

# Genetic and temporal patterns of multiple parasitism by brown-headed cowbirds (*Molothrus ater*) on song sparrows (*Melospiza melodia*)

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**Abstract:** Identifying the factors used by an avian brood parasite to select host nests is important in understanding the determinates of individual reproductive success, yet such factors are poorly known for most parasitic species. Insights into these factors may come from understanding the conditions under which female parasites lay more than one egg per host nest (multiple parasitism). Using genetic techniques we examined patterns of multiple parasitism on a preferred host, the song sparrow (*Melospiza melodia*), to determine some basic patterns of multiple parasitism. Multiple parasitism involved equal frequencies of the same female parasitizing the same nest again and two or more females parasitizing the same nest. The frequency of multiple parasitism increased as the season progressed. We also documented a high frequency of parasitism that was not synchronized with host laying. These laying patterns may be the result of cowbirds "making the best of a bad situation" or of suboptimal host choice by inexperienced, nonselective females.

**Résumé :** L'identification des facteurs qu'utilisent les parasites des nids d'oiseaux pour choisir les nids de leurs hôtes est essentielle à la compréhension des variables déterminantes du succès de leur reproduction individuelle, et pourtant ces facteurs sont mal connus pour la plupart des parasites. La compréhension des conditions dans lesquelles les parasites femelles pondent plus d'un oeuf par nid (parasitisme multiple) peut jeter de la lumière sur la question. Nous avons tenté de déterminer les patterns de base du parasitisme multiple au moyen de techniques génétiques chez un hôte de prédilection, le bruant chanteur (*Melospiza melodia*). Le parasitisme multiple est le fait tant des femelles qui pondent deux fois ou plus dans le même nid, que de plusieurs femelles qui pondent dans le même nid. La fréquence du parasitisme multiple augmente à mesure que la saison progresse. Nous avons également observé plusieurs cas de parasitisme multiple non synchronisé avec la ponte de l'hôte. Ces patterns sont probablement des pontes de vachers qui tirent le meilleur parti possible d'une situation boiteuse au départ ou la conséquence d'un choix d'hôte sub-optimal par une femelle non sélective et inexpérimentée.

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## Introduction

Studies of avian brood parasitism have largely reflected a fascination with the coevolutionary relationship between hosts and parasites. Relatively few studies, however, have explored the proximate and ultimate ecological factors that influence the parasite's reproductive behaviour and tactics. The choice of which nest to parasitize has an important impact on a parasite's reproductive success. Nevertheless, little is known about how brood parasites select nests from among those

available (but see Martínez et al. 1998b; Clotfelter and Yasukawa 1999; Massoni and Reboreda 2001).

Until recently, brown-headed cowbirds (*Molothrus ater*, hereinafter cowbirds) have been described as laying indiscriminately among host nests (e.g., Friedmann 1929; Rothstein 1976, 1990). However, evidence for host preference is mounting, indicating that, in fact, cowbirds may select host nests adaptively from among those available (e.g., Smith and Myers-Smith 1998; Alderson et al. 1999a; Hahn and Hatfield 2000), possibly through selecting hosts between or within species that are most likely to fledge their offspring (e.g., Grant and Sealy 2002). In cowbirds, the occurrence of more than one parasitic egg in a host's nest, i.e., multiple parasitism, has been widely documented (e.g., Friedmann et al. 1977; Rothstein and Robinson 1998; Trine 2000). Understanding the factors that influence levels of multiple parasitism should provide insights into the mechanisms that dictate how female cowbirds choose their hosts. For example, multiple parasitism may reflect host preference or it may be a response to a shortage of alternative host nests (Smith and Myers-Smith 1998). Because multiple parasitism usually reduces cowbird productivity (Rothstein and Robinson 1998; Trine 2000; but see Weatherhead 1989), a female should not parasitize a nest more than once or, if she can recognize a nest parasitized by another female, should avoid laying in it (Ortega et al. 1994;

