An Experimental Study of Nest Desertion by the Clay-colored Sparrow (*Spizella pallida*) in Response to Cowbird Parasitism

by

Dorothy Phyllis Hill

A thesis
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in fulfillment of the
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AN EXPERIMENTAL STUDY OF NEST DESERTION BY THE CLAY-COLORED SPARROW (*Spizella pallida*) IN RESPONSE TO COWBIRD PARASITISM

BY

DOROTHY PHYLLIS HILL

A Thesis submitted to the Faculty of Graduate Studies of the University of Manitoba in partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE

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For my mother and father,
Shirley and Ronald Hill

ABSTRACT

The hypothesis that Clay-colored Sparrows (*Spizella pallida*) desert nests to counter parasitism by the Brown-headed Cowbird (*Molothrus ater*) was tested. In a population of sparrows near Delta Marsh, Manitoba, the breeding season was longer than that of the cowbird's, and clutches initiated later in the season were rarely parasitized. No seasonal decline in breeding success or clutch size was recorded. Thus, nest desertion appeared to be a viable strategy for parasitized Clay-colored Sparrows.

Clay-colored Sparrows did not desert experimentally parasitized nests, whether or not a cowbird model was placed on the nest to simulate parasitic laying. However, sparrows attacked the model at almost 61% of the nests tested. Changes in clutch composition (i.e. combination of host and cowbird eggs) and the presence of "broken" eggs in the nest also did not elicit nest desertion. "Broken" eggs were intact Clay-colored Sparrow eggs with a small piece of eggshell glued to them. Sparrows ejected "broken" eggs from their nests or removed the piece of eggshell. The latter response probably indicated a failed ejection attempt. Only reductions in total clutch volume elicited nest desertion.

Almost 60% of naturally parasitized nests were subsequently deserted. Parasitized nests that were deserted usually experienced greater egg loss around the time of parasitism than those not deserted. This observation substantiated the experimental results indicating that Clay-colored Sparrows desert nests in response to reduced clutch volume. In 1990, 17% of nests depredated at the egg stage experienced partial clutch reduction (PCR). Seventy-one percent of these nests were deserted. Responses to partial clutch reduction cannot be considered anti-parasite defences since PCR is not unique to cowbird parasitism and Clay-colored Sparrows do not distinguish between the agents of reduction. Thus, Clay-colored Sparrows do not use nest desertion to counter cowbird parasitism.

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GENERAL INTRODUCTION

Approximately 1% of the world's bird species are obligate brood parasites (Hamilton and Orians 1965, Payne 1977). These birds make no nest of their own, but instead lay their eggs in the nests of other birds, the hosts. Once the parasite has deposited its egg, it contributes nothing further to its young. Incubation of the parasitic egg and raising the parasitic nestling to independence are burdens of the host. Thus, obligate brood parasites depend upon other species for their survival.

Brood parasitism is usually detrimental to hosts. For example, birds parasitized by the Common Cuckoo (*Cuculus canorus*) lose all of their own young because the newly hatched cuckoo evicts all host young and eggs from the nest (Chance 1922, Wyllie 1981). Great Spotted Cuckoo (*Clamator glandarius*) nestlings outcompete their Magpie (*Pica pica*) nestmates by 'super-begging', which causes host young to starve (Redondo and Reyna 1988). Solitary Vireo (*Vireo solitarius*) nestlings grow slower in nests parasitized by the Brown-headed Cowbird (*Molothrus ater*) than in unparasitized nests (Marvil and Cruz 1989). Consequently, there is selection pressure on hosts to counter these effects (see Rothstein 1975a, 1990; Payne 1977; Davies and Brooke 1988), and many hosts have evolved defences against brood parasitism. These include egg ejection (Rothstein

1975a, Davies and Brooke 1988), nestling recognition (Friedmann 1960), and, possibly, nest defence (Robertson and Norman 1976, 1977; Hobson and Sealy 1989). In turn, brood parasites have evolved counter-defences that include egg and nestling mimicry (Chance 1921, Friedmann 1960, Davies and Brooke 1988, 1989; Redondo and Reyna 1988; Higuchi 1989), shortened incubation periods (Briskie and Sealy 1990), and rapid egg laying (Hann 1941, Nolan 1978: 371, Wyllie 1981: 125, Davies and Brooke 1988). The progression of adaptations and counter-adaptations by brood parasites and their hosts has been termed an 'evolutionary arms race' (Dawkins and Krebs 1979, Davies and Brooke 1988). For this reason, brood parasitism is an ideal system with which to study coevolution (see Rothstein 1990 for a review).

However, the temptation exists to attribute coevolution to host behaviours without evidence that the selective pressure of brood parasitism has ultimately lead to them. One way to examine the ultimate causes of a behaviour is to explore the proximate stimuli that elicit that behaviour. For example, if the proximate stimulus leading to a host behaviour is unrelated to brood parasitism, we must conclude that brood parasitism is not the basis for that behaviour and therefore the behaviour is not an example of coevolution between host and parasite.

One example of a host behaviour that has been interpreted as an anti-parasite defence, but whose origins are contentious, is nest desertion (e.g. Rothstein 1975a, 1990). Nest desertion has been recorded in apparent relation to brood parasitism in several hosts (e.g. Salt 1966, Best 1978, Clark and Robertson 1981, Zimmerman 1983, Wolf 1987, Davies and Brooke 1988, Graham 1988, Higuchi 1989, Moksnes and Røskaft 1989), but seldom has it been examined experimentally (e.g. Rothstein 1986, Davies and Brooke 1988, Higuchi 1989, Moksnes and Røskaft 1989). Without experimentation, we lack the critical evidence that nest desertion is a legitimate anti-parasite defence.

In the present study, I examined nest desertion in the Clay-colored Sparrow (*Spizella pallida*), a frequent host of the Brown-headed Cowbird (Mayfield 1965, Friedmann et al. 1977). By experimentally determining the proximate factors that elicit nest desertion in this species, I was able to examine whether the sparrows use desertion as an anti-parasite defence and hence, whether this behaviour is an example of the coevolution between host and parasite. Proximate factors examined included the presence of a cowbird egg in the nest, sight of or interaction with a female cowbird at the nest, reduction in clutch volume, replacement of sparrow eggs with the same volume of cowbird eggs (hereafter, changes in clutch composition), presence of broken eggs in the nest, and human nest visitation. I also monitored naturally parasitized nests to correlate some of the above factors with the desertion of these nests.

INTRODUCTION

Parasitism by the Brown-headed Cowbird can be detrimental to host species in several ways. Female cowbirds often remove one or more host eggs from the nests they parasitize (see Sealy 1992 for a review). Eggs may break and incubation may be hampered when the often-larger cowbird egg is added to host clutches (Payne 1977, Weatherhead 1991). As well, the cowbird has evolved a short incubation period (Friedmann 1929, Briskie and Sealy 1990) and its young often hatch before the host's young. The presence of the newly hatched cowbird in the nest can induce hosts to switch from incubation attentiveness to nestling feeding, which may lead to fewer host eggs hatching (e.g. Petit 1991). Furthermore, early hatching, coupled with the nestling cowbird's (usually) larger size, may put host nestlings at a competitive disadvantage and further reduce host broods through starvation, crowding, or suffocation (Nolan 1978: 387, Marvil and Cruz 1989, contra Hatch 1983). Thus, it is expected that natural selection would favour host behaviour that minimizes the impact of cowbird parasitism (Rothstein 1975a, Payne 1977, May and Robinson 1985).

Many hosts exhibit behaviours that have been interpreted as anti-parasite defences. The best studied of these is egg ejection. Rothstein (1975a, b; 1976; 1978;

1982a) examined egg ejection experimentally and termed species that eject foreign eggs as 'rejectors' (see also Bazin 1991). However, despite the apparent benefits of ejecting cowbird eggs from their nests, thereby avoiding the impact of lowered hatching and nestling success, few of the more than 160 known cowbird host species actually exhibit this behaviour (Rothstein 1975a). One reason may be that egg ejection does not eliminate the cost to the host of egg removal by cowbirds (Rothstein 1970). Furthermore, there may be costs associated with ejection behaviour itself. For example, small hosts may damage their own eggs while attempting to eject the foreign egg (see Rohwer and Spaw 1988, Rohwer et al. 1989). Therefore, the most effective host defence may be to avoid being parasitized in the first place (Rothstein 1970; Robertson and Norman 1976, 1977). Robertson and Norman (1976, 1977) proposed that one way hosts may avoid being parasitized is by aggressively preventing female cowbirds from gaining access to their nests (see also Folkers 1982, Hobson and Sealy 1989).

