



Host use and fecundity of individual female brown-headed cowbirds

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Descriptions of the laying behaviours of obligate brood parasites such as the brown-headed cowbird, *Molothrus ater*, typically fall into one of two categories. These categories are 'shotgun behaviour', where females are predicted to distribute their eggs apparently at random between available host nests, or 'host selection behaviour', where females lay their eggs discriminately, placing them into the most suitable host nests. To test these hypotheses, data on individual female fecundity and host use patterns are required, but until recently, such information has been largely unavailable. We used field observations and genetic parentage analysis to describe the fecundity and laying behaviours of individual female cowbirds over six breeding seasons at Delta Marsh, Manitoba, Canada. Although some females used more than one host species both within and between breeding seasons, other females parasitized specific host species regardless of their availability. This nonrandom host use suggests some degree of host selection in this population. We also found that realized female fecundity was low ($\bar{X} \pm \text{SD} = 2.3 \pm 0.6$ eggs per female) compared with previously published estimates. Our results suggest that female laying behaviour lies on a gradient between the two extreme categories of pure 'shotgun' or 'host selection' laying behaviours, and females may optimize their reproductive effort by varying their behaviours as environmental conditions dictate. When high-quality hosts are not available for parasitism, cowbirds may switch to parasitizing lower-quality hosts. Flexibility in cowbird laying behaviour may be an adaptation that enables individuals to successfully exploit local and temporal variation in the availability of different hosts.

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Birds that are obligate brood parasites abandon the care of their young to host parents, which raise the parasite young. Consequently, a female parasite's reproductive success depends largely on the ability of the host parents to care for her young. The choice of which host to parasitize, therefore, is a crucial reproductive decision made by female parasites. Among avian brood parasites that lay their eggs in the nests of more than one species of host, there is considerable evidence that the potential hosts vary in their quality as surrogate parents. This variability is due to several factors that include the likelihood that hosts will eject the parasite egg(s) or abandon parasitized nests (Rothstein 1975), the intensity of

resource competition between host and parasite offspring (Dearborn & Lichtenstein 2002) and the suitability of the diet fed to parasite young by host parents (Rothstein 1975; Middleton 1977). These factors may result in substantial variation between host nests in the number of cowbirds that fledge per cowbird egg laid (Ortega 1998).

As a result of the differences in the potential success of parasite young between host species, selection should favour individual parasites that lay eggs in the nests of the host most likely to fledge the parasite young and that avoid unsuitable hosts. The 'host selection' hypothesis (Kattan 1997; Rothstein & Robinson 1998; Grant & Sealy 2002) predicts that individual parasites should distribute eggs between high-quality hosts to maximize the potential success of each offspring. As a result, individual females should lay fewer eggs because each egg cared for by suitable host parents should have a higher likelihood of surviving to reproduce. Alternatively, the 'shotgun' hypothesis suggests that a more successful strategy is to produce large numbers of eggs that are distributed randomly between host nests (Scott & Ankney 1983; Holford & Roby 1993; Rothstein & Robinson 1998).

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A long-standing controversy is which of these hypotheses better describes host use in one of the best-studied generalist brood parasites, the brown-headed cowbird, *Molothrus ater* (hereafter cowbird) (Scott & Ankney 1983; Rothstein 1990; Holford & Roby 1993; Rothstein & Robinson 1998). Evidence for the 'shotgun' hypothesis comes from studies that document high potential fecundity and apparently random population-level distributions of cowbird eggs between the available hosts in a community (Rothstein 1976, 1990). However, other studies have documented patterns of laying behaviour that are more consistent with the 'host selection' hypothesis. For example, although cowbirds are known to parasitize over 220 host species (Friedmann & Kiff 1985), several studies have documented cowbirds avoiding inappropriate hosts and selectively parasitising particular host species regardless of their relative availability (Mayfield 1977; Franzreb 1985; Gryzbowski et al. 1986; Sealy & Bazin 1995; Smith & Myers-Smith 1998). Additionally, Ortega et al. (1994) showed that cowbirds avoid laying eggs in previously parasitized nests, possibly to reduce the costs of conspecific competition for parental care. These findings suggest that under some circumstances cowbirds may lay eggs discriminately, thereby increasing the probability of success for each offspring. It is also possible that individual laying behaviours lie between the scenarios stated in these hypotheses. Females may optimize their behaviour by using tactics that fall between two extremes of 'shotgun' and 'host selection' behaviour depending on the circumstances. For example, Alderson et al. (1999a) documented the presence of both 'generalist' and 'specialist' females within their study population, which suggests that the populations of generalist parasites consist of both 'generalist' and 'specialist' individuals.

