Cues used by brood parasites and predators
to locate nests

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by

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CUES USED BY BROOD PARASITES AND PREDATORS

TO LOCATE NESTS

BY

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A Thesis submitted to the Faculty of Graduate Studies of the University of Manitoba
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MASTER OF SCIENCE

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ABSTRACT

Predators and avian brood parasites must locate potential prey or hosts. They use a variety of cues to do this. This thesis examines five cues that could be used by predators and brood parasites to locate nests of Clay-colored Sparrows (*Spizella pallida*) to depredate or parasitize, respectively: nest concealment, nest height, supporting vegetation, parental activity, and parental aggression. Nest concealment, nest height and supporting vegetation were recorded for each active nest found and related to nest outcome. Parental activity was examined using nest placements simulating different levels of activity (an empty nest, a full clutch, one egg per day until a full clutch was achieved, one egg per day plus a model Clay-colored Sparrow perched near the nest, one egg per day plus a model plus a playback of a recorded Clay-colored Sparrow song). Parental aggression was studied using model testing using four models, a Brown-headed Cowbird *Molothrus ater* (a brood parasite), a Common Grackle *Quiscalus quiscula* (an avian predator), a Franklin's ground squirrel *Spermophilus franklinii* (a mammalian predator) and a Fox Sparrow *Passerella iliaca* (a control). None of the cues examined seem to be used by either predators or parasites to locate nests. Nest concealment, whether viewed from a parasite's point of view or a predator's was not related to nesting outcome. Most nests (67%) were highly concealed with 80-100% concealment. Neither nest height nor supporting vegetation affected nesting success. Most nests (41%) were built at heights of 101-200 mm and were placed in snowberry *Symphoricarpos occidentalis* (77%). None of

the five levels of simulated parental activity elicited parasitism. Predation frequencies remained unaffected. Parental aggression could not be used to locate nests, as Clay-colored Sparrows were found not to be aggressive towards the models.

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GENERAL INTRODUCTION

To survive, animals must overcome many obstacles. Among other things, they must eat, reproduce and find shelter. Predators and parasites must locate appropriate prey and hosts; prey and hosts must avoid being eaten and parasitized. Nest predators and avian brood parasites must search for suitable nests. Little is known about how they do this and what cues they use. This thesis explores experimentally some of the possible cues to which nest predators and parasitic birds respond.

Predation is responsible for up to 55% of brood losses (Ricklefs 1969, Martin 1992a). Most mammalian predators rely on olfaction to locate prey whereas avian predators are visual (Colwell 1992). Predators do not choose a particular set of species to depredate. Individual species of predators seem to be less selective than Brown-headed Cowbird (*Molothrus ater*) parasitisms. This is demonstrated by the large variety of species' nests affected by predation (see Ricklefs 1969). Predators may search an area and opportunistically prey upon nests and hence specific cues may not be that important.

A second cause of nest failure is avian brood parasitism, which may be responsible for up to 40% of nest losses (Ricklefs 1969). Brood parasitism is an alternative reproductive strategy in which an individual of one species (the parasite) lays its eggs in the nests of an individual of another or the same species (the host). The host then incubates the eggs and raises the parasite's young. Parasitism

frequently is costly to the host, in the form of lost reproductive effort such as egg removal (Sealy 1992), eviction of eggs or young (Wyllie 1981, Gill 1983), inefficient incubation (Petit 1991), or competition between parasitic and host young (Rothstein 1975, Payne 1977).

An obligate parasite, the Brown-headed Cowbird has always been thought to employ a generalist strategy in its use of hosts. Brown-headed Cowbirds have been reported parasitizing 216 species, although only 139 have been reported successfully raising young cowbirds (Friedmann et al. 1977). These numbers show, however, that although many species are potential hosts, some are preferred over others, for reasons that are not yet fully understood. In fact, several studies have also shown that cowbirds parasitize nests of some species much more frequently than others in the same community (e.g., Hill 1976, Elliott 1978, Fleischer 1986, Briskie et al. 1990). This suggests that cowbirds may be choosing among the available hosts, i.e. not employing a generalist strategy.

Payne (1977) discussed several characteristics that might influence host selection. Cowbirds require high-protein food, which makes certain seed-eating species such as American Goldfinches (*Carduelis tristis*) incompatible as hosts (see Middleton 1977, 1991). If host eggs are too large, the cowbird's eggs may not be effectively incubated (Payne 1977). Payne also mentioned that the more abundant host species are more likely to be parasitized (also see Friedmann 1929). Wiley (1988) identified several other characteristics important for host selection. The timing of the breeding seasons of both host and parasite must overlap (see also Carey 1982,

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Burgham 1985) for the eggs to hatch in time for the young to be raised successfully. Nest defence by the host, through aggression or nest guarding, may influence host selection by making some hosts more dangerous to parasitize (Slack 1976, Neudorf and Sealy 1992). The final and perhaps most important characteristic is that hosts accept the parasitic egg. Rothstein (1975) identified accepters and rejecters of cowbird eggs by artificially parasitizing nests of approximately 50 actual and potential hosts of the Brown-headed Cowbird. He found that about a dozen species consistently ejected the cowbird egg whereas other species accepted it. It is important to the cowbird that a potential host accept parasitism; otherwise its egg is wasted. Ankney and Scott (1980) suggested that a cowbird would lay in an rejecter's nest if an accepter's nest was not available at the time of parasitism.

Some workers have suggested that cowbirds lay their eggs at random in any nest they happen upon (Mayfield 1965). Others have suggested that cowbirds discriminate among available nests in which they lay (Elliott 1977). Preston (1948) was the first to examine the distribution of cowbird eggs and to compare it to a Poisson (random) distribution. He looked at five data sets and found that only two fit a Poisson distribution, whereas the others did not. He then analyzed the data assuming that the first cowbird egg was not placed at random and all subsequent eggs were. Using this assumption he found that all five data sets fit a Poisson distribution, i.e. that cowbirds lay all subsequent eggs randomly. Elliott (1977) found similar results in the community he studied and concluded that cowbird egg distribution is non-random, which implies that cowbirds choose nests to parasitize. Linz and Bolin

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(1982) also had similar results, whether they looked at the total number of nests or only those parasitized.

Mayfield (1965), however, concluded that cowbirds lay at random, including their first egg. He examined eight studies and five of these conformed to a Poisson distribution. In the other three studies, he corrected a bias for deserted nests. This approach, however, introduced a new bias that may be just as important as the bias for deserted nests (see Elliott 1977). Mayfield had equivocal results with five cases supporting a random distribution of eggs and three cases supporting nest selection. Lowther's (1984) results were similar to Mayfield's. Lowther separated nests without cowbirds eggs into (1) nests undetected by cowbirds and (2) nests found but not parasitized. He included only the second category in his calculations and found that only four of 14 cases departed from a Poisson distribution, with each of the species receiving a high frequency of parasitism. Lowther concluded that female cowbirds select nests opportunistically.

The idea that cowbirds choose nests is gaining support as several studies have shown different parasitism frequencies on various species in a given community (Carter 1986, Fleischer 1986, Wiley 1988, Briskie et al. 1990, Ortega et al. 1994). This indicates that cowbirds are able to choose which nests they parasitize.

Nest predators and avian brood parasites must first locate nests from which to obtain food and to parasitize, respectively. Parasites are faced with the additional problem of selecting the "best" nest from those found. Predators may also select the most profitable prey from those found (Krebs and Cowie 1976). Predators and

parasites may locate nests by looking for the actual nest, watching the parents building nests, flying over an area and flushing an incubating parent off the nest, smelling the parent on the nest or the eggs or nestlings, seeing the eggs or eggshells, detecting movements and hearing the sounds of the nestlings or by responding to alarm calls of the parents (Prescott 1965, Gottfried and Thompson 1978, Collias and Collias 1984, McLean et al. 1986). Predators may use all or some of these cues, depending on the prey and type of predator (olfactory versus visual; Clark and Nudds 1991, Colwell 1992).

In this study, I examined experimentally some of the cues that brood parasites and predators might use to locate nests. I did not examine whether these same cues may be used by parasites and predators to select nests.