However, Rohwer and Spaw (1988) argued that neither egg ejection nor nest defence are options available to small host species (but see Hobson and Sealy 1989). For these birds, nest desertion may be the only way to counter cowbird parasitism. Desertion can occur under several circumstances (Rothstein 1975a) and may have costs associated with it (Rohwer and Spaw 1988). Therefore, two things must be established before it can be concluded that a species uses nest desertion as an anti-parasite strategy. Firstly, desertion must be shown to be a viable option for that species and, secondly, it must be demonstrated that the species indeed is responding to parasitism and not to some other factor when it deserts its nest.

In some cases, nest desertion may cost more than accepting cowbird parasitism and, therefore, acceptance may be a better strategy (Wolf 1987, Rohwer and Spaw 1988, Rohwer et al. 1989). For example, in a study of intraspecific brood parasitism, Gibbons (1986) found that because of a substantial seasonal decline in nesting success, Moorhens (*Gallinula chloropus*) lost fewer young on average by accepting parasitism than by deserting parasitized clutches and renesting. It may be expected that species in which nesting success declines over the season would be less likely to desert parasitized nests. Related to this, Rohwer and Spaw (1988) noted that species reported to desert nests parasitized by the Brown-headed Cowbird usually have breeding seasons considerably longer than that of the cowbird.

Identifying the factor(s) that elicits nest desertion is also important. When a bird deserts a nest parasitized by a cowbird, it may be responding to the presence of the cowbird egg in its nest, the sight of or interaction with the female cowbird at the nest, an alteration of clutch volume or composition, or broken eggs in the nest (Rothstein 1975a, Graham 1988, Kemal and Rothstein 1988). Anti-parasite defences are behaviours that have evolved specifically to counter brood parasitism and species that possess such defences respond to the parasitic egg and/or the parasite itself. Although broken eggs and clutch alterations may result from actions by the parasite, they are independent of the actual act of parasitism and can be caused by other agents such as a predator. Thus, it is necessary to identify to which of these proximate stimuli hosts respond. An experimental approach is essential because it is impossible to control for these individual factors at naturally parasitized nests (Rothstein 1975a).

Disturbance at the nest by the female parasite may influence whether or not a bird deserts its nest. Reed Warblers (*Acrocephalus scirpaceus*) are more likely to abandon nests experimentally parasitized with an artificial cuckoo egg after they have seen a stuffed, female Common Cuckoo (*Cuculus canorus*) on their nests (Davies and Brooke 1988). Possibly such interactions also affect cowbird hosts. Graham (1988) noted that artificial parasitism experiments on cowbird hosts (e.g. Rothstein 1975a) resulted in fewer desertions than natural parasitisms did and he hypothesized that the difference may have been due to the presence of the female cowbird in the latter case (contra Burgham and Picman 1989).

For Meadow Pipits (*Anthus pratensis*), it is the combination of egg and parasite that serves as an important cue. These birds continue tending their nests after receiving an artificial cuckoo egg or after a stuffed cuckoo has been placed near their nest. However, the combination of these two factors can result in as many as 50% of the nests being abandoned (Moksnes and Røskaft 1989).

Broken eggs can leak and jeopardize entire clutches and therefore it is adaptive for birds to eject such eggs to protect those that remain (Kemal and Rothstein 1988). Broken eggs may also stimulate birds to desert their nests. Hofslund (1957) documented two cases in which Common Yellowthroats (*Geothlypis trichas*) abandoned parasitized nests that contained punctured eggs, possibly damaged by the parasitizing cowbird's claw.

Partial clutch reduction (PCR) is the loss of some, but not all, of a bird's clutch (Rothstein 1986). Female cowbirds often remove one or more eggs from the nests they parasitize (e.g. Hann 1941, Zimmerman 1983, Sealy 1992) and this removal may promote desertion (Wolf 1987). Several studies have implicated PCR in nest desertions (e.g. see Zimmerman 1966, Finch 1983, Wolf 1987). As both cowbirds and predators remove eggs, desertions that result from such reductions are not a response unique to cowbird parasitism (Wolf 1987).

Finally, experimental parasitism must control for the affect of human nest visitation since some species have been reported to desert when disturbed by human observers at the nest (e.g. Zwickel and Carveth 1978, Safina and Burger 1983).

Among cowbird hosts that have been recorded deserting parasitized nests are several species in the genus *Spizella*: Field Sparrow (*S. pusilla*; Best 1978, Walkinshaw 1978), Chipping Sparrow (*S. passerina*; Graham 1988), Brewer's Sparrow (*S. breweri*; Rich 1978, Biermann et al. 1987), and Clay-colored Sparrow (*S. pallida*; Fox 1961, Salt 1966, Knapton 1978). Typically, desertion rates vary among and within these species, both annually and apparently geographically. Rich (1978) recorded desertion of all parasitized Brewer's Sparrow nests, while Biermann et al. (1987) observed a 69% desertion rate for this species. Field and Chipping sparrows have been recorded deserting 63% (Best 1978) and 52% (Graham 1988) of parasitized nests, respectively.

Desertion rates recorded for the Clay-colored Sparrow seem to be especially variable. Salt (1966) claimed that this species deserted all parasitized nests but other investigators recorded rates of 50% (Shortt *in* Bent 1968: 1204), 37.5% (Fox 1961), and 25% (Lane *in* Bent 1968: 1204). Most puzzling are Knapton's (1978) observations from southwestern Manitoba, where he reported desertion rates of

15.8% and 60.0% from two sites only 12 km apart. Knapton invoked evolutionary lag (see Rothstein 1982b, Rothstein 1990) to explain this variation and suggested that anti-parasite defences are not yet fully developed in the Clay-colored Sparrow (Knapton 1978). Alternatively, if Clay-colored Sparrows respond to the laying cowbird, rather than the cowbird egg, variation in sparrow-cowbird encounters could account for variation in sparrow responses to parasitism.

In this study, I determined whether or not nest desertion is a viable option available to Clay-colored Sparrows. I recorded the length of breeding seasons of both the sparrow and Brown-headed Cowbird and examined seasonal changes in sparrow clutch size and nesting success. I also examined experimentally possible stimuli that elicit nest desertion in the Clay-colored Sparrow to assess whether this species uses desertion as an anti-parasite strategy. I quantified the responses of Clay-colored Sparrows to experimental parasitism with and without the presence of a female cowbird at the nest, changes in clutch volume and composition, broken eggs, and visits to the nest by a human.

METHODS

Study Site

The study was conducted during the spring and summer of 1990 and 1991 on 185 ha of old-field succession, prairie, and wet meadows adjacent to a woodlot known locally as the Oxbow Woods. This woodlot grows in association with an oxbow formation along the southern edge of Delta Marsh, Manitoba (50° 10'N, 98° 22'W), on the property of the University of Manitoba Field Station (Delta Marsh). Dominant shrubs in this community include snowberry (*Symphoricarpos occidentalis*), wild rose (*Rosa* sp.), and raspberry (*Rubus strigosus*) (Gamble 1980). The woodlot and surrounding plant communities are described by Evans (1972) and Gamble (1980).

Clutch initiation and nesting success

Habitat was searched daily from mid-May to the end of July for sparrow nests that, when found, were numbered with flagging tape placed at least 1.5 m away. The date of clutch initiation was known precisely for nests found before or during egg laying. Clutch initiation dates were estimated for other nests by back-counting 11 days from hatching to the laying of the penultimate egg (see Fox 1961, Harrison 1975) and then subtracting two or three days depending on the final clutch size. Nests for which an initiation date could not be estimated were eliminated from this analysis. This method was used both for data collected in the field during the present study and those obtained from the Prairie Nest Records Scheme (PNRS, Manitoba Museum of Man and Nature, Winnipeg, Manitoba).

