Importance of nest size and materials in host choice of the Brown-headed Cowbird

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Introduction

Nests are defined as structures that aid in the survival of the eggs and young. When the nest provides suitable protection, for example, from cold, heat, solar radiation, predators, it can greatly increase the fitness of the breeding pair (Collias and Collias 1984). This potential to increase reproductive output indicates that nest-building behaviour and nest structure are under intensive selective pressures (Nores and Nores 1994).

Predation is one of the major selective forces shaping reproductive strategies in passerines (Ricklefs 1969). Ricklefs (1969) noted that predation accounted for more than 50% of the nest losses in many studies of passerine birds. Like predation, avian brood parasitism is also an important mortality factor because it lowers and sometimes eliminates the reproductive output of the individuals parasitsed (Rothstein 1975, 1990; Payne 1977).

Unlike predation, which can occur at any nest at any time, brood parasites must select certain nests at certain times in order to reproduce successfully. Although the Brown-headed Cowbird is known to parasitise many species (216), only 139 of these species have been reported to successfully raise cowbird young (Friedmann *et al.* 1977). Several studies have shown that although many species are potential hosts, some are preferred over others, even within the same community (Hill 1976; Fleischer 1986; Briskie *et al.* 1990). This preference indicates that cowbirds can differentiate between the available hosts.

Host selection has been studied by many researchers, but it is still not fully understood. Host characteristics, such as abundance, timing of breeding season, egg size, incubation period, diet and tolerance of parasitism, seem to contribute to the likelihood of a cowbird parasitising a particular species (Friedmann *et al.* 1977; Rothstein 1975; Payne 1977; Wiley 1988; Sealy and Bazin 1995).

More specifically, host choice may also be due to the nest-searching strategies of the Brown-headed Cowbird. First, the female cowbird has been observed silently watching the host build. The second strategy involves the female walking silently over the forest floor and stopping sometimes to watch the movements of birds in the forest canopy. The third nest searching behaviour involves the female making a series of short flights a few feet above the nest shrubbery, essentially flushing the host from its nest (Friedmann 1929; Hann 1941; Payne 1973; Norman and Robertson 1975). These methods make (1) host aggression (host reacting to cowbird nearby), (2) nest placement (height, supporting vegetation, concealment that could hide or make nest finding difficult) and (3) nesting building activity (the cowbird can easily follow a nest builder with a bill full of materials back to the nest location) all possible cues that a female cowbird could use to find a potential host and its nest (Rothstein 1975; Slack 1976; Thompson and Gottfried 1981; Fleischer 1986; Orians *et al*. 1989; Briskie *et al*. 1990; Colwell 1992; Neudorf and Sealy 1992).

Because cowbird fitness depends on selecting an appropriate host, there may be other selective pressures acting on the parasite to choose a breeding pair that provides the highest probability of producing a cowbird chick. Due to the high density of nesting Yellow Warblers at Delta Marsh (14.4 pairs /ha, MacKenzie *et al.* 1982) it is plausible that a cowbird may choose certain breeding pairs over others in the population. This would require the cowbird to recognise good-quality hosts based on behaviour, nest characteristics, territory quality and/or other conspicuous features (Soler *et al*. 1995).

Nests are viewed as extensions of the phenotypes of their builders, thus morphology may reflect important variation among the quality of individuals within a population (Lent 1992). Nest size has been identified as one nest characteristic that the Great Spotted Cuckoo (*Clamator glandarius*) uses to assess the quality of its Magpie (*Pica pica*) hosts in Spain (Soler *et al.* 1995). Thus hosts with high-quality territories built larger nests and were parasitised more frequently than neighbours with nests of smaller volume.

Muller (1991) observed that Barn Swallows (*Hirundo rustica*) severely restrict their use of feathers and other conspicuous nesting material to reduce depredation. As brood parasites and nest predators are known to inflict similar selection pressures on nesting birds (Ricklefs 1969), it is possible that nest design may be influenced to reduce the probability of parasitism.

At Delta Marsh, Yellow Warblers have been sympatric with cowbirds for hundreds of years. Thus with an intense selective pressure on cowbirds to choose appropriate hosts and concomitant pressures on Yellow Warblers to reduce the effects of parasitism, differences between parasitised and non-parasitised nests can be examined. I will test to see whether cowbirds preferentially parasitise certain Yellow Warbler nests (size, mass and materials) over others within the community.