INTRODUCTION

Both predators and cowbirds must locate nests and choose a suitable one from among those found. They may use similar cues, as brood parasites can be considered a type of predator (Wiley 1982). Very little is known about how predators locate nests (Smith 1974, Collias and Collias 1984). Few studies have looked at the predator/prey interaction from the point of view of the predator. Much of the literature describes tactics used to avoid being eaten or what occurs after food has been found or procured (but see Bell 1991). There is a large body of literature on optimal foraging that discusses what happens once the prey has been found (reviews in Krebs and McCleery 1984, Pyke 1984), which indicates that predators should choose the most profitable prey given their current condition.

Andersson (1981) described three general methods of searching by predators: (1) continuous movement, (2) sitting and waiting, and (3) pausing and travelling. Different animals use different techniques. Many avian predators often use the sit and wait and the pause and travel techniques. Birds have been documented perching and scanning, hovering and soaring in search of food (Carlson 1985, Viitala et al. 1995). Avian predators that hunt on the ground and mammalian predators are believed to find prey using directional, systematic searching or random search movements (Zach and Smith 1981, Benhamou 1992).

Three methods of searching, in this case for nests to parasitize, have also been documented for Brown-headed Cowbirds: (1) watching hosts at their nests, (2) silently

searching for nests, and (3) flushing hosts off nests (Norman and Robertson 1975, Wiley 1988). The most common method is watching hosts (Friedmann 1929, Hann 1941, Payne 1973).

Two behaviours predators and cowbirds could cue in on are activity and aggression of nest owners, which may indicate that there is an active nest in the area and draw the predator or parasite to the nest. Some other cues that might be used include song rates of adults and parental aggression to indicate the bird's quality (Smith 1981, Arcese and Smith 1988), activity around the nest to indicate nesting stage, nest placement (e.g., height, supporting vegetation, concealment), and nest type (Thompson and Gottfried 1981, Fleischer 1986, Orians et al. 1989, Briskie et al. 1990, Colwell 1992). These cues may lead predators or cowbirds to nests, may help them select nests and perhaps even provide information on the fitness of the adults (Smith 1981). For example, the more time a male can devote to singing, the more fit it may be (see Greig-Smith 1980, 1982; Reid and Sealy 1986).

In this study, I examined experimentally five cues that might be used by both predators and parasites to locate nests: nest concealment, nest height, vegetation supporting the nest, parental activity, and parental aggression.

Some researchers have suggested that predation is related to concealment for predators who rely primarily on sight to locate prey (Knapton 1978b, Wray and Whitmore 1979). Following this, visual predators should have more difficulty locating well-concealed nests with the result that these should be preyed upon less frequently. Predators who hunt by smell should be able to better locate nests regardless of

concealment simply because they do not rely primarily on visual cues (Clark and Nudds 1991, Holway 1991). Thus, if the major predators in an area use olfaction to find nests, predation frequencies should be independent of concealment.

For Clay-colored Sparrows (*Spizella pallida*), Knapton (1978b) found that better-concealed nests were depredated less frequently. Studies on other species have shown similar results but only for visual predators (Clark and Nudds 1991, Colwell 1992). The extent of this relationship for olfactory predators, however, is unknown. Knapton (1978a) concluded that ground squirrels were visual predators from his observation that they depredated well-concealed nests in snowberry (*Symphoricarpos occidentalis*) less frequently. However, most mammals use their sense of smell to locate food (Young 1957). Further, studies specific to rodents have demonstrated that they rely primarily on olfactory cues to locate prey (Howard et al. 1968, Jennings 1976). It is reasonable, therefore, to assume that ground squirrels are olfactory predators contrary to Knapton (Boonstra et al. 1990, Colwell 1992, but see Norment 1993). I predicted, therefore, that concealment is not related to nesting success of Clay-colored Sparrows because the Franklin's ground squirrel (*Spermophilus franklinii*) is its main predator.

Cowbirds are visual animals and it is reasonable to expect that they would parasitize less concealed nests more frequently simply because they are easier to locate. This raises a paradox, however, because other studies suggest that birds should select nest sites that reduce predation of their young (Murphy 1983). As better concealed nests suffer less predation (McLean et al. 1986, Sugden 1987,

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Brown and Fredrickson 1989), cowbirds should parasitize better-concealed nests because they will also benefit from this reduced level of predation (see Gates and Gysel 1978). Further, highly concealed nests may also allow cowbirds to gain access to nests unnoticed by hosts so that they can lay their egg unmolested. The apparent importance of laying unnoticed by hosts is suggested by the fact that cowbirds take only a few seconds to lay their eggs and do so before sunrise when it is still fairly dark and many hosts are away from their nests (Scott 1991, Neudorf and Sealy 1994, Sealy et al. 1995). I predicted that these latter factors are more important to the cowbird than the difficulties in locating well-concealed nests and thus cowbirds should parasitize well-concealed nests more frequently.

Nest height and supporting vegetation may in fact be used as cues to locate nests. If nests are at a set height or in a particular species of plant, this would allow predators and parasites to form search images and "know" where to look. Briskie et al. (1990) showed that lower nests were parasitized more frequently. Filliater et al. (1994) discussed five hypotheses that explain how both nest height and vegetation could provide cues for predators when looking for nests. These hypotheses involve nest inaccessibility, nest height (high, mid-height and low nests) and vegetation (common and rare plants). They indicate that there is a wide variety of possible explanations for where nests are placed depending on the type of predators in the area. I predicted that nests that were built higher in the vegetation would be less successful because they are more obvious. I predicted that the vegetation supporting

the nest would influence nesting outcome, in that some vegetation offers better protection from nest threats than others.

Parental activity at nests may be used by cowbirds to locate nests (Friedmann 1929, Hann 1941, Buech 1982, Wiley 1988). I tested this by placing out old nests (see Thompson and Gottfried 1981). For parental activity to assist the cowbird in finding nests, activity must be centred near or at the nest and occur when parasitism is appropriate. These activities may include nest building, mate guarding, nest visits and egg laying. Several studies have shown that when old nests were placed out, even with eggs, cowbirds did not lay eggs in them (e.g., Laskey 1950, Thompson and Gottfried 1976). Therefore, Lowther (1979) and Thompson and Gottfried (1981) attempted to simulate parental activity by adding one egg per day to each nest, but still recorded only a low frequency of parasitism (see also Wiley 1988). This suggests that more obvious parental activity is indeed necessary. I investigated this by simulating five levels of increasing parental activity: empty nests, nests with full clutches, nests in which one egg was placed per day, nests with model hosts and nests with song. I predicted that the frequency of parasitism will increase with increasing amounts of parental activity.

Predators may also use parental activity at the nest to locate nests (review in Collias and Collias 1984). The activity of adults may direct the predator to the nest site or may cue it to an active nest nearby. Here, too, I predicted that simulating increasing amounts of activity of nest owners at artificial nests should cause the frequency of predation to increase.

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Parental aggression has usually been thought to discourage both predators and parasites (Buitron 1983, Smith et al. 1984, Martin 1992b). Some hosts can distinguish cowbirds from other potential nest threats (Nice 1937, Robertson and Norman 1976, Hobson and Sealy 1989, Neudorf and Sealy 1992). Enemy recognition can be tested experimentally by placing models of different enemies near nests and quantifying the birds' responses to them. Some species react more aggressively to a cowbird model, thus providing a potential cue for cowbirds to locate active nests (Robertson and Norman 1977, Smith 1981). For a variety of species, e.g. Red-winged Blackbird (*Agelaius phoeniceus*), parental aggression such as chases, alarm calls, attacks and strikes is directed towards a female cowbird (Hobson and Sealy 1989, Neudorf and Sealy 1992). It has been suggested that individuals that defend their nests more aggressively will be parasitized more frequently because they are more likely to be near their nests and reveal their positions (Robertson and Norman 1977, Smith 1981, Carter 1986). This has become known as the nest-cue hypothesis. Smith (1981) also suggested that parental aggression may reflect parental quality. Parental aggression being used by nest-searching cowbirds has been viewed as "maladaptive" (Smith 1981, Smith et al. 1984) because it potentially lowers the reproductive output of hosts. Smith et al. (1984) suggested that the use of parental aggression as a cue to nest location could have come about when the potential benefits of successfully driving off some predators with aggressive behaviour outweighed the potential cost of attracting cowbirds. For the nest-cue hypothesis to be supported, nesting birds must respond to a threat at a distance that would enable the cowbird to use the

behaviour to locate the nest. If the birds do not react until the cowbird is very close (e.g. 0.5 m or less), then the nest probably has already been found and the nest-cue hypothesis is invalidated (Neudorf and Sealy 1992). If the level of aggression increases as the nest is approached, then the nest-cue hypothesis may be borne out (Duckworth 1991). I predicted that hosts will react to a nest threat at distances greater than 0.5 m, thus allowing parental aggression to be a mechanism for finding nests.