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Hahn et al. 1999) unless she first removes the other parasitic egg. Multiple parasitism resulting from laying by two or more females in the same nest (hereinafter multiple-female nests) may occur where cowbirds are abundant, if suitable nests are in short supply (Smith and Myers-Smith 1998), or if female cowbirds do not recognize already-parasitized nests (Ortega et al. 1994; Hahn et al. 1999). By contrast, multiple parasitism involving a female parasitizing a nest more than once (single-female nests) should occur only when suitable nests are limited (Martínez et al. 1998b; Alderson et al. 1999a). The few published estimates of the frequency of either type of multiple parasitism are based on studies that assumed that individual female cowbirds lay morphologically distinct eggs (e.g., McGeen and McGeen 1968; Elliott 1977) or on genetic studies that involved small sample sizes (Alderson et al. 1999a; Hahn et al. 1999; Woolfenden 2000).

Whereas multiple parasitism may or may not be a form of unsuitable host nest use, eggs are always wasted when laid too early or too late (Kattan 1997; Strausberger 1998; Mermoz and Reboresda 1999). Unsynchronized parasitism may occur when suitable nests are not available, as a consequence of the low cost of egg production in cowbirds (Scott and Ankney 1980; Kattan 1997). The occurrence of inappropriately timed eggs has generally been considered a rare event that is “a last resort in an emergency” (Friedmann 1929, pp. 186–187). This description contrasts with the “shotgun” strategy, which suggests that some brood parasites lay in any nest they encounter, and many researchers believe that some wastage of eggs or improper nest choice is an unavoidable cost of the generalist laying strategy (e.g., Rothstein 1976; Kattan 1997).

Understanding the causes of multiple parasitism and the use of unsuitable hosts requires information on the laying strategies of individual female cowbirds (e.g., Alderson et al. 1999a). Recently, parentage analysis using highly variable genetic markers has begun to provide information on the laying patterns of individual female parasites and, hence, the distributions of eggs in host nests through space and time (but see Martínez et al. 1998b; Alderson et al. 1999a; Hahn et al. 1999; Woolfenden 2000).

We investigated patterns of parasitism by brown-headed cowbirds on song sparrows (*Melospiza melodia*) at Delta Marsh, Manitoba. The song sparrow was the most frequently parasitized host in this community and was consistently multiply parasitized (S.G. Sealy, unpublished data). Our primary objective was to determine the frequency of multiple parasitism by a single female versus more than one female. In addition, we examined the timing and synchronization of parasitism on song sparrows in general.

## Methods

### Study site and host-nest monitoring

We studied song sparrow nests in the forested dune ridge and adjacent marsh and fields at Delta Marsh, Manitoba (habitats described in MacKenzie et al. 1982; Weatherhead 1989). The data are of two types. In 1994–1998, song sparrow nests were discovered opportunistically throughout the site and no effort was made to find all nests. Our primary goal was to obtain a large sample of nests for recording parasitism frequencies. Individual nest histories were largely extrapolations based on a few inspections. Hence, data from

these nests were used to record only the occurrence of multiple parasitism by one or more females, unless nest histories were fully known. In 1999, we searched daily for nests within a core area of the study site and were aware of the locations of all singing males and, hence, potential nests. Point counts and territory mapping of song sparrows conducted in a previous year yielded an estimate of approximately 35 song sparrow nests, including renests, in the area (Woolfenden 2000). Thirty-seven nests were found in 1999, hence, we were confident that we had found most song sparrow nests initiated during the cowbird laying season. In 1998 and 1999, these nests were checked daily for cowbird parasitism and the date of clutch completion, depredation, abandonment, or fledging was recorded. Nest stage was determined for nests at which host laying events were recorded or by backdating from hatch at nests found during incubation. Nests were not checked during rain, at wind speeds >30 km/h, or at temperatures <10°C. In 1999, depredated, abandoned, and fledged nests were checked every few days for up to a week until 2–3 days postfledging or failure to detect parasitism.