Methods

Searches for Yellow Warbler nests were conducted daily on the forested dune ridge. Nests were checked every second day to ensure that the nest was promptly collected after use (deserted, depredated or young fledged). All nests were located in the willow community (south side of ridge) to ensure that the vegetation used in nest building was similar. All nests were stored in plastic or paper bags until examined.

The nests were dried (at 80°C) in brown paper bags until dry mass was recorded, that is, no change in mass occurred after two consecutive measurements, 24 hours apart. Dried nests were cut in half. Stratification of layers was visible by colour and texture. One-half of the nest was used as a reference from which measurements (see Fig. 1 for definition) were taken and colour was determined for each layer (colour followed Smithe 1974). The other half was teased apart. Each material within the nest was separated, classified according to groupings and weighed to the nearest 0.05 g. Groupings that weighed less than 0.05 g were designated a set mass of 0.02 g, indicating that it was present in that layer.

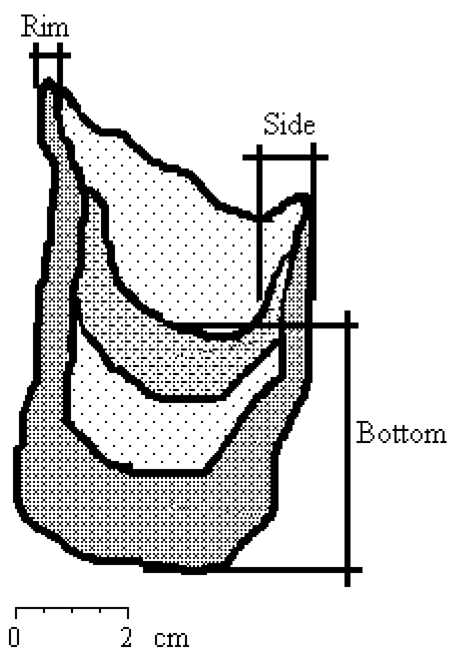

Figure 1. Dimensions used to measure the cut portion of a Yellow Warbler nest.

All the material within the nest fell into one of six groupings: nettles/hops *(Urtica dioica*/*Humulus lupulus*), grass, deer hair, feathers, fruits, and other. Other consisted of fox hair, duff (crystalline particles from feather sheaths of the young birds), insects (mostly Order Diptera and spider webs), excrement, man-made materials (fishing line, window screening, toilet paper, string, plastic), rootlets, wild cucumber (*Ecinocystis lobata*) tendrils, wood/bark, egg shell bits, leaves, and three unknowns which were found in three nests. Insects, duff and excrement were removed from the "other" category because they were not materials that were selected by the nest builder during nest construction. The exception was spider webs within the insect category. It was observed that Yellow Warblers collected the webs and placed them on the outside of the nest and around the surrounding support branches of the nest shrub (pers. obs.). However, they were collectively weighed within the insect category in which the majority of the insects were of the Order Diptera.

Due to the differences in nests between years, only nests from 1995 were used in testing the hypothesis. Of the 65 nests collected in 1995, 13 nests were parasitised by Brown-headed Cowbirds (parasitised nests). The remaining 52 nests were non-parasitised.

The mass of nesting materials was converted into a proportion of the half nest to compensate for differences in nest mass and errors in cutting the nest in half. Since the data were in proportions, they were transformed to arcsine by taking the arcsine of the square-rooted proportions and expressing the data in degrees. To ensure that the data were normally distributed and variances equal, a K-S Lillifores test and Levene's Test was employed, respectively (a=0.05). A two-sample T^2 statistic was used to determine if there was a difference in proportion of nesting materials between parasitised and non-parasitised nests (Kenkel lab program).

Nest size (base depth, side width, rim width, see Figure 1 for definition) and mass of parasitised and non-parasitised nests were log transformed (log+1). The data was then normally distributed with equal variances (K-S Lillifores test and Levene's Test for Equality of Variances). A two-sample T^2 test was administered to nest size and a Students t-test to nest mass (two-tailed test, alpha = 0.05) to compare between parasitised and non-parasitised nests.