The median clutch initiation date was used to distinguish between early- and late-nesting attempts in each year. "Early" nests were initiated on or before the median date and "late" nests were initiated later. Combining data from 1990 and 1991, I tested for a seasonal decline in clutch size by comparing mean clutch sizes of early and late nests. A one-tailed, Wilcoxon 2-sample test (equivalent to the Mann-Whitney U test, Siegel 1956: 116-126) was used for this analysis. These data were also analyzed for differences in mean clutch size between years using the 2-tailed version of the Wilcoxon 2-sample test. Nests in which the clutch size was ambiguous due to parasitism or predation were deleted from the analysis. I used Mayfield's (1961, 1975) method to determine the nest success of early and late nests. Only data collected in 1990 were used for this analysis because experiments conducted in 1991 influenced nest outcomes. The Mayfield method incorporates nest-days of exposure (one nest-day is equivalent to one nest exposed to predators for one day) and, therefore, controls for the bias introduced when nests are found at different stages. The proportion of nest-days with losses in early and late nests were compared using a Chi-square test for two independent samples in 2X2 contingency table (Siegel 1956: 107-109).

Experimental procedures

Seven experimental treatments were performed, three in 1990 and four in 1991. In 1990, nests were assigned randomly to 1) the control nests (human disturbance), 2) cowbird-egg treatment, or 3) cowbird-egg plus model treatment (hereafter, model treatment). In 1991, nests were assigned to one of four groups: 1) broken-egg treatment, 2) broken-egg plus cowbird-egg treatment, 3) clutch-reduction treatment, or 4) clutch-reduction plus cowbird-egg treatment.

Upon receiving its experimental treatment, each nest was checked daily for five days and after that, every second or third day until the young fledged or the nest failed. Nests that were naturally parasitized were monitored in the same way. To ascertain whether a nest was active, I recorded changes in the number of eggs present, whether eggs were warm or cold to the touch, and the presence of sparrows on or near the nest. Nests were checked between 0600 hr and 2100 hr (Central Daylight Time) and experiments were conducted between 0530 hr and 1200 hr (CDT).

Control nests were monitored as described above, but their contents were not manipulated. Five-day monitoring began only after a control nest had received at least one sparrow egg to keep this treatment consistent with the experimentally manipulated nests. On the first day of checking, I touched the edge of the nest to simulate my behaviour at the experimentally parasitized nests.

Nests that received the cowbird-egg treatment were parasitized with an artificial cowbird egg. These eggs were made of plaster-of-Paris from moulds formed from real cowbird eggs and painted with acrylic paints and polyurethane using Rothstein's (1970, 1975b) method (see Figure 1). Artificial eggs averaged approximately 0.2 g (6.4%) heavier than real cowbird eggs from the study area (cowbird egg masses in Sealy 1992). In controlled experiments, Rothstein (1975b) found no difference in host responses to real and artificial eggs. At the end of the five-day monitoring period, artificial cowbird eggs were checked for puncture marks to determine whether the sparrows had attempted to puncture-eject them. Sparrow responses to the cowbird-egg treatment were compared to those elicited by experimentally introduced real cowbird eggs from data provided by S.G. Sealy.

At nests receiving the model treatment, I placed a taxidermically prepared female cowbird in laying position (see photograph in Hann 1941) on the nest prior to introducing the artificial cowbird egg into the nest. The legs of the cowbird were removed to avoid damaging the nest

Figure 1: Artificial cowbird eggs used in the experiments (bottom) and real cowbird eggs found on the study site (top).


CM
1
2
3
4
5
6
7
8
9
10
11
12
13

contents. A portable blind was set up 2-10 m from the nest, depending on the thickness of the surrounding cover. I recorded how long the sparrows took to return to the nest and whether one or more sparrows responded. I left the cowbird model on the nest for approximately one minute from the time the sparrows had returned. A time of one minute was chosen since it takes female cowbirds usually only 30-60 seconds to lay an egg (see Hann 1941, Nolan 1978: 371). I recorded whether the sparrows flew at, pecked, or knocked the model off the nest. I also noted if they uttered alarm calls. After one minute, I removed the model, placed an artificial cowbird egg into the nest, and retreated from the area as quickly as possible. The nest was then monitored for five days, after which the artificial cowbird egg was checked for punctures. No sparrow eggs were removed during any of the above manipulations.

Nests that received the "broken" egg treatment had one sparrow egg replaced by a broken egg. Broken eggs were intact sparrow eggs to which small pieces of eggshell were glued at 45° angles (Type I eggs of Kemal and Rothstein 1988) (Figure 2). In addition to monitoring these nests for desertion, evidence that sparrows ejected the broken eggs was recorded. Nests that received the broken-egg plus cowbird-egg treatment had an artificial cowbird egg added at the time of egg switching. Otherwise, these nests were treated exactly the same as those in the broken-egg treatment.

Figure 2: "Broken" Clay-colored Sparrow eggs used in the experiments.

14a

Clutch reduction, with and without the introduced artificial cowbird egg, involved reducing the sparrow's clutch by two eggs. Removal of two sparrow eggs enabled me to keep the total clutch volume constant in the clutch-reduction plus cowbird-egg treatment since cowbird eggs are approximately twice the volume of Clay-colored Sparrow eggs. In order to calculate egg volume, the maximum length (L) and breadth (B) of 140 sparrow eggs were measured to the nearest 0.10 mm with sliding calliper (Appendix). Egg volume was then calculated using the formula: volume = $0.51LB^2$ (Hoyt 1979). Mean sparrow egg volume, 1.40 (SE=0.01 ml), was compared to the cowbird egg volume, 2.82 (SE=0.33 ml), that appears in Sealy (1992) and was found to average 49.6% the volume of cowbird eggs. Both three- and four-egg clutches were used for these experiments, therefore I determined the final clutch size before performing the manipulation. Responses to these treatments were compared with a 2-tailed Fisher exact probability test (Siegel 1956: 96-104).

Briskie and Sealy (1987) elicited nest desertion in Least Flycatchers (*Empidonax minimus*) by parasitizing nests at the pre-egg stage. However, Rothstein (1975a) noted that many nesting attempts are aborted during nest building whether or not they are parasitized. Clay-colored Sparrow nests found during nest building were monitored daily to determine the frequency of desertion at this stage. No experimental manipulations were performed until a nest had received at least one sparrow egg.

Natural cowbird parasitism

I recorded the number of nests naturally parasitized and the number of cowbird eggs each nest received. I also noted whether host eggs disappeared from these nests. The total number of sparrow eggs removed from parasitized nests was estimated by recording changes in clutch size. As sparrow eggs were not numbered, it was sometimes impossible to determine the exact number of eggs removed. For example, in some nests it was unclear whether one or two eggs had disappeared. In these cases, I used the smaller number for the estimate. Clay-colored Sparrows were recorded deserting nests or accepting natural cowbird parasitism by the same five-day criterion described above. I used a 2-tailed Fisher exact probability test to compare desertion rates of naturally and experimentally parasitized nests (Siegel 1956: 96-104).

Data from the Prairie Nest Records Scheme were used to quantify the magnitude of egg removal from parasitized Clay-colored Sparrow nests by comparing the mean sizes of sparrow clutches in parasitized and unparasitized nests. These results were compared with a 2-tailed Wilcoxon 2-sample test (Siegel 1956: 116-126).

Nest predation

In 1990, I recorded the number of nests depredated at the egg stage (egg laying and incubation) and the proportion of these that involved PCR. Sparrow responses to predator-induced PCR were then compared to those elicited by the clutch-reduction and clutch-reduction plus cowbird-egg experiments using 2-tailed Fisher exact probability tests (Seigel 1956). This test was also used to compare sparrow responses to PCR and to natural cowbird parasitism.