Empirical tests of hypotheses regarding laying behaviours of female parasites require information about both the fecundity and patterns of host use by individual females. Until recently, descriptions of individual behaviours were largely unavailable, due to the lack of a priori information regarding where a female lays her eggs and the difficulties associated with obtaining descriptions of the laying behaviours of individual females based solely on observations. Therefore, most of the available descriptions of cowbird laying behaviour have been inferred from population-level studies of the patterns of cowbird parasitism relative to habitat features (e.g. Brittingham & Temple 1983; Robinson 1992; Strausberger 1998; Avrill-Murray et al. 1999), host community composition (Strausberger 1998) and host behaviour (Clark & Robertson 1979; Briskie & Sealy 1989; Rothstein 1990; Neudorf & Sealy 1992; Sealy 1995). Although these studies are important for understanding factors that may determine patterns of parasitism at the population level, they provide no insights into the reproductive choices made by individual female cowbirds (but see Payne et al. 2000).

Recently developed DNA-based genetic markers provide a novel way of linking parents with individual offspring in the absence of such a priori information regarding the location of a particular female's eggs. To date, only two studies (Alderson et al. 1999a, b; Hahn et al. 1999) have

used genetic parentage analysis to describe the laying behaviour and fecundity of individual female cowbirds, and both have provided some evidence for discriminating host use by individual females. These studies support the host selection hypothesis by documenting that females are capable of discriminating between hosts, perhaps on the basis of their quality as surrogate parents (Woolfenden 2000; Grant & Sealy 2002) and suggest that the inference of individual behaviours based on population-level interactions may be inaccurate.

We used a combination of observational and genetic techniques to describe the fecundity and patterns of host use by female cowbirds at Delta Marsh, Manitoba, over 6 years. We relate these patterns to the availability and quality of host nests to understand how host availability affects host use by individual female parasites and to make inferences about individual cowbird laying behaviours.

METHODS

Field Methods

Field work was conducted at the Delta Marsh Field Station, Delta Marsh, Manitoba (98°23'W, 50°11'N). Details of the study area are provided by Alderson et al. (1999a, b) and (Woolfenden et al. 2001). During the cowbird breeding seasons of 1993–1998, we captured, individually colour-marked and monitored over 95% of all adult cowbirds (based on weekly transect censuses; for details see Woolfenden 2000; Woolfenden et al. 2001, 2002) on a 60-ha central study site. At first capture, a blood sample (Hoysak & Weatherhead 1991) was taken from each adult. Trapping and observation protocols are provided in Woolfenden et al. (2001).

We thoroughly searched the central study area (average 24 person-hours per day) and opportunistically searched the surrounding habitat for potential host nests. In every year the most abundant host species were yellow warblers, *Dendrocia petechia*, red-winged blackbirds, *Agelaius phoeniceus*, and song sparrows, *Melospiza melodia* (Woolfenden et al. 2001). Nests were marked and the contents monitored every other day. To obtain information on cowbird and host nest densities, we censused two, 2000-m transects, set 100 m apart, through the study area once every 7 days. Trained observers conducted 10-min point counts of the numbers of singing male red-winged blackbirds, yellow warblers and song sparrows. Birds vocalizing within a 50-m radius of each transect point could easily be detected by observers. We estimated our success at finding nests of these three species by dividing the number of nests located by the estimated total of nests (determined by the number of males heard singing during weekly censuses and averaging these values across weeks). We did not attempt to determine the pairing status of singing males of any species or the levels of polygyny in red-winged blackbirds. Consequently, we may have overestimated the number of warbler and sparrow nests and underestimated the number of blackbird nests. Based on this analysis, we estimated that more than 90% of red-winged blackbird