### Cowbird-egg sampling

Upon discovery, all cowbird eggs were removed from nests. In both years eggs were replaced with plaster-of-Paris or wooden models painted to resemble cowbird eggs to maintain the status of parasitism of the clutch. The cowbird eggs were incubated at 37.5°C for up to 10 days to ensure adequate tissue development. Developed eggs were sealed in plastic bags and stored at –20°C.

### DNA extraction, polymerase chain reaction amplification, and genotyping

Of 161 eggs collected, 134 (83%) yielded sufficient DNA for genetic analysis. Eggs that did not yield DNA were either infertile or otherwise did not develop. DNA was isolated from tissue samples removed from the eggs by organic-solvent purification (Sambrook et al. 1989). Allelic variability and genotypes were assessed using up to nine microsatellite loci, including five cowbird-specific loci (BHCO10, -20, -23, -25, and -29), two isolated from yellow warblers (*Dendroica petechia*; YW15 and -16) (Dawson et al. 1997), and two isolated from Swainson's thrushes (*Catharus ustulatus*; T4 and -10) (Gibbs et al. 1999). We used polymorphic loci from these additional species to improve resolution and the power to determine probabilities of kinship. Procedures for genotyping were described in Alderson et al. (1999b).

### Assessment of sibling kinship

We examined kin relationships among 58 groups of cowbird eggs found in the same nest, using kinship analyses that compare estimates of pairwise relatedness ( $r$ ; see Queller and Goodnight 1989), conducted with the program KINSHIP, version 1.1.2 (Goodnight et al. 1997). We used population allele frequencies for the five cowbird and two yellow warbler loci from the adult cowbird population sampled at Delta Marsh since 1994 (B.E. Woolfenden, unpublished data). Allele frequencies for the two thrush loci were assessed from a sample of 20 randomly selected adult cowbirds (10 males, 10 females) captured and bled in 1998 and 1999. KINSHIP used these allele frequencies to generate null distributions and expected 95% confidence intervals for full-

sibling ( $r = 0.5$ ), half-sibling ( $r = 0.25$ ), and unrelated ( $r = 0$ ) pairwise relationships using 5000 randomizations. Because these relatedness distributions overlapped extensively, we used the following criteria to infer kin relationships among pairs of eggs on the basis of expected  $r$  values for each type of kin group. First, we classified pairs of eggs as full siblings only if the  $r$  value was above the upper 95% confidence interval for half-siblings and, similarly, as unrelated only if the  $r$  value was below the lower 95% confidence interval for half-siblings. Values of  $r$  that fell within regions of overlap for different kin groups were dealt with in the following way. We used KINSHIP significance testing ( $\alpha = 0.05$ ) for null distributions of various kinship levels and classified as unrelated all pairs that fell within the overlap between unrelated siblings and half-siblings that failed to reject the null hypothesis in a likelihood test of half-siblings versus unrelated siblings ( $p > 0.05$ ). Likewise, we classified as full siblings all pairs that fell within the overlap between half-siblings and full siblings that rejected the null hypothesis in a test of full siblings versus half-siblings. Hence, we considered full siblings only those pairs of individuals where a KINSHIP test of full siblings versus half-siblings yielded  $p < 0.05$  or when the null hypothesis was not rejected but the pair had an  $r$  value greater than the upper 95% confidence limit for half-siblings. These criteria were used to minimize the occurrence of Type I errors, i.e., misclassifying unrelated siblings or half-siblings as full siblings, or unrelated siblings as half-siblings. The power of these tests was 0.95 and, hence, fewer than 5% of pairs were classified as unrelated when in fact they were full siblings. By these criteria, the estimate of the frequency of either type of multiple parasitism may be slightly biased toward parasitism by different females.

