sites were surrounded by nesting Red-wings. At a third site, Red-wings nested with a few Yellow-heads in a marsh approximately 100 m from the main Yellow-head colony. In all three marshes, some Yellow-heads nested away from the main colony, yet none were parasitized. In a few cases, Red-wings that nested <10 m away were parasitized. However, if the Yellow-head is not a suitable cowbird host because most individuals nest in dense colonies, then individual Yellow-heads that nest on the periphery or away from the main colony may benefit from the cowbird's association of the species with high nest density. Relative to the Red-wing, both Tri-colored Blackbirds and Yellow-heads have a shorter breeding season (Orians 1980), and both species are rarely parasitized by cowbirds (Friedmann et al. 1977, Friedmann and Kiff 1985).

In both years of the Yellow-head study, we commonly found hundreds of mites crawling on our hands and arms within seconds of handling Yellow-head nestlings. Although we did not quantify differences between Red-wing and Yellow-head ectoparasites, we did not find a similar infestation of mites in Red-wing nests.

If ectoparasites reduce the suitability of Yellow-heads as hosts, we should have found higher mortality, lower growth rates, or both in cowbird nestlings reared by Yellow-heads than in those reared by Red-wings. Other birds, such as Virginia Warblers (*Vermivora virginae;* pers. obs.) and Yellow-shouldered Blackbirds (*Agelaius xanthomus;* Post 1981), are parasitized by both ectoparasites and brood parasites. Furthermore, ectoparasites were not found in nests during the egg-laying stage. We believe that ectoparasites are not a likely proximate influence in the absence of parasitism. Heavy ectoparasitism on Yellow-heads historically may have influenced cowbird host choice, especially with more suitable hosts available.

Nests of both Yellow-heads and Red-wings are similar with respect to construction, conspicuousness, and placement. Presumably Yellow-head and Red-wing nests are equally susceptible to detection by cowbirds. Cowbirds may use high perches to search for nests to parasitize (Berger 1951, Wiens 1963). When marsh-nesting species are parasitized, they are more heavily parasitized in peripheral and easily accessible portions of cattail marshes (Linz and Bolin 1982) and more frequently in upland bushes than in cattail marshes (Friedmann 1963, Robertson and Norman 1976, Linz and Bolin 1982, pers. obs.).

Orians (1980) found that Yellow-heads did not nest in marshes adjacent to woody vegetation. In our study, all three Yellow-head marshes were adjacent to cottonwoods. However, if the majority of Yellow-heads nest in the absence of trees, then this association could have an influence in the cowbird's choice of not parasitizing the Yellow-head.

We suggest that there is not a single host defense or parasite constraint which, by itself, can explain the lack of parasitism on Yellow-heads. Predation, host egg size, diet, acceptance of cowbird eggs, and growth of host nestlings are not constraints upon the cowbird's ability to successfully parasitize Yellow-heads. Yellow-head breeding characteristics that may make it a less suitable host than the Red-wing are synchrony and early timing of breeding, high rate of abandonment at the end of the breeding season, high nest density, heavy ectoparasite infestation, habitat, and perhaps large adult size. Short incubation could make both blackbird species less suitable than hosts with longer incubation periods. When more desirable hosts are available, the additive effect of many Yellow-head breeding characteristics may influence host choice. In other years and in other populations, if food resources and predation place more constraints on reproductive success, Yellow-heads may not appear to be an attractive host to cowbirds.

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