Table 1. Total number of egg, nestling and fledgling brown-headed cowbird samples collected each year, the number that were successfully genotyped and the number that were assigned a female parent based on exclusion analysis

	Location	1993	1994	1995	1996	1997	1998	Total	Annual $\bar{X} \pm SD$
Offspring sampled	Study area	35	90	32	37	42	66	302	50.3±23.0
	Outside	0	0	8	19	22	20	69	11.5±10.2
	Total	35	90	40	56	64	86	371	61.8±22.9
Offspring genotyped	Study area	27	64	28	28	33	60	240	40.0±17.21
	Outside	0	0	7	19	20	13	59	9.8±8.9
	Total	27	64	35	47	53	73	299	49.8±17.3
Samples assigned a female parent*	Study area	16 (3)	56	25 (4)	28	30	48 (15)	203 (22)	33.8±15.1 (7.3±6.7)
	Outside	0	0	5 (1)	8 (1)	8 (2)	11 (8)	32 (12)	32.0±8.0 (8.0±3.0)
	Total	16 (3)	56	30 (5)	36 (1)	38 (2)	59 (23)	235 (34)	39.2±16.2 (6.8±9.2)
% Samples assigned a female parent†	Study area	59.2	87.5	89.3	100	90.1	80.0	84.6	88.6±7.0
	Outside			71.4	42.1	40.0	84.6	54.2	59.5±20.0
	Total	59.2%	87.5	85.7	75.6	71.7	80.8	78.6	80.0±6.0

Data are grouped according to where they were collected (within the study area or in surrounding areas of host nesting habitat).

*Total number of samples assigned a parent whose identity was unknown (virtual females) is indicated in parentheses.

†Percentage includes samples assigned a virtual female parent.

and yellow warbler nests and approximately 50% of the song sparrow nests were located each year.

From 1994 to 1998, 923 host nests were inspected: 394 (42.7% of total nests) red-winged blackbird nests, 82 (8.9%) song sparrow nests and 447 (48.4%) yellow warbler nests. Across all years, the average date of first laying by cowbirds was 28 May. Data from the first year of the study are not included in this summary because nest searching and monitoring were not as intensive in 1993 as in subsequent years; therefore, the nests we monitored probably did not accurately represent host availability in that year. In all years, cowbird eggs were removed as they were found and in most cases replaced with model eggs to maintain clutch volume and reduce the probability of host abandonment. Cowbird eggs were artificially incubated for approximately 9 days to ensure adequate tissue development, then frozen and stored at -20°C . When nestling cowbirds were discovered in host nests or fledgling cowbirds were trapped, a blood sample was taken from the alar vein and the cowbirds were returned to the capture site.

Over six breeding seasons (1993–1998), we collected 345 cowbird eggs: 95 from 442 red-winged blackbird nests, 111 from 467 yellow warbler nests and 119 from 89 song sparrow nests. The remaining cowbird eggs were found in nests of the alder flycatcher, *Empidonax alnorum* ($N=2$), American robin, *Turdus migratorius* ($N=1$), clay-coloured sparrow, *Spizella pallida* ($N=2$), grey catbird, *Dumetella carolinensis* ($N=5$), Savannah sparrow, *Passerculus sandwichensis* ($N=4$), swamp sparrow, *Melospiza georgiana* ($N=5$), veery, *Catharus fuscescens* ($N=1$) and two in the abandoned nests of unidentified hosts. The remaining 26 samples were taken from fledglings and could not be assigned to a particular host species.

Instances of multiple parasitism were documented in the nests of the three most abundant host species in most years (B. E. Woolfenden, H. L. Gibbs, S. G. Sealy & C. M. McLaren, unpublished data). Overall, 29.2% of all parasitized nests were multiply parasitized. Multiple parasitism was most common in song sparrow nests (39.7% of

available nests, 65.5% of parasitized nests), followed by red-winged blackbird nests (3.1% of available nests, 24.5% of parasitized nests) and yellow warblers (0.7% of available nests, no instances of multiple parasitism).