RESULTS

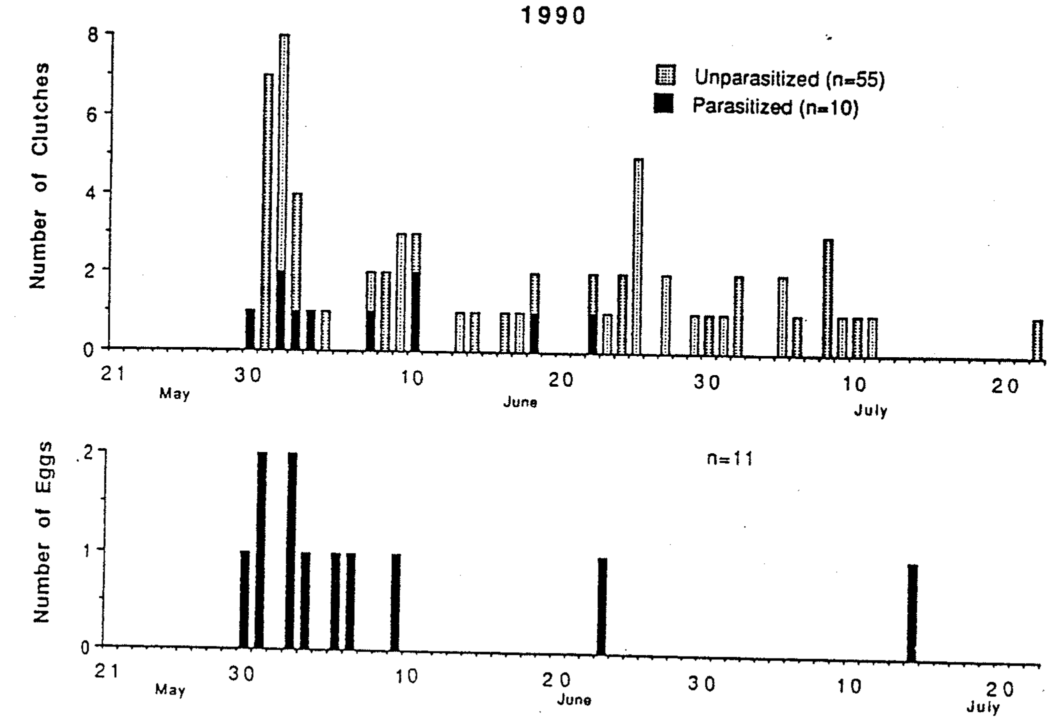
Clutch initiation and nesting success

Clay-colored Sparrows initiated clutches from 30 May to 22 July, 1990 and from 24 May to 17 July, 1991 (Figure 3). Median clutch initiation dates for 1990 and 1991 were 13 and 2 June, respectively. Mean clutch sizes did not differ between early ($x=3.77$, $SE=0.06$) and late ($x=3.74$, $SE=0.06$) season nests ($z=-0.130$, $p > 0.05$) nor between 1990 ($x=3.70$, $SE=0.06$) and 1991 ($x=3.80$, $SE=0.05$)($z=-1.47$, $p > 0.05$). In both cases, differences were not detected because the means were very close (Figures 4 and 5). Maintaining observed variances and sample sizes, differences as small as 0.2 and 0.5 eggs, respectively, were detectable with a power level of 80% (Borenstein and Cohen 1988). Comparison of the number of nest-days with and without losses showed that clutches initiated after 13 June 1990 were just as successful as clutches initiated on or before this date ($\chi^2 = 1.251$, $df=1$, $p > 0.05$) (Table 1). Cowbird parasitism rarely occurred after the third week in June (Figures 3 and 6). In the present study, clutches initiated later in the breeding season generally were not parasitized (Figures 3).

Experimental parasitism

Acceptance was 100% for the cowbird-egg treatment, model treatment, and control (Table 2). Puncture marks were

Figure 3: Initiation dates of parasitized and unparasitized Clay-colored Sparrow nests and dates cowbird eggs were laid during 1990 and 1991.


1990
Number of Clutches
0
2
4
6
8
▨ Unparasitized (n=55)
■ Parasitized (n=10)
21
May
30
10
June
20
30
10
July
20
Number of Eggs
0
1
2
n=11
21
May
30
10
20
June
30
10
20
July