Predators also may use aggression to locate nests. Some studies have found that more aggressive pairs were depredated more frequently (Searcy 1979, Röell and Bossema 1982), whereas other studies have found the opposite (Greig-Smith 1980, Blancher and Robertson 1982). I predicted that if predators are able to use aggression to locate nests, nest owners must respond aggressively towards a model at different distances from their nests, perhaps becoming more aggressive as the model is placed closer to the nest and the threat increases. Knapton (1978a) stated that nest defense does not prevent predation. This may also apply to parasitism because cowbirds are larger than Clay-colored Sparrows. Sealy (1994) presented many observations of both predators and parasites being successful despite the presence of the nest owners, including nests of Clay-colored Sparrows (see also Neudorf and Sealy 1994, but see Buitron 1983). Therefore, if sparrows have little chance of deterring predators or cowbirds, concealment of the nest and minimizing their activity around the nest may be alternative strategies to increase their reproductive output. Minimizing the activity around the nest could be accomplished

in two ways: (1) males could avoid the nest during building and egg laying, or (2) the adults could temporarily abandon the nest site when a nest threat is approaching (Burgham 1985).

In the present study, I examined the importance of parental activity and aggression to Brown-headed Cowbirds and predators in locating nests. I also determined if nest concealment, supporting vegetation and nest height were used as cues to locate nests. The study species involved is the Clay-colored Sparrow, an accepter species (Hill and Sealy 1994).

METHODS

Study Site

This study was conducted at the University of Manitoba Field Station, Delta Marsh (50° 10′ N, 98° 22′ W), Manitoba, during the springs of 1993 and 1994, in an area known as the Oxbow Woods. Situated along the southern edge of Delta Marsh, this woodlot is surrounded by old-field succession dominated by snowberry and wild rose (*Rosa* sp.) (see Evans 1972, Gamble 1980, Hill 1992, Hill and Sealy 1994).

Locating Nests

All experiments except those relating to parental activity were conducted with active Clay-colored Sparrow nests. I searched the southern portion of the study site for sparrow nests daily from mid-May to the end of June. I searched the habitat thoroughly, checking every tuft of grass and snowberry bush. I flagged and numbered each nest approximately 2 m away, and inspected each nest daily until the fourth day of incubation for signs of predation, i.e. broken eggs, eggshells, tipped nests, missing eggs (see Major 1991, Sealy 1994) and parasitism, i.e. presence of a cowbird egg.

Nest Concealment

I quantified the degree of concealment at each nest by assigning cover values on a scale from 1-5, that corresponded to increasing concealment of the nest (1=0-20% concealed, 2=20-40% concealed, etc.). Estimates were made from eight

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compass directions, at two heights (nest height and the observer's eye level) and one value from above the nest. I then calculated an average concealment value. All measurements were taken one meter from the nest (see Holway 1991). These measurements simulated the cowbird's or avian predator's vantage point (observer's eye level; see Gochfeld 1979) and a mammalian predator's vantage point (nest height). The concealment estimate from above was intended to reflect what a cowbird may see when perched. I estimated the cover value on the day the nest was tested (see below) or on the day the last Clay-colored Sparrow egg was laid. This ensured that the nest was active (Friedmann 1929, McGeen 1971). I then correlated concealment values with the nest outcome (predation, parasitism or success). I considered a nest successful if the clutch was still intact three days after the last egg was laid. The three-day cutoff was chosen because Clay-colored Sparrows are sometimes parasitized shortly after the clutch is complete. The chosen time frame includes four days of incubation. However, most parasitism occurs during the egg-laying period (Hill 1992). I ended the experiment before fledgling success was known because I wanted a comparable time frame for both parasitism, which occurs near the beginning of the nesting cycle, and predation, which occurs throughout the nesting cycle.

Nest Height and Supporting Vegetation

I recorded the height of the nest rim from the ground. For analysis, I broke the heights into increments of 100 mm, the approximate height of a single nest. The

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dominant plant species in which the nest was placed was recorded to determine if there was any relationship to nest outcome.

Parental Activity

Old Clay-colored Sparrow nests (collected by D.P. Hill in 1991, and by me in 1993) were placed randomly in Clay-colored Sparrow nesting habitat from 3 to 18 June in 1993 and 6 to 21 June in 1994. Nests were placed in sites with known (controlled) concealment values (Lowther 1979) for eight days, which simulates one day as an empty nest, four days of egg laying and three days of incubation (four-egg clutches are the modal clutch size for Clay-colored Sparrows at Delta (Hill 1992)). I placed the nests 3 m apart along a transect, 1 to 2 m alternately to the left or right of a rope stretched along the transect. I flagged each nest location along the rope so that I could relocate the nests. With this spacing, nests were 4 to 6 m apart, as they were placed on alternate sides of the rope and 1 to 2 m from it. I chose this spacing because Clay-colored Sparrow territories are small (natural nests are sometimes within 5 m of each other (Knapton 1979)). Nests received one of five treatments: (1) no eggs (nest was left empty), (2) full clutch of four artificial eggs was introduced on day 1, (3) one artificial egg was introduced per day until a full clutch was achieved, (4) treatment 3 with the addition of model Clay-colored Sparrow perched near the nest, or (5) treatment 4 with the addition of a playback of a recorded Clay-colored Sparrow song (Thompson and Gottfried 1981). I discuss the manufacture of artificial eggs and treatments 4 and 5 in greater detail below. Each

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treatment, consisting of 20-35 nests, simulated laying and different amounts of parental activity to determine if parental activity influenced predation and parasitism frequencies (see Wiley 1988). Comparisons were made between treatments for the three nest outcomes to determine if parental activity affected nesting outcome.

The eggs were made of plaster-of-Paris and painted to resemble Clay-colored Sparrow eggs (Rothstein 1975). The eggs were slightly larger and heavier than real Clay-colored Sparrow eggs (2.2 g versus 1.6 g; 17.5 mm x 13.4 mm versus 17.1 mm x 12.7 mm; measurements from Walkinshaw 1944 and Bent 1968). The slightly greater mass and size should not affect the study because predators were able to remove the eggs (pers. obs.) and there is some natural variation in egg size (Bent 1968). Cowbirds should not be affected because they are known to parasitize species with eggs that are larger than those of Clay-colored Sparrows (e.g. Fleischer 1986). I placed nests in active territories as the study was conducted during the breeding season of Clay-colored Sparrows. Thus, there was an increased level of activity near the experimental nests that was in addition to the simulated levels of activity. This may have been a problem but the activity probably was similar for each artificial nest. This problem was not addressed in other studies using artificial nests in active territories (see Lowther 1979, Thompson and Gottfried 1981).

The models used in treatment 4 and 5 were Clay-colored Sparrows, freeze-dried and mounted on poles, and placed facing the nest. The models were placed 0.5 m from the nest for 30 minutes every morning from 0630-1000 (Central Standard Time) for 7 days (Wiley 1988). Cowbirds are active in nesting areas in the morning

and then move off these areas to feeding areas during the late morning or early afternoon (Rothstein 1984). Treatment 5 utilized songs of Clay-colored Sparrows that had been recorded in 1993 and transferred to a loop tape at a rate of 9 songs/minute, a rate that fell within the natural song rate (Bent 1968). Song was played back for 30 minutes on a cassette recorder placed at the base of the pole. The model treatment and model plus song treatment were randomly assigned to nests and to a different 30-minute period every day so that each nest received the treatment over each 30-minute period during the experiment. Two runs of nest placements were conducted to increase sample size.

For nest concealment, nest height, supporting vegetation, and parental activity, Fisher exact tests (2-tailed) were used for desired comparisons of each cue and nest outcome because the populations were not normally distributed and had cell sizes smaller than five (Conover 1980, Zar 1984).