Results

The majority of both parasitised and non-parasitised Yellow Warbler nests had three layers: 92% (n=13) of parasitised nests and 75% (n=52) of non-parasitised. Due to the differences between two- and three-layered nests, two-layered nests were dropped from further analysis. Range of colour for parasitised and non-parasitised nest was similar with the exception that non-parasitized nests sometimes had a greyish frame (Fig. 2). Parasitized nests had similar nest materials ($F = 1.835$, $F_{0.05,6,45} = 2.64$, $p>0.05$; Fig. 3), nest size ($F = 3.171$, $F_{0.05,3,48} = 3.363$, $p > 0.05$; Fig. 4) and nest mass (t-value = -1.11, df = 63, $p>0.05$; Fig. 5) to non-parasitised nests. Trends within the data indicate that parasitised nests had less grass and more other materials and are generally heavier. Among other materials, rootlets and man-made materials occurred in higher frequency in parasitised than non-parasitised nests (Table 1).

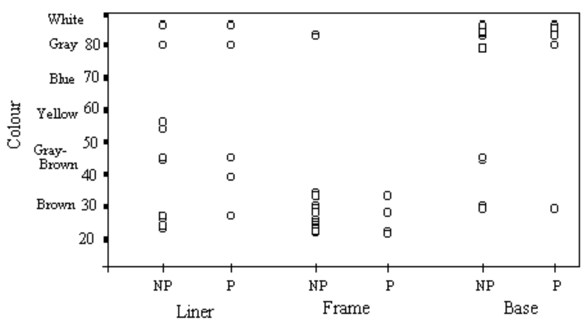

Figure 2. Comparison of colour (Smithe 1974) between non-parasitised (NP; n=39) versus parasitised (P; n=12) nests for the three layers.

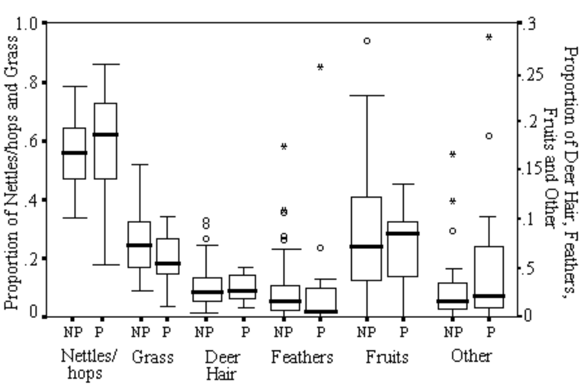

Figure 3. Comparison of the proportion of nesting materials between non-parasitised (NP; n=39) versus parasitised (P; n=12) nests. Note that the left and right axis are of different scale. Boxplot represents median, 25th and 75th percentiles, whiskers extend to the highest and lowest values, excluding outliers (o) and extreme values (*).

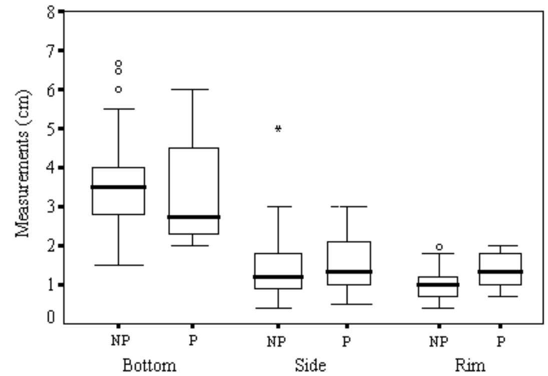

Figure 4. Comparison of nest size between non-parasitised (NP; n=39) versus parasitised (P; n=12) nests. See Figure 7 for definition of measurements. Boxplot as in Fig. 3.

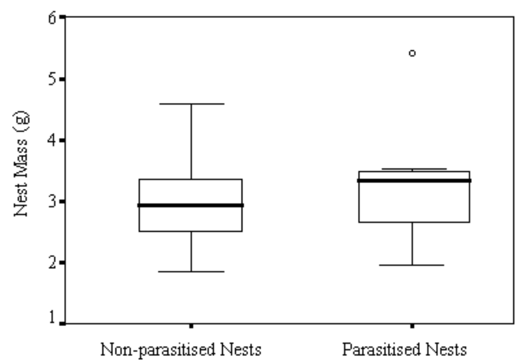

Figure 5. Comparison of mass between non-parasitised (39) versus parasitised (n=12) nests. Note that nest mass is based on one-half nests. Boxplot as in Fig. 3.