### Synchrony of cowbird laying

The first day of host laying (LD 1) was the day on which the first host egg was laid. The first day of incubation (ID 1) in host nests was the day following clutch completion, i.e., the day by which the clutch had remained unchanged for 2 consecutive days. We considered cowbird eggs that appeared in active nests before LD 1 and up to and including ID 2 to be appropriately timed and all others to be inappropriately timed. We chose these criteria because incubation periods for song sparrows and cowbirds are approximately 12 days (calculated from the laying of the last egg in sparrows; Nice 1937); hence, cowbird eggs laid after ID 2 likely do not hatch. Inactive nests included abandoned nests, either unattended ones that had never received a host egg or contained eggs that had been cold to the touch for at least 2 consecutive days, depredated nests, and nests from which young had fledged.

We compared the appropriateness of cowbird laying in each category of multiply parasitized nest, i.e., single-female nests versus multiple-female nests, using  $\chi^2$  contingency tests, combining nests from all years. We analysed data by nest, each nest being scored as “all eggs laid appropriately” or “one or more laid inappropriately”, and by egg, each egg being scored as “appropriately laid” or “inappropriately laid”. In the latter case, only eggs laid after the first egg in the nest were considered, unless both eggs appeared the same day, in which case neither was included. Two or more eggs laid by

the same female in the same nest were scored as single-female eggs (see below) regardless of whether they were laid along with one or more eggs of a different female.

## Results

### Kin relationships of eggs in multiply parasitized nests

Of 58 nests, 27 (47%) contained cowbird eggs that were full siblings, i.e., eggs laid by one female, and 31 (53%) contained two or more eggs laid by more than one female. Of the latter group, nine nests contained more than two cowbird eggs, of which at least two were laid by the same female (single-female eggs; see Methods and below) and the remainder were laid by another female. Because these nests resulted from both single-female parasitism events as well as multiple-female parasitism events, we also considered each event independently to determine the frequency at which multiple parasitism involved one female laying in a nest she had already parasitized versus a different female parasitizing an already-parasitized nest. Over all years, 43 (55%) eggs laid in nests that already contained at least one cowbird egg were laid by a female that had already laid an egg in that nest, compared with 35 (45%) eggs that were laid by a female different from any that had already laid in that nest.

### Synchrony of cowbird laying

Many cowbird eggs were not laid in synchrony with the song sparrow nest cycle or were laid in inactive nests. Overall, of 140 parasitism events for which the host nest stage was known, 42 (30%) were inappropriately timed. This estimate is conservative because nests were considered abandoned only if they had remained unattended with cold eggs for at least 2 consecutive days. Thus, for example, in two multiply parasitized nests likely abandoned before they received any host eggs, only the second and third cowbird eggs in the nest were inappropriately laid, and two other nests found with two cold cowbird eggs were deleted from the sample.

Multiply parasitized nests that received inappropriately laid cowbird eggs tended to involve multiple females (multiple-female nests) rather than the same female parasitizing a nest again (single-female nests), although the difference was not significant ( $\chi^2 = 3.404$ ,  $p = 0.065$ ). This trend was also evident in subsequent-to-first eggs laid in these multiply parasitized nests. In this analysis, eggs laid by a female in a nest that already contained another female's egg were more likely to be inappropriately laid than the second egg laid in a nest by the same female, although this difference also was not significant ( $\chi^2 = 2.728$ ,  $p = 0.099$ ).

The Julian date of initiation of nests that received one or more inappropriately laid cowbird eggs ( $148.5 \pm 1.9$  (mean  $\pm$  SE),  $n = 16$ ) did not differ significantly from the initiation date of nests that received only appropriately laid cowbird egg(s) ( $148.0 \pm 1.5$ ,  $n = 24$ ) ( $U = 175.5$ ,  $p = 0.6$ ). However, the laying date of inappropriately laid eggs ( $158.2 \pm 1.6$ ,  $n = 31$ ) was significantly later than the laying date of appropriately laid eggs ( $152.8 \pm 1.0$ ,  $n = 55$ ) ( $U = 530.5$ ,  $p = 0.004$ ).