Parental Aggression

Enemy recognition

To test whether Clay-colored Sparrows recognized different nest threats, I used the data on responses by sparrows to three models (female Brown-headed Cowbirds, Franklin's ground squirrel and Common Grackle *Quiscalus quiscula*) placed 0.5 m from active nests from the distance testing experiment (see below). I added a fourth model, a Fox Sparrow (*Passerella iliaca*), to serve as a control. The sparrow is a good control because it is similar in shape and size to female cowbirds

but neither parasitizes nor preys upon Clay-colored Sparrow nests. It is found on the study area only during migration and therefore should rarely interact with Clay-colored Sparrows. Thus, I expected the Fox Sparrow to elicit low levels of aggression (see Hobson and Sealy 1989, Neudorf and Sealy 1992, Bazin and Sealy 1993). These models allowed determination of responses to different potential enemies. In this series of tests, I included only tests where birds responded because I was interested in the actual aggressive responses of the birds and not whether they responded by avoiding the nest.

The tests were conducted during the egg-laying stage. Data were tape-recorded and later transcribed. The responses of Clay-colored Sparrows were recorded following the methods of Smith et al. (1984), as modified by Hobson and Sealy (1989). Responses were: (a) time spent <2 m, 2 m to 5 m or >5 m from the model, (b) vocalizations (chip, quiet chip), (c) hidden in the vegetation, (d) attacks, (e) feeding, (f) incubating, (g) perching, (h) out of area, and (i) singing. I scored categories a, c, e, f and h as the number of 10-second intervals in which they occurred while I scored all other categories as the actual number of times they occurred in the 5-minute test (refer to Table 1). The time Clay-colored Sparrows took to react to the model was also recorded as an indication of parental attentiveness. The responses of both male and female were combined as the sexes could not be distinguished in this unmarked population. Each test was run for 5 minutes with 15-minute rest periods between successive model presentations to reduce carry-over aggression. Observations were made from a blind 5 to 10 m from the nest. The

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models used in the distance testing were taxidermically mounted in upright, non-threatening postures. Models were placed facing the nest. Nests were tested from 0600 to 1900 (CST) and each nest was tested only once at all three distances. The test was started when a bird returned to within 5 m of the model. If no bird showed up within 30 minutes, the test was ended and this was considered no response.

Distance testing

To test the nest-cue hypothesis, I placed a female cowbird model 0.5 m, 2.5 m and 4.5 m from nests to determine at what distance Clay-colored Sparrows reacted to a cowbird. The farthest distance was selected on the basis of territory size, which sometimes placed nests as close as 5 m apart (Knapton 1979). This test permitted determination of the possibility that a cowbird could use parental aggression to locate nests. To determine if predators elicited aggressive behaviour that could be used as a cue, model testing at the same three distances was done using an avian predator (Common Grackle) and a mammalian predator (Franklin's ground squirrel). The grackle was chosen as the avian predator because it breeds in the study area.

I chose the Franklin's ground squirrel as the mammalian predator because it is found on the study area in substantial numbers and is known to prey on bird nests (Sowls 1948, Knapton 1978b, Sargeant et al. 1987). To act as a control, I tested four nests with a model Fox Sparrow placed at the three distances.

For the distance-model testing, Friedman analysis of variance was used due to the nonparametric nature of the data. For the enemy recognition testing, I used

the Kruskal-Wallis test. If a significant difference was found between the distances or models, I then used nonparametric multiple comparisons to determine where the difference was (Conover 1980, Conover and Iman 1981; also see Neudorf 1991).

TABLE 1: Definitions and units of measurement for behavioural responses recorded during the parental aggression experiments.

Response	Description	Unit of measurement
< 2 m	Distance of parent(s) from model	Number of 10-sec intervals each parent spent at this distance during the 5 min trial
2-5 m	Distance of parent(s) from model	Number of 10-sec intervals each parent spent at this distance during the 5 min trial
> 5 m	Distance of parent(s) from model	Number of 10-sec intervals each parent spent at this distance during the 5 min trial
Incubation	Female on nest	Number of 10-sec intervals the female spent on the nest during the 5 min trial
In vegetation	Parent(s) hidden in vegetation	Number of 10-sec intervals each parent spent in the vegetation during the 5 min trial
Leave area	Parent(s) no longer in sight	Number of 10-sec intervals each parent was out of sight during the 5 min trial
Chip	Alarm call given by parent(s)	Number of times the call occurred during the 5 min trial
Quiet chip	Communication call given by parent(s)	Number of times the call occurred during the 5 min trial
Close passes	Parent(s) swoop over model	Number of times behaviour occurred during the 5 min trial
Perch changes	Parent(s) hop from perch to perch	Number of times behaviour occurred during the 5 min trial
Return time	Time it took one or both parents to return to nest area	Seconds

RESULTS

I found 112 Clay-colored Sparrow nests, of which 13 were parasitized (11.6%), 12 were preyed upon (10.7%), and 87 were successful (77.7%) in the first eight days of the nesting cycle. The three outcomes of the nests did not differ between the two years (Fisher exact test, $p=0.712$).

Nest Concealment

Most nests (>67%) were highly concealed (concealment values between 4 and 5). For all concealment values taken at both eye-level and nest-level (Table 2), the three outcomes did not differ significantly (eye-level, Fisher exact test, $p=0.391$; nest-level, Fisher exact test, $p=0.642$). Concealment values measured from above also did not differ significantly for the three possible outcomes (Fisher exact test, $p=0.149$).

Nest Height and Supporting Vegetation

Nest height did not affect nest outcome (Fisher exact test, $p=0.203$). Forty-one percent of the nests were built at heights from 101 to 200 mm (Table 3). Snowberry was the dominant plant with 77% of nests built in this species (Table 4). Nest outcome was not related to supporting vegetation (Fisher exact test, $p=0.826$).

TABLE 2: Frequency of parasitism, depredation and nest success of Clay-colored Sparrow nests for five concealment value categories taken at eye-level and nest-level.

Concealment[a] values (% concealed)	Nest Outcome[b]			
	Parasitized (%)[c]	Depredated (%)[c]	Successful (%)[c]	Total (%)[c]
Eye-level				
40-60	2 (1.8)	0	7 (6.3)	9 (8.1)
60-80	1 (0.9)	4 (3.6)	23 (20.5)	28 (25.0)
80-100	10 (8.9)	8 (7.1)	57 (50.9)	75 (66.9)
Total	13 (11.6)	12 (10.7)	87 (77.7)	112 (100.0)
Nest-level				
40-60	0	0	0	0
60-80	1 (0.9)	0	3 (2.7)	4 (3.6)
80-100	12 (10.7)	12 (10.7)	84 (75.0)	108 (96.4)
Total	13 (11.6)	12 (10.7)	87 (77.7)	112 (100.0)

[a] Includes eight directions and above that emulate what a cowbird or an avian (eye-level values) or mammalian (nest-level values) predator would see.
[b] No nest fell in the 0-20% or the 20-40% concealment categories.
[c] Number of total nests. Percentage of total nests in parentheses.

TABLE 3: Frequency of parasitism, depredation and nest success of nests for 13 height categories.

Nest height (mm)	Nest Outcome			
	Parasitized (%)[a]	Depredated (%)[a]	Successful (%)[a]	Total (%)[a]
0-100	2 (1.8)	1 (0.9)	8 (7.1)	11 (9.8)
101-200	4 (3.6)	3 (2.7)	39 (34.8)	46 (41.1)
201-300	3 (2.7)	7 (6.3)	31 (27.7)	41 (36.7)
301-400	2 (1.8)	1 (0.9)	7 (6.3)	10 (9.0)
401-500	1 (0.9)	0	2 (1.8)	3 (2.7)
501-650	1 (0.9)	0	0	1 (0.9)
Total	13 (11.6)	12 (10.7)	87 (77.7)	112 (100.0)

[a] Number of total nests. Percentage of total nests in parentheses.

TABLE 4: Frequency of parasitism, depredation and nest success of nests for five supporting vegetation species.

Plant Species	Nest Outcome			
	Parasitized (%)[a]	Depredated (%)[a]	Successful (%)[a]	Total (%)[a]
Snowberry	11 (9.8)	8 (7.1)	67 (59.8)	86 (76.7)
Rose	0	1 (0.9)	4 (3.6)	5 (4.5)
Grass	2 (1.8)	3 (2.7)	13 (11.6)	18 (16.1)
Raspberry	0	0	2 (1.8)	2 (1.8)
Gooseberry	0	0	1 (0.9)	1 (0.9)
Total	13 (11.6)	12 (10.7)	87 (77.7)	112 (100.0)

[a] Number of total nests. Percentage of total nests in parentheses.