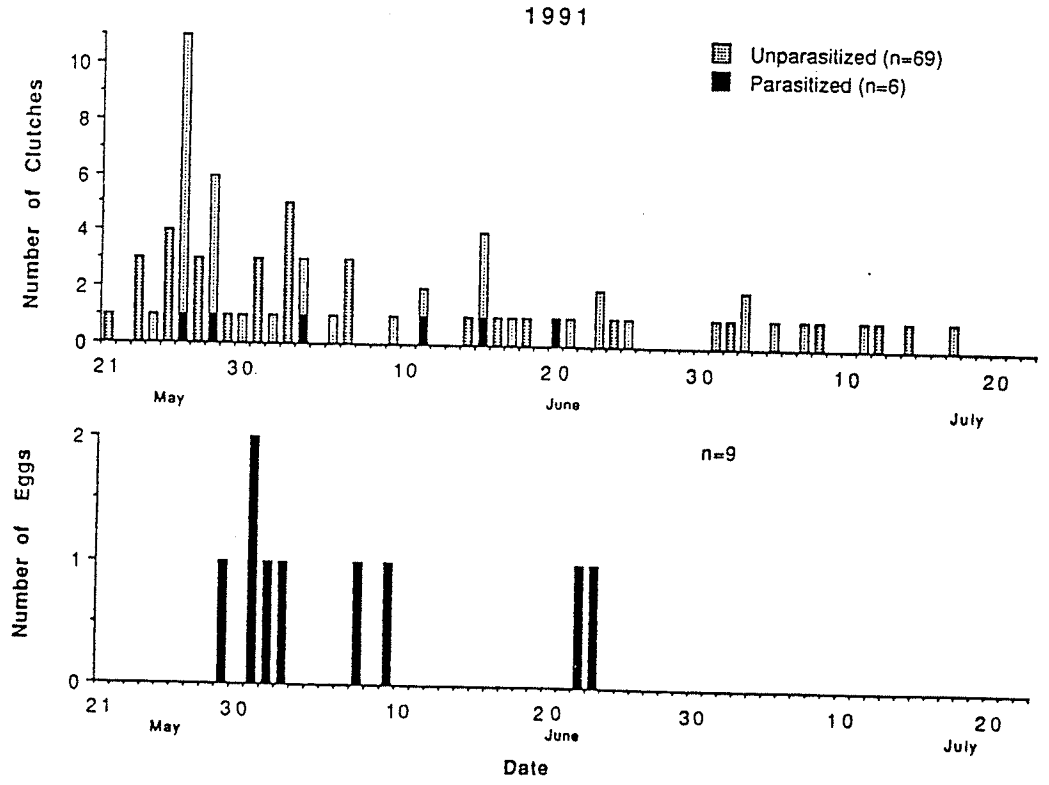
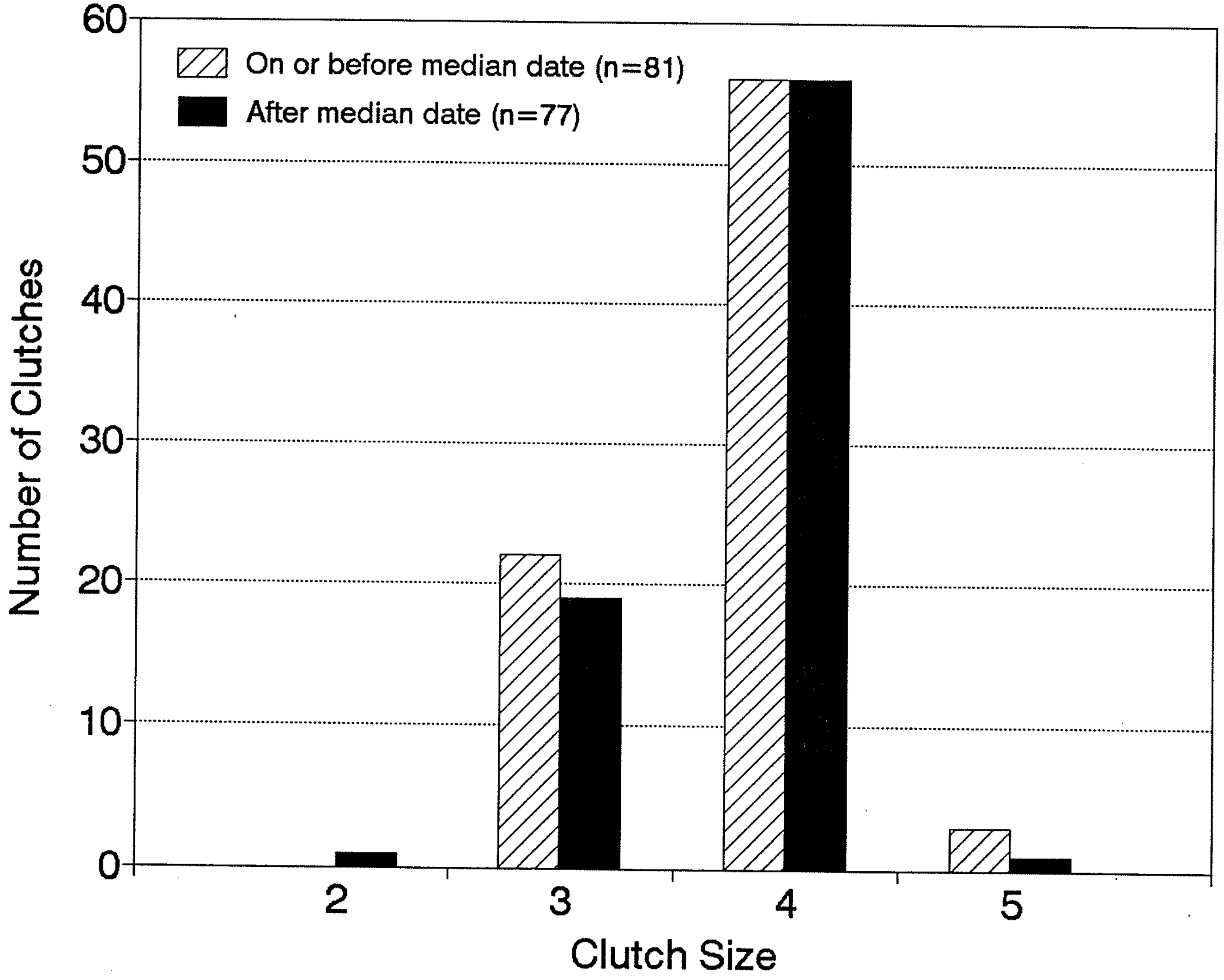
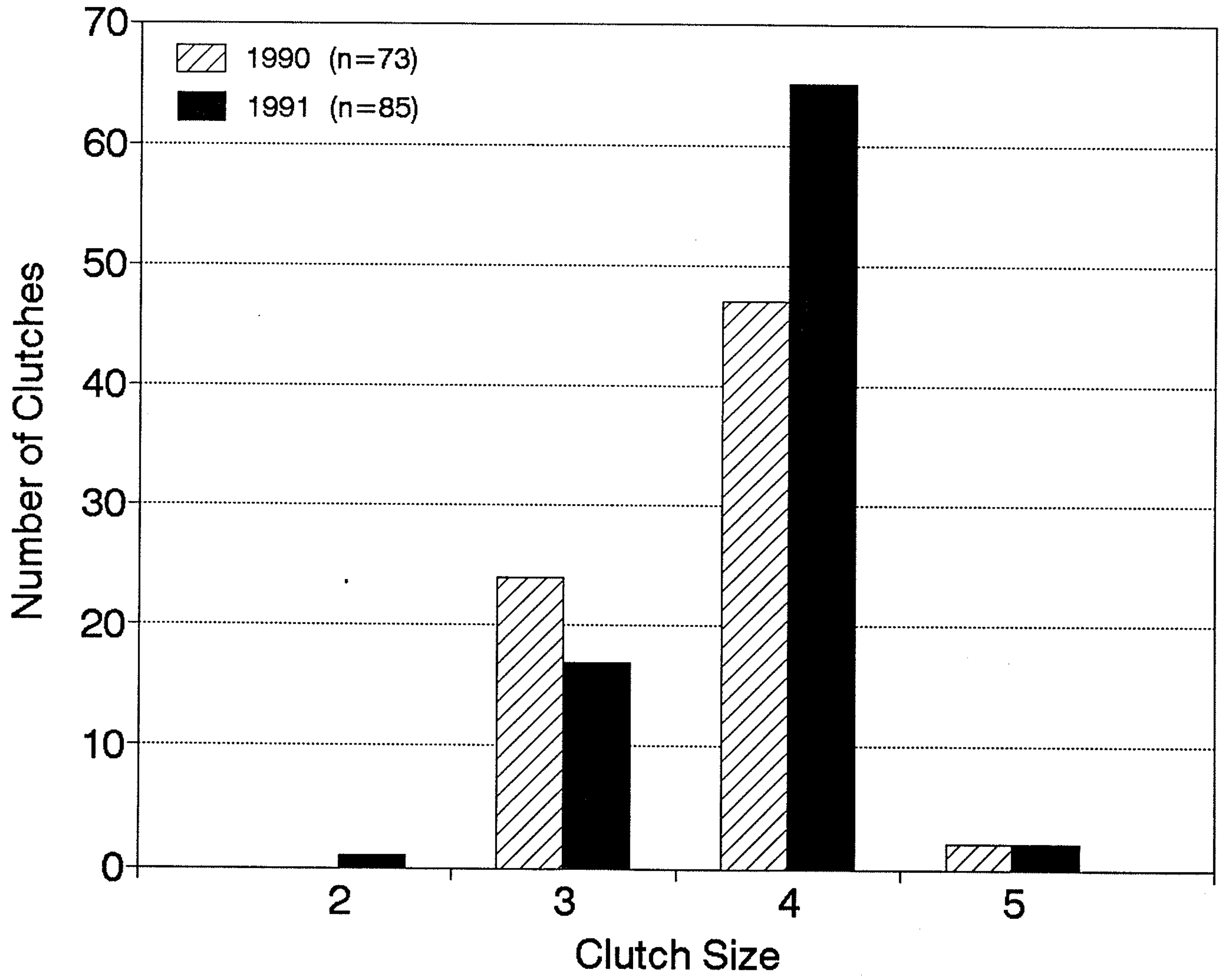

1991
Number of Clutches
0
2
4
6
8
10
▨ Unparasitized (n=69)
■ Parasitized (n=6)
21
May
30
10
20
June
30
10
20
July
Number of Eggs
0
1
2
n=9
21
May
30
10
20
June
30
10
20
July
Date

Figure 4: Sizes of clutches initiated on or before and after the median clutch initiation date, 13 June 1990 and 2 June 1991.



60
50
40
30
20
10
0
Number of Clutches
▨ On or before median date (n=81)
■ After median date (n=77)
2
3
4
5
Clutch Size

Figure 5: Sizes of clutches initiated in 1990 and 1991.



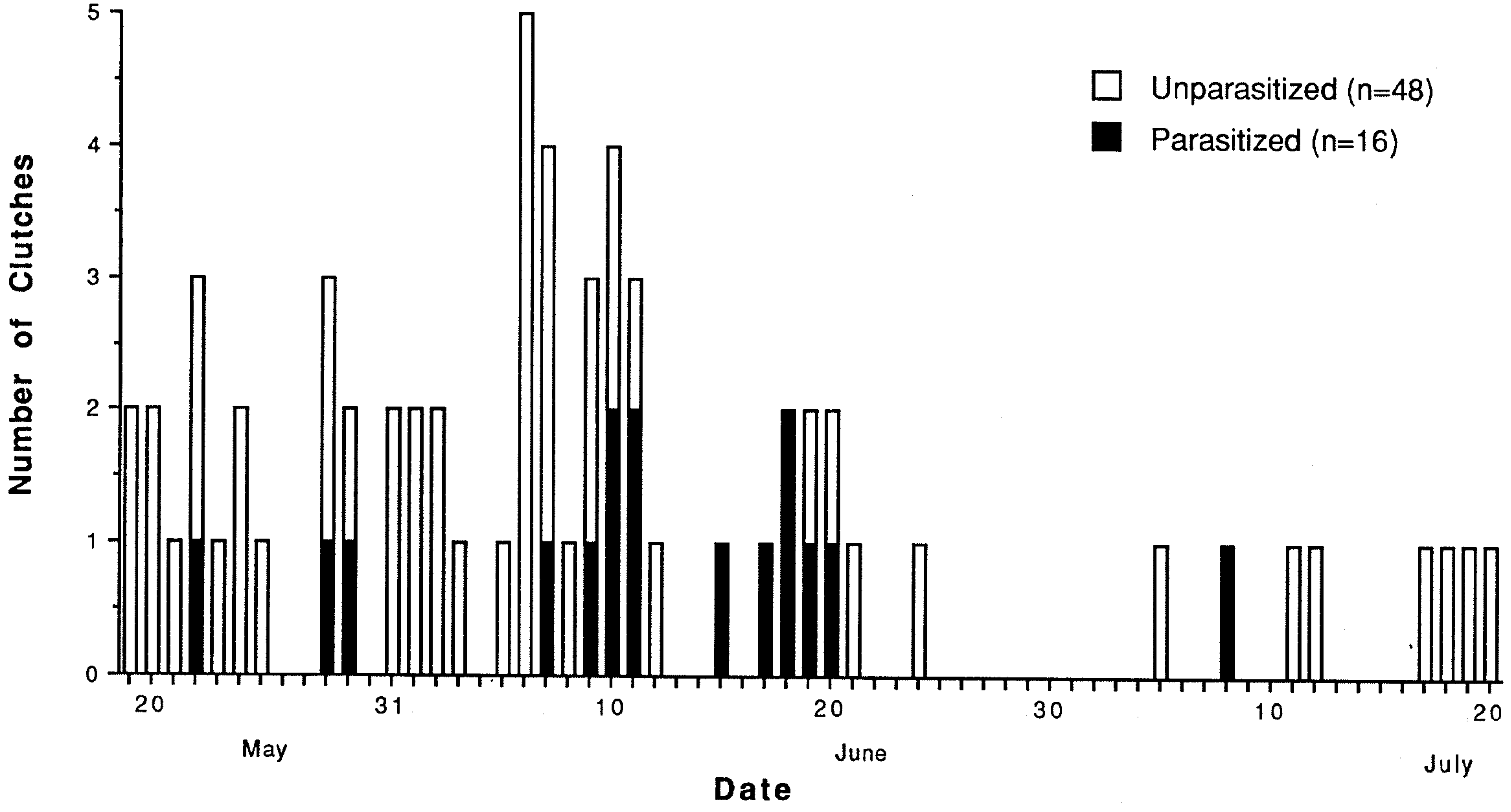
70
60
50
40
30
20
10
0
Number of Clutches
▨ 1990 (n=73)
■ 1991 (n=85)
2
3
4
5
Clutch Size