### Timing of cowbird laying and multiple parasitism

Although inappropriately timed eggs were more likely laid in multiple-female nests and laid later, cowbird eggs appear-

ing in multiple-female nests were not laid significantly later in the season (Julian date =  $155.8 \pm 2.2$  (mean  $\pm$  SE),  $n = 22$ ) than eggs laid in single-female nests (Julian date =  $155.2 \pm 1.5$ ,  $n = 22$ ) ( $U = 228$ ,  $p = 0.7$ ). This was because multiple-female nests occurred throughout the season, some earlier ones with appropriately timed eggs and some later ones with inappropriately timed eggs.

## Discussion

### Single versus multiple females

Female cowbirds parasitized nests again almost as often as females parasitized nests already parasitized by another female. In the only other study in which patterns of multiple parasitism were examined, Martínez et al. (1998b) found that the frequencies of both parasitism and multiple parasitism were influenced by nest availability, likely because synchronous host initiation of clutches reduced the probability that each nest was parasitized (Martínez et al. 1996). However, they found that nests parasitized again by female great spotted cuckoos (*Clamator glandarius*) tended to occur independently of the availability of Eurasian magpie (*Pica pica*) nests. They suggested that these nests were reused because they were preferred in some way, the preference being perhaps related to host quality (Soler et al. 1995). Even so, Martínez et al. (1998a) suggested that in a previous year at the same site, availability may instead have influenced host choice: multiply parasitized nests were mostly “shared” nests that contained eggs laid by different females, and temporal patterns of laying suggested that cuckoos parasitized carrion crows (*Corvus corone*) when magpie nests were not available. Similarly, Strausberger (1998) suggested that multiple parasitism points to host preference in cowbirds. At Delta Marsh, the community of potential hosts is diverse, but many hosts nested at low density or rejected cowbird eggs (S.G. Sealy, unpublished data). Other abundant hosts include the red-winged blackbird (*Agelaius phoeniceus*), which nests semi-colonially in the marsh and may have group defense, which prevents parasitism (Robertson and Norman 1977; Clotfelter and Yasukawa 1999), and the yellow warbler (*Dendroica petechia*), which apparently is less preferred because it often rejects cowbird eggs (Sealy 1995). If the song sparrow is a preferred host, patterns of parasitism on it may be unaffected by the relative availability of other hosts. Our results suggest that nests may be parasitized more than once by the same female when few new song sparrow nests are available, whereas nest parasitism by more than one female frequently involves females laying indiscriminately. A female may parasitize a nest more than once because she prefers it over a nest of a lower quality host species. This assumes that a female remembers which nests she has parasitized. Indirect evidence based on the relative size of the hippocampus suggests that female cowbirds can remember nest locations (Sherry et al. 1993), but there is little evidence from the field to validate the assumption.

Strausberger (1998) suggested that if cowbirds are physiologically constrained to produce eggs even when no suitable nest is available (Rothstein 1976), they may “make the best of a bad situation” and reparasitize already-parasitized nests. His data did not support this hypothesis, however. Hahn et al. (1999, pp. 216) speculated that multiple parasitism re-

sults from “opportunistic laying by a yearling female cowbird”. They cited Darley’s (1983) observation that younger females usually do not hold home ranges and suggested that these females parasitize any nest, irrespective of its stage or whether it has been parasitized. Multiple parasitism may be a consequence of a nonterritorial system or the presence of some nonterritorial individuals (Martínez et al. 1998b; Alderson et al. 1999a), but there is no information on the ages of the females involved. Yearling female cowbirds arrive at breeding sites later (Darley 1983; Woolfenden 2000) and, hence, breed later (Fleischer et al. 1987). It is possible, therefore, that later and inappropriately timed cowbird eggs were laid at Delta Marsh by younger females. Thus, there may be two types of female cowbird, those that lay selectively and those that lay indiscriminately.