Parental Activity

Only one of the five treatments affected nest outcome. The fifth treatment (one egg/day plus model plus song) was significantly different from the other treatments (Fisher exact test, p=0.009), because no nests in this treatment were depredated. None of the nests from any treatment was parasitized (Table 5). Distribution of nests according to concealment values for both eye-level and nest-level was similar to active nests. Most nests fell in the 80-100% concealment category (compare Table 2). Concealment also did not affect the outcome for any treatment at eye-level (Table 6). However, for concealment values at nest-level (Table 7), 80%-100% concealment had a significant effect on the outcome for treatment five (Fisher exact test, p=0.001). Again this was due to the lack of predation on nests in this treatment.

Parental Aggression

Enemy recognition

The 0.5-m distances from the model testing described below were used to test for enemy recognition. Two of the recorded responses, namely time intervals spent less than 2 m from the model and time intervals spent greater than 5 m from the model, differed significantly among the models presented (Table 8). Clay-colored Sparrows spent more time closer to the cowbird model than any of the other three models and they also spent more time farther from the Fox Sparrow model than the

others. The 'chip' alarm call (Walkinshaw 1944) frequency also increased slightly in response to the cowbird and sparrow models but not for either predator model.

TABLE 5: Frequency of parasitism, depredation and nest success of artificial nests with five levels of simulated parental activity.

Simulated parental activity[a]	Nest Outcome		
	Parasitized (%)[b]	Depredated (%)[b]	Successful (%)[b]
No eggs (n=33)	0	10 (30.3)	23 (66.7)
Full clutch (n=33)	0	11 (33.3)	22 (66.7)
One egg/day (n=34)	0	13 (38.2)	21 (61.8)
One egg/day + model (n=21)	0	5 (23.8)	16 (76.2)
One egg/day + model + song (n=21)	0	0	21 (100.0)

[a] Sample size (n) = number of nests in each level of simulated activity.
[b] Percentage of total nests for each level of simulated activity.

TABLE 6: Frequency of parasitism, depredation and nest success on artificial nests with five levels of simulated parental activity by concealment category taken at eye-level.

Concealment values (% concealed)	No eggs			Full clutch			One egg/day			One egg/day+model			One egg/day+model+song		
	P[a] (%)	D[a] (%)	S[a] (%)	P (%)	D (%)	S (%)	P (%)	D (%)	S (%)	P (%)	D (%)	S (%)	P (%)	D (%)	S (%)
0-20	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
20-40	0	0	0	0	0	1 (3.1)	0	1 (2.9)	1 (2.9)	0	0	0	0	0	0
40-60	0	0	0	0	0	2 (6.3)	0	0	1 (2.9)	0	0	2 (9.5)	0	0	4 (19.1)
60-80	0	2 (6.1)	8 (24.2)	0	3 (9.4)	4 (12.5)	0	3 (8.6)	1 (2.9)	0	1 (4.8)	5 (23.8)	0	0	6 (28.6)
80-100	0	8 (24.2)	15 (45.5)	0	8 (25.0)	14 (43.8)	0	9 (25.7)	19 (54.3)	0	4 (19.1)	9 (42.9)	0	0	11 (52.4)

[a] P = parasitized, S = successful, D = depredated.

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TABLE 7: Frequency of parasitism, depredation and nest success on artificial nests with five levels of simulated parental activity for the 80-100% concealment category at nest-level.

Simulated parental activity	Nest Outcome[a]		
	Parasitized (%)	Depredated (%)	Successful (%)
No eggs	0	10 (30.3)	23 (69.7)
Full clutch	0	12 (36.7)	20 (60.6)
One egg/day	0	13 (38.2)	20 (58.8)
One egg/day + model	0	5 (23.8)	15 (71.4)
One egg/day + model+song	0	0	19 (90.5)

[a] No nest fell in the 0-20% or 20-40% concealment ranges. One successful nest fell in the 40-60% concealment range for the full clutch treatment. Four successful nests fell in the 60-80% concealment range: one in the one egg/day treatment, one in the one egg/day+model treatment and 2 in the one egg/day+model+song treatment.

TABLE 8: Summary of responses of Clay-colored Sparrows to four models presented at 0.5 m from the nest, and results of Kruskal-Wallis test.

| Response[a] | Type of model presented | | | | p-value[d] |
	BHCO[b] (17)[c]	COGR (10)	FGSQ (10)	FOSP (4)	
< 2 m	31.8 ± 4.8	9.6 ± 4.2	9.7 ± 4.0	0.3 ± 0.3	0.0014
2-5 m	7.1 ± 2.2	18.3 ± 5.1	15.8 ± 5.3	18.3 ± 12.9	0.1745
> 5 m	1.4 ± 0.8	3.1 ± 2.5	3.3 ± 3.2	11.8 ± 4.8	0.0171
Incubation	3.4 ± 2.3	0.0	0.0	0.0	0.4625
In vegetation	5.4 ± 2.1	13.3 ± 4.2	9.8 ± 4.7	18.0 ± 10.1	0.2612
Leave area	0.8 ± 0.5	4.0 ± 2.7	3.7 ± 2.7	8.0 ± 4.6	0.5975
Chip	8.1 ± 2.7	1.0 ± 0.7	2.7 ± 2.7	5.0 ± 4.7	0.0562
Quiet chip	3.0 ± 1.8	1.3 ± 0.7	1.9 ± 0.6	0.5 ± 0.5	0.4223
Close passes	0.5 ± 0.4	0.0	0.0	0.0	0.4625
Perch changes	28.9 ± 6.2	29.3 ± 11.5	21.0 ± 5.8	11.5 ± 4.2	0.6872
Return time (s)	484.1 ± 152.2	922.0 ± 254.3	446.3 ± 174.6	394.8 ± 1126.9	0.0900

Responses are given as mean ± s.e.
[a] Refer to Table 1 for explanation of behaviours and units.
[b] BHCO=Brown-headed Cowbird, COGR=Common Grackle, FGSQ=Franklin's ground squirrel, FOSP=Fox Sparrow.
[c] Combined sample sizes for male and female are given in parentheses.
[d] Results of the Friedman test for comparisons among the four models.

Distance testing

Seventeen nests were tested with a model female cowbird placed at three distances from the nest. Of the recorded responses to the model, only four differed significantly among the distances: time intervals spent less than 2 m from the model, time intervals spent 2-5 m from the model, frequency of chips, and frequency of perch changes (Table 9). The birds spent more time closer to the nest when the model was closer to the nest and centred their activities around the nest. The frequency of chip calling and the frequency of perch changes increased as the model was placed closer to the nest. The time females incubated was greatest when the model was placed the farthest from the nest, although this difference was only slight (Table 9). None of the more aggressive behaviours, such as flybys and chips, differed significantly among the distances because each was rare. The time adults took to respond and the number of adults that responded also were not significantly different for all three distances.

Clay-colored Sparrows did not react aggressively to the model Franklin's ground squirrel as only one behaviour recorded differed significantly among the three distances, the quiet chip (Table 10). Incubation and perch changes showed distinct but not significant trends. Incubation increased as the model distance from the nest increased, whereas perch changes decreased.

Clay-colored Sparrows did not react aggressively to the model Common Grackle, as only two behaviours recorded differed significantly among the three distances, time intervals spent less than 2 m from the model and time intervals spent

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greater than 5 m from the model (Table 11). The sparrows spent more time closer to the model when it was closer to the nest and more time farther from the model when it was farthest from the nest. This indicates that the birds centred their behaviour around the nest, not around the model. Perch changes showed a strong trend but it did not differ significantly among the distances, decreasing in frequency as the model was placed farther from the nest. Only the quiet chip differed significantly among the distances for the Fox Sparrow model (Table 12). Chipping decreased as the model was placed farther away, this decrease did not, however, differ significantly among the three distances.

TABLE 9: Summary of responses of Clay-colored Sparrows to cowbird models presented at three distances from the nest, and results of Friedman test.