Table 1. Separation of other materials and frequency in non-parasitised and parasitised nests.

Material	Freq. in non-parasitized nests (n=46)	Freq. in parasitised nests (n=12)
Fox fur	22	8
Insects	59	66
Leaves	41	33
Wood/Bark	17	0
Man-made Materials	17	33
Rootlets	11	25
Wild cucumber tendrils	13	8

Discussion

Generalist brood parasites, such as Brown-headed Cowbirds, are faced with the assortment of potential hosts to parasitise. Although there is some evidence of brood parasites using nest characteristics to select high-quality hosts, it does not appear to be the case with Yellow Warblers, despite their high density at Delta Marsh.

The majority of studies of host selection in the Brown-headed Cowbird does not pay attention to variation in nest and nest structure (Lowther 1979). King (pers. comm. *in* Lowther 1979) found that nest variation is of minor importance in comparison to egg appearance, especially egg size. However, Lowther (1979) found that nest dimensions covaried with egg size across species such that smaller eggs were in nests with smaller nest dimensions and larger eggs in larger nests. Nest characteristics may play an important part in determining the suitability of the host, especially when the host or its eggs are absent upon discovering a nest. At Delta Marsh, Yellow Warblers build similar looking nests to the rarely parasitised Least Flycatcher. Despite this similarity, cowbirds are still able to differentiate between these two species, although other characteristics, such as nest height and increased host aggression may account for the difference in parasitism rate (see Briskie *et al*. 1990).

Lowther (1979) also stated that any search image that cowbirds may use in selecting host nests could still alter aspects of nest construction. Friedmann *et al*. (1977) suggested that cowbirds form search images for common host species in the same manner as some predators are believed to form search images for the most abundant prey (Tinbergen 1946; Opdam 1979). Mueller (1991) observed that Barn Swallows restricted their use of feathers and other conspicuous nesting material to reduce depredation. Although there was no significant difference in nesting materials, grass occurred in lower proportions and other in higher proportions in parasitised than non-parasitised nests. Although the increased use of other could not be exceedingly conspicuous to a cowbird (it occurred in such low proportions), it is possible that it may reflect territory characteristics. For example, rootlets and man-made materials occurred in higher frequency in parasitised nests than non-parasitised nests (Table 1). Rootlets are found in and on the ground and may be available only if the surrounding area is relatively clear of litter and cover, making it easy for the female Yellow Warbler to collect. Also man-made materials such as string, plastic and fishing line were materials commonly found near and around the cottages. The presence of clearings as well as high structures (houses, telephone wires, trees) are optimal for the nest-searching behaviour of cowbirds, since they can sit elevated and observe the nest-building activities around them (Friedmann 1929; Hann 1941; Payne 1973; Norman and Robertson 1975).

When looking for appropriate hosts at Delta Marsh, it is plausible that the female cowbird forms a search image of a grey mass of nesting materials (base colour of Yellow Warbler nests; Figure 2). All Yellow Warbler nests dissected contained a high proportion of nettles/hops (Figure 3) so is an effective search image. However, it would not distinguish between high and low quality Yellow Warbler breeding pairs.

Soler *et al*. (1995) reported that the Great Spotted Cuckoo used nest size, which reflected high quality territories, to assess the quality of its host. Although, territory quality was not examined in this study, all the nests collected for this study were within the south willow ridge which is the preferred habitat of the Yellow Warbler (Sealy, pers. comm.). This may explain the absence of nest size differences. However, the north ridge, which has suitable habitat for breeding Yellow Warbler pairs, is also parasitised by Brown-headed Cowbirds. Thus it is improbable that cowbirds are only selecting high quality Yellow Warbler hosts.

As nests are viewed as extensions of their builders, nest morphology may reflect important variations among the quality of individuals within a population (Lent 1992). Because the Brown-headed Cowbirds are visual searchers, variations in nest characteristics could be used to differentiate quality of hosts within a species. However, this does not appear to be the case with Yellow Warblers. Thus cowbirds may be utilising other cues to determine host quality characteristics (territory quality, host behaviour), or are simply parasitising any available Yellow Warbler nest.

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