Table 1: Nest-days with and without losses for clutches initiated on or before and after 13 June 1990.

	Nest-days		
Clutches initiated	With losses	Without losses	Total
On or before 13 June	24	394	418
After 13 June	22	506	528
Total	46	900	946

Note: $\chi^2=1.251$, df=1, $p>0.05$.

Figure 6: Initiation dates of parasitized and unparasitized Clay-colored Sparrow nests, 1927-1989 (source: Prairie Nest Records Scheme).



Number of Clutches
0
1
2
3
4
5
☐ Unparasitized (n=48)
■ Parasitized (n=16)
20
31
10
20
30
10
20
May
June
July
Date

Table 2: Responses of Clay-colored Sparrows to the experimental treatments.

Treatment:	Response accept	 desert	 eject	 total
CB[a] egg	19	0	0	19
Model	19	0	0	19
Clutch reduction	5	10	0	15
Clutch reduction + CB egg	14	1	0	15
Broken egg	8[b]	0	10[c]	18
Broken egg + CB egg	10[b]	0	8[c]	18
Control	19	0	0	19
Total	94	11	18	123

[a] CB = cowbird.

[b] Sparrows damaged the broken egg by breaking off the broken piece, but then accepted the remaining intact egg.

[c] Sparrows ejected broken eggs, but not cowbird eggs.

never found on the artificial cowbird eggs. Given the sample size (n=19 nests in each treatment), power level was estimated to be 80% (estimated from Fleiss 1981). In other words, the sample size should have been large enough to detect 80% of the desertions had they occurred. Two nests in the egg treatment and one nest each in the model treatment and the control accepted the experimental procedure for four days but were depredated by the fifth day. At these nests, the experimental treatments were considered accepted. The experimental procedure was accepted for at least five days at all other nests included in the results. The number of Clay-colored Sparrow eggs present on the day the above treatments were initiated were as follows: 17 nests contained 1 egg, 6 contained 2, 10 contained 3, and 24 contained 4 eggs. Acceptance was also 100% at twenty-nine Clay-colored Sparrow nests experimentally parasitized in 1987 with real cowbird eggs by S. G. Sealy (pers.comm.). There was no difference in sparrow response to real and artificial cowbird eggs.

Clay-colored Sparrows took a mean of 17.04 ± 3.55 (SE) minutes to return to their nests during the model trials. Two sparrows, probably the mated pair, responded in 73.9% of the trials while one sparrow responded 26.1% of the time (n=23). In 14 (60.9%) model trials, the sparrows pecked the cowbird model and in five cases they knocked it off the nest. Ten of those birds that pecked the model also flew at it repeatedly. Pecking was always accompanied by a high-pitched hissing alarm call and only once was this call given when the sparrows did not peck the model.

One incident of natural cowbird parasitism was observed. Two Clay-colored Sparrows responded to the laying cowbird by hissing and pecking at it. The sparrows deterred the parasite during its first attempt (arrival at 04:46 CDT), but it returned one minute later and laid successfully in the nest. The sparrows continued pecking the cowbird while it was on the nest. In contrast to the Clay-colored Sparrows, the cowbird laying bout was approximately one minute. The female sparrow returned to the nest to lay an egg 97 minutes after the parasitism. The sparrows accepted the cowbird egg in this instance.

Responses to broken eggs and clutch reduction

No nest into which a "broken" egg was introduced was deserted, whether or not a cowbird egg was added (n=18 nests in each treatment). Again, sample sizes were large enough to detect 80% of the desertions had they occurred (estimated from Fleiss 1981). Ten and eight broken eggs were ejected in the broken-egg and broken-egg plus cowbird-egg treatment, respectively. Eggs that were not ejected were damaged by the sparrows, which occurred when they broke off the glued piece of eggshell, possibly while attempting to eject the egg. The sparrows accepted and incubated the remaining intact eggs. Egg ejection and damage occurred both with and without the addition of a cowbird egg.

Ten (66.7%) of the 15 reduced clutches were deserted. In contrast, only one nest (6.7%) was deserted in the clutch-reduction plus cowbird-egg treatment (n=15 nests). The responses to these two treatments differed significantly (Fisher exact probability test, $p < 0.002$). Five of the 15 clutches that were reduced, but given a cowbird egg, were 3-egg clutches. These clutches were reduced to one sparrow egg plus one cowbird egg. None of these clutches was deserted.

Eighty-one nests were discounted from the experiments because of predation, natural parasitism, or other factors. Responses to the experimental treatments are summarized in Table 2.

Natural cowbird parasitism

Twenty-two of 204 nests (10.8%) on my study site were naturally parasitized. Three nests (13.6%) received two cowbird eggs, one nest (4.6%) received three, and each of the other 18 nests (81.8%) was parasitized once. In contrast to the response elicited by experimental parasitism (cowbird-egg and model treatments), thirteen (59.1%) naturally parasitized nests were deserted, eight (36.4%) were accepted, and at one (4.5%) nest the outcome was unknown. These responses differed significantly from those elicited by experimental parasitism (Fisher's exact probability test, $p < 0.001$). Eleven (50%) of the deserted nests lost at least one host egg around the time of parasitism. Two of three nests (66.7%) parasitized during the nest building stage were deserted. However, eleven (30.5%) of 36 unparasitized nests found during nest building were also deserted. Of the eight nests at which natural parasitism was accepted, four lost no sparrow eggs, three lost either zero or one egg, and one nest may have lost two eggs. An estimated 32 sparrow eggs were removed from 22 parasitized nests or approximately 1.5 eggs removed per parasitized nest.

Data obtained from the PNRS indicated that 288 unparasitized and 86 parasitized nests contained means of 3.77 (SE=0.03) and 2.31 (SE=0.08) Clay-colored Sparrow eggs, respectively. These means differed significantly ($z=-13.58$, $p < 0.0001$). Parasitized nests contained 1.46 fewer eggs than unparasitized nests.

Nest predation

Forty of 96 (41.7%) nests found in 1990 were depredated at the egg stage and seven (17%) of these involved PCR. Of clutches involving PCR, five (71.4%) were deserted, one (14.3%) was accepted, and the outcome of the other was unknown. These responses differed significantly from those elicited by the clutch-reduction plus cowbird-egg experiment

(Fisher's exact probability test, $p < 0.05$). Differences in responses to predator-induced PCR and the clutch-reduction experiment were not detected, but sample size was small. Similarly, no difference in sparrow responses to natural cowbird parasitism and predator-induced PCR was found, but again, sample size was small.