Response[a]	Distance (m)			p-value[c]
	0.5 (16)[b]	2.5 (16)	4.5 (17)	
< 2 m	33.5 ± 4.3	22.4 ± 4.0	6.8 ± 3.1	0.0001
2-5 m	5.6 ± 1.8	14.6 ± 2.8	29.5 ± 2.6	0.0001
> 5 m	1.2 ± 0.8	2.1 ± 1.5	1.8 ± 0.8	0.6176
Incubation	3.4 ± 2.3	2.5 ± 1.9	13.0 ± 3.6	0.0529
In vegetation	5.4 ± 2.1	9.7 ± 2.2	8.5 ± 2.4	0.2408
Leave area	0.9 ± 0.5	1.7 ± 1.2	4.4 ± 2.5	0.7662
Chip	9.8 ± 2.9	7.3 ± 2.8	1.0 ± 0.7	0.0166
Quiet chip	1.3 ± 0.8	3.1 ± 1.6	0.6 ± 0.3	0.2218
Close passes	0.5 ± 0.4	0.0	0.0	0.1302
Perch changes	30.8 ± 5.9	21.2 ± 5.0	12.2 ± 3.3	0.0018
Return time	2545.9 ± 2059.3	556.6 ± 137.9	298.7 ± 113.7	0.9860

Responses are given as mean ± s.e.
[a] Refer to Table 1 for explanations of behaviours and units.
[b] Combined sample sizes for male and female are given in parentheses.
[c] Results of the Friedman test for comparisons among the three distances.

TABLE 10: Summary of responses of Clay-colored Sparrows to Franklin's ground squirrel models presented at three distances from the nest, and results of Friedman test.

Response	Distance (m)			p-value
	0.5 (9)	2.5 (8)	4.5 (8)	
< 2 m	9.7 ± 4.0	0.50 ± 0.5	3.8 ± 3.7	0.3254
2-5 m	15.8 ± 5.3	25.5 ± 4.5	22.4 ± 5.6	0.8883
> 5 m	3.3 ± 3.2	7.6 ± 2.6	5.8 ± 3.3	0.1088
Incubation	0.0	2.0 ± 2.0	6.0 ± 4.1	0.1567
In vegetation	9.8 ± 4.7	14.3 ± 4.2	14.4 ± 4.9	0.3731
Leave area	3.7 ± 2.7	4.0 ± 2.7	5.6 ± 3.9	0.2541
Chip	2.7 ± 2.7	0.1 ± 0.1	0.1 ± 0.1	0.8432
Quiet chip	1.9 ± 0.6	2.6 ± 1.0	5.3 ± 1.7	0.0443
Close passes	0.0	0.0	0.0	-
Perch changes	21.0 ± 5.8	13.9 ± 5.6	7.6 ± 3.0	0.1885
Return time	446.3 ± 174.6	778.4 ± 196.3	894.5 ± 215.1	0.5204

Responses are given as mean ± s.e. Conventions as in Table 9.

TABLE 11: Summary of responses of Clay-colored Sparrows to Common Grackle models presented at three distances from the nest, and results of Friedman test.

Response	Distance (m)			p-value
	0.5 (7)	2.5 (8)	4.5 (10)	
< 2 m	9.6 ± 4.2	2.9 ± 2.0	0.0	0.0111
2-5 m	18.3 ± 5.1	23.8 ± 3.8	16.8 ± 4.3	0.7495
> 5 m	3.1 ± 2.5	14.6 ± 5.2	20.2 ± 4.1	0.0361
Incubation	0.0	2.0 ± 2.0	0.0	0.3690
In vegetation	13.3 ± 4.2	15.9 ± 4.8	20.6 ± 4.8	0.2858
Leave area	4.0 ± 2.7	0.1 ± 0.1	2.7 ± 2.0	0.2739
Chip	1.0 ± 0.7	1.9 ± 1.6	0.3 ± 0.2	0.8600
Quiet chip	1.3 ± 0.7	4.0 ± 1.2	2.7 ± 0.9	0.4282
Close passes	0.0	0.0	0.0	-
Perch changes	29.3 ± 11.5	17.0 ± 4.4	15.2 ± 3.2	0.1027
Return time	922.0 ± 254.3	729.4 ± 206.9	613.9 ± 216.4	0.2082

Responses are given as mean ± s.e. Conventions as in Table 9.

TABLE 12: Summary of responses of Clay-colored Sparrows to Fox Sparrow models presented at three distances from the nest, and results of Friedman test.

Response	Distance (m) 0.5 (4)	2.5 (4)	4.5 (4)	p-value
< 2 m	0.3 ± 0.3	0.5 ± 0.5	2.5 ± 1.9	0.1537
2-5 m	18.3 ± 12.9	3.0 ± 0.7	11.5 ± 4.1	0.1780
> 5 m	13.0 ± 4.8	18.0 ± 6.1	10.5 ± 5.0	0.8240
Incubation	0.0	0.0	5.0 ± 5.0	0.4219
In vegetation	18.0 ± 10.1	9.0 ± 4.9	4.3 ± 3.9	0.2746
Leave area	8.0 ± 4.6	9.0 ± 6.4	6.5 ± 4.3	0.9334
Chip	5.0 ± 4.7	0.3 ± 0.3	0.0	0.1537
Quiet chip	0.5 ± 0.5	2.8 ± 0.6	0.5 ± 0.5	0.0029
Close passes	0.0	0.0	0.0	-
Perch changes	11.5 ± 4.2	6.8 ± 3.4	9.8 ± 2.8	1.0000
Return time	394.8 ± 126.9	347.4 ± 128.0	83.0 ± 36.7	0.4219

Responses are given as mean ± s.e. Conventions as in Table 9.

DISCUSSION

Despite the high frequency of predation and parasitism on bird nests in general, little is known about how predators and parasites find nests. They probably use a variety of cues to locate them. Depending upon the importance of nest contents in their diets, predators may often find nests opportunistically. Brood parasites, however, must find host nests in order to reproduce. Some cues used by predators and brood parasites to find nests may be able to be identified by correlations from observations of natural predation and parasitism. However, appropriate experiments should offer the best way of revealing cues that potential predators and brood parasites use to find nests. Using an experimental approach in some cases, I investigated the importance of five potential cues that could provide information to predators and/or parasites on the location of nests or nest sites. These cues were nest concealment, nest height, supporting vegetation, parental activity and parental aggression. The results in some cases supported the hypotheses, but not in others.

Nest Concealment

The non-significant findings suggest that there is no relationship between nest concealment and nest outcome. Several workers have reported that more concealed nests were less likely to be depredated (Martin and Roper 1988, Brown and Fredrickson 1989, Clark and Nudds 1991). In a review of the literature, Clark and

Nudds (1991) reported that the importance of nest concealment was dependent on the predator community. They found that concealment of duck nests was important when avian predators were present but when mammals or both birds and mammals were present, nest concealment was less important. Best and Stauffer (1980) found that nest concealment was not related to nesting outcome for a community consisting of 15 different species when there was a mix of avian and mammalian predators. Their results showed that nests with poor concealment had success frequencies of 49%, those with good concealment had success frequencies of 44% and those with excellent concealment had success frequencies of 35%. Best (1978) concluded that for Field Sparrows (*Spizella pusilla*) nest concealment does not affect snake predation but he did not look at concealment from above and could not relate concealment to cowbird parasitism. Smith (1981) presented similar results where the main predator was avian. He also looked at parasitism and found that concealment was also not related to nest success. He unfortunately does not give any details as to his findings. Anderson and Storer (1976) found more cowbird eggs in dense cover, indicating that for Kirtland's Warbler (*Dendroica kirtlandii*) more-concealed nests were parasitized more frequently (0.70 cowbird eggs per nest in heavy nest concealment versus 0.47 cowbird eggs per nest in light nest concealment). However, this relationship was not significant. Buech (1982) also found that parasitized nests tended to be better concealed than non-parasitized nests. He also suggests that parental activity may be important in finding these nests. Nice (1937:93-94) and Nolan (1978:401) found that better-concealed nests were parasitized and depredated less often than poorly

concealed nests. Nice divided nests into those with excellent concealment and those with good, fair or poor concealment. Nests in the first group had success frequencies of 55% versus 36% success in the second group. Nolan divided concealment into nests with above average concealment and those with below average concealment. Success of the below average group was 0% versus 21% for the above average group. Finally, Holway (1991) found that nest sites were more concealed than random points (40% versus 20% concealed) but successful and depredated nests did not differ in concealment levels (both were approximately 40% concealed). He did not mention the type of predators in the area but suggested that if predators find nests by olfactory cues then visual concealment may not be important.