### Timing and synchronization

The frequency of unsynchronized parasitism (30% of all cowbird eggs laid in song sparrow nests) is one of the most highly documented for any host species of the brown-headed cowbird. In most studies, frequencies of inappropriate laying involve fewer than 10% of all cowbird eggs laid (e.g., Berger 1951; Strausberger 1998), but frequencies between 10 and 20% have also been reported (e.g., Nolan 1978; Sealy 1992). In only four studies were frequencies >20% (Weatherhead 1989; Freeman et al. 1990; Davis 1994; Scott and Lemon 1996). We did not record cowbirds laying during the song sparrow nestling stage, although such cases have been documented occasionally in several other host species (e.g., Furrer in Friedmann et al. 1977; Davis 1994; Sealy 1995).

Cowbirds may not preferentially parasitize song sparrow nests during laying, either because they cannot assess the stage or because they are forced to lay at other stages because of a shortage of other known nests. Weatherhead (1989) similarly suggested that evolutionary lag explained the lack of refinement in timing of parasitism on red-winged blackbirds, which suggests that selection for the ability to ascertain the stage of the host nest has been slow. Freeman et al. (1990) observed that red-winged blackbird nests in marshes surrounded by more trees contained fewer inappropriately laid cowbird eggs and concluded that cowbirds that perched near the marsh gained better information to use in deciding when to parasitize nests. In the shiny cowbird (*Molothrus bonariensis*), poor synchronization resulting in “shotgun” parasitism may result when cowbirds have difficulty gaining access to nests in cavities or domed nests (Kattan 1997; Mermoz and Reboreda 1999). The two examples of poor synchronization in red-winged blackbirds (Weatherhead 1989; Freeman et al. 1990) may be similarly explained if group defense (see above) prevented cowbirds from monitoring nests closely enough. This explanation, however, likely does not explain poor synchronization in solitary-nesting species such as the song sparrow and other grassland hosts. Perhaps cowbirds are less likely to monitor ground nests because of the costs associated with finding them again to determine their contents or because of the difficulty of observing host behaviour from distant perches.

Cowbirds may be forced to parasitize nests after the hosts have laid because cowbird densities are high, as high cowbird-to-host ratios may jeopardize cowbird selectivity by forcing competing females to avoid conflict at host nests (Smith

1999). Despite extremely high cowbird-to-host ratios at Delta Marsh, there are nonrandom patterns of parasitism across all hosts in the community (B.E. Woolfenden, H.L. Gibbs, and S.G. Sealy, unpublished data). As well, some song sparrow nests escaped parasitism, therefore competition for host nests in the laying stage should not force cowbirds to lay indiscriminately.

If the smaller number of nests established later in the season are more difficult to locate, more eggs should be laid inappropriately at this time (Friedmann 1929; Hoy and Ottow 1964). This assumption was supported by the results of the examination of the laying dates of individual eggs, but not by the comparison of initiation dates of clutches classified as either all eggs appropriately timed or some eggs inappropriately timed. The latter comparison eliminated the bias that is inherent in the contrast, because inappropriately laid eggs include those laid later in the host-nest cycle and, hence, also later in the season. This test may still be biased somewhat, however, because eggs for which laying dates were not known precisely were not included. These tended to be laid earlier in the host cycle, i.e., in nests found after clutch completion but before hatch, and, hence, were appropriately laid and therefore also laid earlier in the season. In any event, the fact that fewer nests were available later in the season did not account for the inappropriate layings.

Laying eggs in already-parasitized nests or at inappropriate stages is a trade-off with the costs of locating a better nest. Describing the laying behaviour of individual female cowbirds as optimal strategies in the sense of game theory requires an understanding of several different aspects of single and multiple parasitism (Payne 1977): the criteria used by cowbirds to rank the quality of host nests, differences in nest-searching experience among individual females, differences in the ability to obtain and maintain territories, and the contributions of different females to multiply parasitized nests. We have provided data to clarify the last point. More information on the first three points will contribute to a general understanding of selection pressures that act on the reproductive behaviour of cowbirds.

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