DISCUSSION

Clutch initiation and nesting success

Clay-colored Sparrows neither laid smaller clutches over the breeding season nor experienced greater nest failure as the season progressed. Overall, a seasonal decrease in the breeding success of Clay-colored Sparrows was not apparent. Furthermore, data analyzed in this study indicate that sparrow clutches initiated later in the breeding season were seldom parasitized. Based on these results, I suggest that nest desertion should be a viable alternative for Clay-colored Sparrows parasitized by the Brown-headed Cowbird.

Rohwer and Spaw (1988) suggested that the acceptance of cowbird parasitism actually may be adaptive (e.g. Petit 1991), especially in species that exhibit seasonal declines in clutch and brood size and seasonal increases in nest failure. Seasonal decreases in clutch size have been observed in several species, including many passerines (see Klomp 1970 for a review). Rohwer and Spaw (1988) also suggested that the probability of a renesting attempt being parasitized will further influence whether hosts desert their currently parasitized nests.

However, delaying breeding may still be disadvantageous despite consistent nesting success throughout the season. Arcese and Smith (1985) found that Song Sparrows (*Melospiza* *melodia*) fledged early in the season dominated those fledged from later nests, regardless of parentage. As dominant individuals were more likely to survive than subordinate birds, they suggested that selection may favour females that lay early. Pianka and Parker (1975) hypothesized that the survivorship and hence, reproductive value, of young decreases as the breeding season progresses. Weatherhead (1989) supported this hypothesis by recording a corresponding decrease in nest defence by Song Sparrows over the season. Wolf (1987) asserted that the combined costs of nest desertion and renesting sometimes may exceed that of accepting parasitism (see also Rohwer and Spaw 1988).

Rothstein (1990), on the other hand, argued that hosts should almost always desert their nests rather than accept brood parasitism. In many passerines nest desertion delays breeding by only 5-7 days, which is not long enough to influence productivity (Clark and Robertson 1981, Rothstein 1990). Failure to desert parasitized nests may indicate a failure to recognize parasitism and this may be related to the type of stimulus that alerts birds to the occurrence of cowbird parasitism.

Experimental vs. natural parasitism

None of the Clay-colored Sparrows deserted its nest in response to experimental parasitism, with or without the cowbird model. As the sparrows neither responded to the parasitic egg nor the parasite itself, I conclude that this species is an acceptor of parasitism.

Only one cowbird host, the Cedar Waxwing (*Bombycilla cedrorum*), frequently deserts experimentally parasitized nests (Rothstein 1976, 1990), although other authors have reported hosts deserting nests implicitly as a result of natural cowbird parasitism (e.g. Clark and Robertson 1981, Wolf 1987, Graham 1988, Sedgwick and Knopf 1988, Burgham and Picman 1989, contra Rothstein 1986). The difference in responses to experimental and natural parasitism could result from two sources: either the proximate factor that elicits the response was absent during the experiment (see Rothstein 1975a) or the experiment was unrealistic (see Graham 1988).

Graham (1988) suggested that one way in which experimental parasitism may be unrealistic is in its timing relative to the host's egg-laying cycle. Cowbirds frequently parasitize nests early in the host's laying cycle but nests are often experimentally parasitized at later stages (2+ eggs; e.g. Rothstein 1975a). Early parasitism is potentially very costly to hosts. The cowbird has evolved a short incubation period (Briskie and Sealy 1990) and its young often hatch before the host young. A cowbird egg deposited in the early stages of the host's breeding cycle takes full advantage of this shortened incubation and places host young at a competitive disadvantage. For example, Solitary Vireo (*Vireo solitarius*) nestlings survive better when their cowbird nestmate is younger or the same age as themselves than they do when the cowbird is older (Marvil and Cruz 1989). From this point of view, it makes sense for hosts to desert nests parasitized early in the laying cycle. This is exactly what the Yellow Warbler (*Dendroica petechia*) does. Cowbird eggs deposited before the mid-point of egg laying are generally rejected by desertion or clutch burial, while those deposited later are usually accepted (Clark and Robertson 1981, Sealy 1992). Other species also show this pattern of behaviour (Ficken 1961, Rothstein 1975a). However, the experiments performed in the present study should not have differed from natural parasitism since I experimentally parasitized nests both before and after the mid-point of host laying and the sparrows' responses did not vary with the timing of parasitism.

Cowbirds sometimes parasitize nests prior to host egg-laying (e.g. Sealy 1992) and some species have been reported more likely to desert nests parasitized at this stage (e.g. Ficken 1961, Nero 1971, Clark and Robertson 1981, Sedgwick and Knopf 1987). Briskie and Sealy (1987) elicited desertion by Least Flycatchers by experimentally parasitizing nests with real cowbird eggs before any host eggs had been laid. It is possible that the variation in desertion rates exhibited by some species reflects variation in nests that were parasitized before or after the onset of clutch initiation. However, Rothstein (1975a) argued that desertion during nest building is common regardless of whether nests were parasitized. Clay-colored Sparrows deserted more than 30% of unparasitized nests found during building and these nests never received sparrow eggs. In contrast, none of the control nests monitored after the appearance of the first egg were abandoned. Several authors have reported Clay-colored Sparrows deserting nests that contained both cowbird and sparrow eggs (e.g. Fox 1961, Salt 1966, Knapton 1978) and, as such, these desertions cannot be accounted for by parasitism at the nest-building stage.

Graham (1988) suggested that another aspect lacking in most experimental parasitism is the presence of the laying parasite. Some hosts of the Common Cuckoo are more likely to abandon nests after they have seen a stuffed cuckoo on or near their nests (Davies and Brooke 1988, Moksnes and Røskaft 1989). Host recognition of the parasite is believed to have lead to several adaptations in the cuckoo that minimize interactions between host and parasite, including the cuckoo's rapid laying time (Davies and Brooke 1988). Similarly, the Brown-headed Cowbird lays quickly (Hann 1941) and Chance and Hann (1942) proposed that its pre-dawn laying time may help it avoid hosts (see also Scott 1991). This suggests that the presence of a cowbird at the nest may be an important cue to hosts and one that plays a role in determining the fate of parasitized nests.

Models typically are used to examine host responses to cowbirds (e.g. Robertson and Norman 1976, 1977, Folkers 1982, Hobson and Sealy 1989, Bazin 1991, Neudorf 1991). However, there has been some criticism as to whether taxidermic mounts really mimic live parasites. Burgham and Picman (1989) did not think models were realistic enough and used, instead, live caged birds in their experiments. Nevertheless, in this study the responses Clay-colored Sparrows exhibited toward the model were strikingly similar to those exhibited during the observed natural parasitism. Sparrows emitted alarm calls and attacked both model and live cowbirds, but ultimately accepted and incubated any introduced cowbird eggs.

Other factors leading to desertion

The other reason why responses to experimental and natural parasitism differ may be that the factor(s) that elicit(s) the response was not present during the experiment. Although few hosts of the Brown-headed Cowbird reject parasitism (Rothstein 1975a), most species respond to broken eggs in their nest (Blankspoor et al. 1982, Kemal and Rothstein 1988, Ortega and Cruz 1988), and to partial clutch reduction (Rothstein 1982b, 1986). These factors may be associated with cowbird parasitism but they are not unique to it and, thus, responses to broken eggs and PCR are not necessarily anti-parasite defences.

In the present study, Clay-colored Sparrows either ejected the "broken" eggs or they damaged them further by breaking off the adhered piece. I considered such damaging of eggs as evidence of failed ejection attempts. These responses occurred whether or not a cowbird egg was also present and, therefore, are not necessarily linked to parasitism. The presence of a broken egg did not elicit nest desertion. Hofslund (1957) noted that two Common Yellowthroats deserted nests that he attributed to broken eggs, but in both cases, the contents of the damaged egg had soiled the nest. Hofslund believed the eggs had been punctured by a cowbird's claw, presumably when it parasitized the nest. A situation like this might be interpreted mistakenly as desertion in response to cowbird parasitism. Desertion has also been attributed to broken host eggs in several other studies (e.g. Hann 1937, Wiens 1963, Lewis 1973, Smith and Atkins 1979).