As the major predator in the Oxbow Woods area on Clay-colored Sparrow nests is the Franklin's ground squirrel, predation frequencies are not expected to be related to concealment because these predators use olfactory senses to locate nests and do not rely solely on sight (Boonstra et al. 1990). As host species do not benefit from a decreased predation frequency with increasing concealment a cowbird egg also would not benefit. Thus, cowbirds apparently lay in any nest regardless of concealment. Indeed, in this study, parasitism frequencies did not increase significantly with decreasing concealment values. Clay-colored Sparrows experience low levels of predation and parasitism, and build fairly well concealed nests (most fell in the range of 4-5 or 80-100% concealed). Therefore, differences in concealment among nests may not provide enough selective pressure for concealment to be used as a nest-finding cue. This cue may work better for a species with a higher frequency

of parasitism, a wider range of nest substrates, variable nest concealment values or whose main nest predator is avian and therefore more likely to be affected by concealment.

Nest Height and Supporting Vegetation

Nest height is not used as a cue by predators nor by parasites to locate Clay-colored Sparrows nests because outcome did not vary with nest height (Table 3). This finding is contrary to what Knapton (1978b) found for Clay-colored Sparrows. He found that pairs that nested within 10 cm above the ground suffered less predation than those that nested higher (39% versus 69%). He had many more nests less than 10 cm from the ground than I did. Most of the nests in the present study were higher than 10 cm (Table 3). This may indicate a population or habitat difference and explains why the results from the two studies differed. Buech (1982) found no differences in nest height between parasitized and non-parasitized nests for three species of *Spizella*, including the Clay-colored Sparrow, results that are similar to my study.

Several studies have shown that higher nests were parasitized more often (e.g. Dappen 1967, Fleischer 1986). Other studies have recorded opposite results (e.g. Briskie et al. 1990), whereas yet other studies have found no relationship between nest height and nest outcome (e.g. Best 1978, Smith 1981). These studies show that there is much variation with respect to the effect of nest height on predation and

parasitism frequencies. It may be that for species with only slight differences in nest height, such as Clay-colored Sparrows, height does not influence nest discovery.

Supporting vegetation also did not affect outcome. Snowberry is abundant and may decrease the chances of a predator or parasite being able to locate a Clay-colored Sparrow nest as there would be too many places to search (see Martin and Roper 1988, Filliater et al. 1994). However, Clay-colored Sparrows seem to prefer snowberry (Walkinshaw 1939, Fox 1961, Salt 1966). In this study, 77% of nests were in this species of plant. Snowberry offers a high degree of nest concealment and protection from the elements and it may be chosen by Clay-colored Sparrows for this reason (Knapton 1978b, Filliater et al. 1994).

Parental Activity

None of the experimental nests was parasitized. The prediction of increased parasitism as parental activity increased was not upheld. Experimental nests were depredated regardless of parental activity level or concealment value for all but the highest level of activity (one egg per day plus model plus song), which experienced no predation. Here, too, the prediction of increased predation as parental activity increased was not upheld. Other studies have produced similar results. Laskey (1950) placed out dummy nests containing small passerine eggs but none was parasitized. Thompson and Gottfried (1976) placed out 240 nests with two quail eggs per nest. Again no parasitism was recorded. These studies indicate that nests alone are not parasitized and that activity around nests is necessary. One objection to

Thompson and Gottfried's study is their use of quail eggs, which are larger than eggs of most cowbird hosts (Payne 1973, Lowther 1979). Lowther (1979) used smaller eggs. He placed one egg per day in 33 nests to produce clutches of 2, 3 or 4 eggs. This simulated some parental activity, and two of his nests were parasitized, possibly due to the simulated parental activity. Thompson and Gottfried (1981) used smaller eggs in a second study. They placed out 25 nests with complete "clutches" on the same day and in a second set of 25 nests they introduced one egg per day. This simulated no parental activity and indirect parental activity, respectively. None of the first set of nests received a cowbird egg, whereas one nest in the second group did. These results also suggest that parental activity is necessary before cowbirds will parasitize nests.

Yahner and DeLong (1992) placed out one egg per day, simulating indirect parental activity. A total of 172 (57%) nests was disturbed by predators but none was parasitized by cowbirds. Wiley's (1988) study on Shiny Cowbirds (*M. bonariensis*) used three levels of parental activity: (1) no activity (empty nest), (2) indirect activity (one egg per day) and (3) direct activity (mounted host) to determine the importance of parental activity in locating nests. None of the empty nests was parasitized, whereas nests with eggs and those with mounted hosts near them received low levels of parasitism (<1%). Although the difference in parasitism frequencies between empty nests and nests with some level of parental activity was not significant, it suggests that parental activity may be an important cue to cowbirds when locating nests. Wiley's experiment with the host mount is similar to treatment

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4 (1 egg per day plus model) of my series of experiments. No previous study has examined the level of parental activity that includes 1 egg per day plus model plus song (treatment 5). Nevertheless, no nests with this highest level of parental activity were parasitized.

In all of the studies, including the present one, parasitism on artificial nests was at a much lower frequency than on natural nests (less than 1% versus 10% or greater). One possible reason why little or no parasitism was observed on artificial nests may be that a critical level of activity or type of activity was not simulated, and before this point is reached, cowbirds will not cue in on model hosts and/or their nests. Perhaps the presence of a living nest owner(s) and/or its movement is required. This was not simulated in the above experiments. Simulation of such movements may be impossible. Blancher and Robertson (1982) found that Eastern Kingbirds (*Tyrannus tyrannus*) did not react aggressively to a stuffed crow model (but see Knight and Temple 1986, Bazin and Sealy 1993). They also mentioned that interactions with live predators could not be standardized. This poses a problem when using these live models. Burgham and Picman (1989) used live models in their experiments and elicited aggressive behaviours. However, they did not address the live model problem. Alternatively, the situations created may be too artificial and the cowbirds recognize them as such. Perhaps the coldness of the artificial eggs is enough to deter parasites.

Cowbirds may need to see birds going to or from their nests to pinpoint the location of nests or to ensure that they are active. Female cowbirds have frequently

been observed perched in trees presumably watching hosts carrying nesting material directly to their nest sites (Norman and Robertson 1975, Wiley 1988). Cowbirds have also been seen flying over nesting areas or flying directly to nests as soon as a host has left. These behaviours ensure that the nest location and stage are known (Wiley and Wiley 1980). Several studies have found that cowbirds occasionally lay in inactive nests suggesting that parental activity is not necessary (Thompson and Gottfried 1981, Wiley 1988, Weatherhead 1989, Sealy 1995). Cowbirds may be interpreting stealing of nesting material from an inactive nest or previous parental activity at a nest as building of an active nest and parasitize these nests inappropriately (Wiley 1988).

Few investigators have looked at predation as well as parasitism using artificial nests (but see Yahner and DeLong 1992). Predation frequencies on artificial nests (Table 5) were similar to that on natural nests (Table 2), which indicates that activity of nest owners is not as necessary for predators to locate nests. No nests in my fifth treatment, however, were depredated, which suggests song may deter predators. A more realistic reason for this finding would be that Clay-colored Sparrows rarely sing above their nest (Knapton 1978a) and if predators attempt to minimize their search effort, they should not look near a singing Clay-colored Sparrow because a nest is probably not below it. This may explain why no nests in treatment 5 were depredated.

Few workers have looked at predation in relation to parental activity simulated at artificial nests or active nests, nor have many references been made to how predators find nests. Collias and Collias (1984) stated that predators probably find

nests by watching birds building them but they did not cite studies to support this claim. Hammond and Forward (1965) stated that avian predators locate duck nests by observing the female's activity. It is reasonable to expect that passerine nest predators use a similar technique to locate nests.

Parental Aggression

Enemy recognition

Rothstein (1990) stated that aggression may be a general response to nest intruders and not a defense against parasites. Smith et al. (1984) found support for this in Song Sparrows. However, other studies have found that hosts recognize the parasite as a unique threat (Hobson and Sealy 1989, Duckworth 1991, Neudorf and Sealy 1992). It may be that some hosts recognize the cowbird as a specific threat and others do not (Neudorf and Sealy 1992). Nest owners have also been shown to recognize different predators. Several studies on both mammals and birds have found that responses varied with different predator models (Patterson et al. 1980, Stone and Trost 1991, Weary and Kramer 1995). Buitron (1983) found responses of Black-billed Magpies (*Pica pica*) to natural predators varied with predator type and situation.

The different responses to the female cowbird model compared to the control suggests that Clay-colored Sparrows recognize cowbirds as a specific threat. Indeed, they responded more aggressively to the cowbird model as more time was spent near the nest and they chipped more frequently (Table 8).

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Clay-colored Sparrows apparently did not distinguish between different predators (Table 8), nor did they react aggressively to the predators. The sparrows only gave quiet chips to the predator models. Bent (1968) described the quiet chip or "tsip" call as a communication call. This suggests that the birds are not disturbed by the presence of the predator models. Another fact that suggests that they were not disturbed is that the birds centred their behaviours around the nest and not the model as would be expected if the model posed a real threat. Neudorf and Sealy (1992) were the first to test an avian predator, the Common Grackle, along with a female cowbird and a control. They showed that some species reacted differently toward the predator and brood parasite whereas others did not. My study is one of the few to test two different types of predators, avian and mammalian (see also Knight and Temple 1988). These tests allowed me to determine if responses varied for different predators and if predators are recognized as unique threats. Clay-colored Sparrows were not highly aggressive and apparently did not recognize unique predators (Table 8). Alternatively, the sparrows may recognize them and choose not to react aggressively because they may not be able to deter them and keeping their nest location hidden may be their only recourse.

The Fox Sparrow elicited some aggression, perhaps due to its similarity in shape and size to a cowbird. The only behaviour that differed significantly among distance was quiet chipping, which suggests that the birds were not disturbed. Bent (1968) described a "tsip" call that is similar to the quiet chip. However, chipping was greatest at the closest distance indicating that the sparrows were slightly disturbed as

chip calls were given as alarm calls (Walkinshaw 1944, Bent 1968). Other studies have found only low levels of aggression elicited from a variety of hosts when presented with a Fox Sparrow model (Hobson and Sealy 1989, Neudorf and Sealy 1992). Clay-colored Sparrows, therefore, may recognize a shape or size and not individual species but due to the small sample size for Fox Sparrow, it is impossible to say with certainty if they recognize cowbirds per se or simply shape and size. Neudorf et al. (unpubl. data) found that bill shape was more important than plumage colour or pattern in recognizing cowbirds. Fox Sparrows and cowbirds have similar bills, although it is slightly shorter in the former. This similarity may account for the slight aggressive responses recorded in these studies.

Robertson and Norman (1977) also tested Clay-colored Sparrows with a cowbird model and three types of sparrow models at 0.5 m from the nest. They found no significant differences in responses among the models but only tested two nests and used a subjective index (see Moran et al. 1981). Sealy et al. (1995) placed a female cowbird on the nest and found that the Clay-colored Sparrows responded aggressively and even knocked the model off the nest, in 5 of 23 trials. Their study demonstrates that Clay-colored Sparrows can be aggressive but they may respond aggressively only to threats right at the nest (see also Neudorf and Sealy 1994, Sealy et al. 1995). They may not react until the threat is at or on the nest so that their behaviour does not reveal the position of their well-concealed nests.

Distance testing

Parental aggression generally has been assumed to deter predators (Blancher and Robertson 1982, Buitron 1983). However, several workers have suggested that parental aggression may be used by both predators and parasites to locate nests (Smith 1981, Smith et al. 1984, Hobson et al. 1988). McLean et al. (1986) found that alarm vocalizations attracted avian predators. Wiley (1988) found that cowbirds were attracted to areas where residents aggressively defended against intruders. These behaviours seem to be "maladaptive" unless they indeed deter parasites and predators, and the nest owners benefit by this behaviour (Smith et al. 1984).

Parental aggression in response to a female cowbird model at three distances was used to test the likelihood that the nest-cue hypothesis is plausible. Clay-colored Sparrows responded but not aggressively at all three distances, which reveals that in theory the nest-cue hypothesis is plausible. Aggressive behaviours were observed infrequently and were not exhibited by all individuals, therefore, aggression probably cannot be used by cowbirds as a reliable cue. However, for those individuals that exhibit aggressive behaviour, cowbirds may be able to cue in on them opportunistically. Cowbirds may be able to gauge the distance between themselves and the host, the number of perch changes made by hosts, and the frequency of chip calls as cues to the presence of a nest. Clay-colored Sparrows, in general, spent more time closer to the model, changed perches and chipped more frequently when the model was closest to the nest. There was also a gradation in responses for time intervals spent greater than 2 m from the model, frequency of perch changes and

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frequency of chip calls, which increased in frequency as the distance from the nest decreased. Chip calls reveal that adults were disturbed and may indicate aggression. These three behaviours may be used by cowbirds to locate nests. For most of the responses, the two closest distances seem to be similar and the responses more frequent than the third and farthest distance. This may indicate a threshold distance, where the adults ignore the model cowbird (intruders) until a certain distance (somewhere between 2.5 and 4.5 m) and then respond as the threat increases (intruder closer to nest).

Clay-colored Sparrows did not react aggressively toward the two predator models. The responses that were significant were not aggressive behaviours and therefore parental aggression is not used as a cue by predators to locate Clay-colored Sparrow nests. The quiet chip was given frequently and seems to be given most often when the birds are foraging or communicating with one another (pers. obs.). This suggests that the birds were not disturbed. The prediction of increased aggression as the predator model was placed nearer to the nest was not supported for either type of predator. Clay-colored Sparrows build well-concealed nests and in order not to draw attention to the nest may not respond aggressively towards predators, thus eliminating this as a nest-finding cue or perhaps they cannot deter predators (Knight et al. 1985, Sealy 1994). The quiet chip for the ground squirrel model increased in frequency as the model distance increased. This may be a positive response, in that the communication chip may indicate that a predator is near and increase in frequency as the predator moves farther away. The apparent lack of response may

be the best strategy for Clay-colored Sparrows because even at half a meter (the closest distance tested) the well-concealed nest may have not been discovered and to respond aggressively would reveal its exact position. The aggressive responses at the nest recorded by Sealy et al. (1995) may be the last attempt to drive the predator away as the nest has now certainly been found.

Model testing at different distances from the nest has only been done in one other study (Gill, S.A., P.M. Grieef and S.G. Sealy unpubl. data). Their results showed that for four different species responses vary with distance. This is important when looking at nest success with respect to cowbird and predator models because conclusions about nest-finding cues and behaviours that attract predators and parasites (McLean et al. 1986) may vary depending on testing distance.

None of the five cues (parental activity, parental aggression, nest concealment, nest height, or supporting vegetation) examined in this study was used by parasites or predators to locate Clay-colored Sparrow nests. These cues may work to varying degrees, either alone or in combination, for other species or in combination for this species. Nest finding is probably species-specific, with nests of some species being found more readily. The question, therefore, still remains: what specific cues do parasites and predators use to find Clay-colored Sparrow nests?

SUMMARY

1. Very low frequencies of predation and parasitism (10.7% and 11.6%, respectively) were recorded for the first 8 days of the nesting cycle. There was a 77.7% success frequency.

2. 67% of nests were highly concealed with values between 80 and 100% concealed. Nest concealment did not affect nesting outcome and is probably not used as a cue to locate Clay-colored Sparrow nests.

3. 41% of nests were built between the heights of 101 and 200 mm. Nest height did not affect nesting outcome and is probably not used as a cue to locate Clay-colored Sparrow nests.

4. 77% of nests were built in snowberry. Supporting vegetation did not affect nesting outcome and is probably not used as a cue to locate Clay-colored Sparrow nests.

5. Simulated parental activity did not elicit parasitism. Predation occurred but did not vary with increasing parental activity. The parental activities simulated in this study did not elicit cowbird egg-laying or increased levels of predation and were probably not used to locate Clay-colored Sparrow nests.

6. Clay-colored Sparrows recognized cowbirds models as unique threats and may recognize predator models as such.

7. Parental aggression cannot be used as a cue to locate Clay-colored Sparrow nests as little aggression was elicited by the four models.

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