Partial clutch reduction can occur when nests are preyed upon (Rothstein 1986), eggs are broken and then removed (Weatherhead 1991), or eggs are stolen by cowbirds (Sealy 1992). Both acceptors and rejectors of cowbird eggs respond to PCR (Rothstein 1982b). When clutches of the Eastern Kingbird (*Tyrannus tyrannus*) were experimentally manipulated such that all but one egg were replaced with cowbird eggs, the kingbird removed all cowbird eggs from its nest and then deserted the remaining lone egg (Bazin 1991).

In contrast, acceptor species do not possess true egg recognition (Rothstein 1982a, 1982b, 1986) and, therefore, will include any eggs present in the nest when assessing their clutch. Eastern Phoebes (*Sayornis phoebe*) assess on the basis of total clutch volume, not number, and as a result, are more likely to desert a clutch of two phoebe eggs than a clutch of two (larger) cowbird eggs (Rothstein 1986).

Similarly, Clay-colored Sparrows also appear to assess clutch volume. Removal of two sparrow eggs resulted in a 67% desertion rate. Most of these were four-egg clutches reduced to two eggs. However, reductions with the addition of a cowbird egg were accepted at 93.3% of the nests, even when the clutch was reduced to one sparrow egg and one cowbird egg (also see Rothstein 1986, Sealy 1992). As in the case of the phoebe, cowbird eggs are approximately twice the size of Clay-colored Sparrow eggs so that the addition of a cowbird egg maintained the original clutch volume.

Timing and intensity of egg removal

Sparrow responses to PCR still do not explain desertion of naturally parasitized nests since cowbirds not only steal host eggs, but also replace them with their own egg. This should compensate for any reduction in clutch volume and, in fact, may even increase clutch volume if only one host egg is removed. I suggest that the timing of egg stealing relative to cowbird laying may be important. Unlike my experiments, removal of host eggs at the time of parasitism has rarely been observed (Prescott 1965: 135, Nolan 1978: 371). Most egg-stealing incidents do not occur during the act of parasitism (Sealy 1992). If egg removal occurs before parasitism, it is possible that the hosts have already deserted their nest by the time the cowbird returns to lay.

However, in a study of Yellow Warblers, only 13% of the egg removals occurred prior to cowbird egg laying (Sealy 1992). In this same population, 41.2% of the cowbird eggs were laid in completed nests but before the warblers had initiated their clutches. In other words, there were no host eggs to remove. Cowbirds bent on removing a host egg at these nests had little choice but to remove it after laying their own. This is in contrast to the present study in which only 13.6% of the parasitisms occurred before clutch initiation.

Cowbirds also appear to remove more host eggs from Clay-colored Sparrow nests than they do from nests of Yellow Warblers. Sealy (1992) found that cowbirds remove a mean of 0.32 eggs per warbler nest, while data obtained from the PNRS show an average loss of 1.46 eggs per parasitized sparrow nest (see Sealy 1992 for rational that this egg loss is due to cowbirds and not predators). Thus, the intensity of host-egg removal appears to be variable. Other studies have recorded egg removal ranging from 1.65 (Zimmerman 1983) to 3.00 (Elliott 1978) eggs per parasitized nest, while Petit (1991) found that egg removal varied throughout the season (see also Zimmerman 1983, Sealy 1992).

In the present study, an estimated 32 eggs disappeared from 22 parasitized nests or approximately 1.5 eggs lost per nest. At most of these nests, sparrow eggs were removed and cowbird eggs appeared between nest checks on consecutive days. Cowbirds have been observed removing host eggs throughout the day (see Sealy 1992 for a review) and lay their own eggs just before dawn (Hann 1941, Scott 1991). Since I usually checked nests in the morning, it is possible that egg removal occurred during the afternoon or evening on the day of the first check and the cowbird egg was laid during the morning of the second check, possibly in an already deserted nest.

The possible relationship between the timing and intensity of host-egg removal is intriguing. Yellow Warbler nests tend to be parasitized in the early stages of the nesting cycle and are subjected to moderate egg removal (0.32 eggs per nest, Sealy 1992), while Clay-colored Sparrow nests are often parasitized after clutch completion and lose more eggs (1.46 eggs per nest, this study). It is possible that partially incubated eggs pose a larger threat to the cowbird in terms of nestling competition and cowbirds parasitizing completed clutches may attempt to reduce this competition as much as possible through increased host-egg removal.

Adaptive value of nest desertion

Rothstein (1982b) argued that acceptance of cowbird parasitism is maladaptive and that the existence of acceptor species can be explained as a result of an evolutionary lag (also see Rothstein 1975a, 1990). Most species respond to partial clutch reduction, but only a few respond specifically to cowbird parasitism (Rothstein 1982b, 1986). Rothstein (1986) suggested the reason for this is that PCR has been a selective pressure longer than has parasitism. He further hypothesized that parasitism is now the stronger selective pressure (Rothstein 1986).

The adaptive value of responses to PCR in countering nest predation is readily apparent (Rothstein 1986), but here I would like to argue that under some circumstances such responses also might be adaptive in terms of cowbird parasitism. Although some cowbird hosts frequently are reported to lose all of their young when parasitized (see Rothstein 1990 for a review), other studies indicate that the major impact of parasitism is host-egg removal (Smith 1981, Hatch 1983, Wolf 1987).

Several studies of Clay-colored Sparrows have shown that fewer sparrows fledge from parasitized than from unparasitized nests (e.g. Fox 1961, Knapton 1978, Buech

1982), but it is unclear how much of this effect is due to egg removal and how much is due to the presence of the cowbird egg or nestling. Further ambiguity arises when authors include nest desertion in their tallies of nest failure due to parasitism. If the major impact of cowbird parasitism on Clay-colored Sparrows is host-egg removal, then it may be adaptive for this species to respond to PCR, rather than to the cowbird egg or female cowbird itself. Some species reported to be impacted mainly by egg removal also desert nests in response to PCR (e.g. Zimmerman 1983, Wolf 1987). Furthermore, nest predation, which also can partially reduce clutches, is prevalent in Clay-colored Sparrow populations. In the present study, almost 42% of the nests found in 1990 were depredated at the egg stage and 17% of these involved PCR. Sparrows deserted 71% of clutches partially reduced by predators. Nest predation is believed to be the single most important factor affecting bird reproductive success (Ricklefs 1969) and responses to PCR can counter both predation and egg removal by cowbirds.

As PCR can occur in the absence of cowbird parasitism, and because Clay-colored Sparrows desert nests regardless of the agent of clutch reduction, nest desertion has not evolved as an anti-parasite defence in this species. Nevertheless, desertion still may be an adaptive response for sparrows confronted by cowbird parasitism and host-egg removal by the parasite.

SUMMARY

1. Clay-colored Sparrows did not desert their nests in response to experimental parasitism with or without the presence of a model cowbird at the nest, changes in clutch composition, or the presence of broken eggs in the nest.

2. Only reductions in total clutch volume elicited nest desertion.

3. Sparrows responded to broken eggs either by ejecting them or by removing the glued piece of eggshell from them. Removal of the piece of eggshell may indicate a failed ejection attempt.

4. Almost 60% of naturally parasitized Clay-colored Sparrow nests were deserted. Deserted nests experienced greater egg loss than nests that were not deserted. Egg loss was probably the result of host-egg removal by cowbirds.

5. In 1990, 17% of nests depredated at the egg-stage lost some, but not all, of their eggs. Clay-colored Sparrows deserted 71% of these nests.

6. Clay-colored Sparrows desert their nests in response to PCR. PCR is not unique to cowbird parasitism and the sparrows do not distinguish between the agents of clutch reduction. Therefore, nest desertion by Clay-colored Sparrows cannot be considered an anti-parasite defence.

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Appendix: Mean length, breadth, and volume of eggs of Clay-colored Sparrows and Brown-headed Cowbirds.

	N	Mean	SE
Sparrow			
Length (mm)	140	16.8	0.07
Breadth (mm)	140	12.8	0.04
Volume (ml)	140	1.4	0.01
Cowbird (from Sealy 1992)			
Length (mm)	77	21.07	0.12
Breadth (mm)	77	16.36	0.09
Volume (ml)	77	2.82	0.33