Parentage Assignment

Of the 371 eggs, nestlings and fledgling cowbirds, 302 were collected in the central study area and 69 in the surrounding habitat (Table 1). Seventy-two of the samples (19.5%) did not yield DNA, because they were from eggs that were infertile or addled. Over the 6-year study, we sampled 293 adult (after-hatch-year, AHY) female cowbirds. Female cowbirds cannot be accurately aged following hatch year (HY), so we were unable to accurately age any females in this study. Not all of these adult females were equally likely to have been breeding on the study area. Many banded females (41.6%) were seen only once, and these probably were migrants or individuals that visited the site to feed at our bait piles (Woolfenden et al. 2001). Therefore, a subset ($N=171$, 58.4% of the total) of females, which were observed or trapped on the site more than once, was used for all further analyses (see also Woolfenden et al. 2002).

Techniques for extracting DNA, genotyping and parentage exclusion analyses followed Alderson et al. (1999a). Based on the set of seven microsatellite markers that we used, the parentage resolution ($P(E)$)=probability that a nonparental female (or male) will be excluded as a parent) (Chakraborty et al. 1988) was 0.9948 and 0.9964, respectively (Alderson et al. 1999a). This result indicates that these markers were sufficiently powerful to exclude over 99% of all nonparental females from the parentage analysis. In cases where seven loci did not provide sufficient resolution to exclude all but a single female as the parent of a given chick we used two additional polymorphic loci (*Cumu4*, *Cumu10*) from the Swainson's thrush, *C. ustulatus* (Gibbs et al. 1999). For both a male and female to be assigned as the genetic parents of the same offspring, each must have contributed a different allele at

each of the seven loci genotyped. In the 10 cases where both the male and female contributed the same allele at one or more loci, the male, female and offspring were genotyped at the two additional loci to determine which was the genetic parent. This additional information allowed us unambiguously to determine which individual was the genetic parent in all cases.

If an offspring was assigned a male but not a female genetic parent, we created virtual female parents based on the relatedness of the offspring within each family group (male parent and his offspring) and the male allelic contribution. Specifically, if the male parent was assigned more than one offspring within the same breeding season, we used the program KINSHIP version 1.12 (Goodnight & Queller 1999) to determine whether the offspring in the family group were full siblings or half-siblings (Alderson et al. 1999b). Briefly, KINSHIP uses allele frequencies (calculated from 462 genotyped adults from this population) to generate null distributions and expected 95% confidence intervals for full sibling and half-sibling relationships using 5000 randomizations. We compared the observed r values (estimated pairwise relatedness) for each pair of offspring in each family group with the range of expected r values for each type of kin group to infer genealogical relationships. We refer to females that were not sampled but for whom genotypes were calculated as VF (virtual female) parents (Alderson et al. 1999b; Woolfenden 2000). This KINSHIP analysis was performed on nine sibling groups. If a sibling group was identified as full siblings, it indicated that the male mated with a single female, and half-sibling groups indicated that the male had mated with two or more females. Multiple mating has been documented in this population (Alderson et al. 1999a, b; Woolfenden et al. 2002).

Host Use Patterns

To determine whether individual variation in host use was related to differences in the relative availability (number of nesting pairs) of each species of host, we compared the frequency with which individual females parasitized hosts relative to the availability of each host species, using a variety of assumptions to estimate which host nests were available. If females lay eggs in nests apparently at random, we predicted that individuals would parasitize hosts in proportion to their availability. Conversely, if females discriminate between hosts, observed parasitism frequencies would be significantly different from those predicted based on host availability. Only females assigned three or more offspring were used in this analysis, and consequently no females from the 1993 breeding season were included. Three eggs were chosen because regression analyses indicated that this was the cutoff to ensure that incomplete sampling did not influence our findings.

Trapping and observation records combined with egg-laying dates, found by determining the dates that eggs assigned to females were laid in host nests, indicated that not all females remained on the study site, or laid eggs throughout the entire breeding season; hence, for analyses of host use patterns, the season was divided into 7-day

intervals. For each female assigned at least four eggs in a given year, we determined the number of eggs laid in nests of each host species and the number of host nests of each species available for parasitism on the central study site in the intervals during which that female was documented on site or known to be laying. We defined the period that a nest was available for parasitism as the 7-day period beginning 1 day before nest initiation (Woolfenden 2000). The validity of this criterion is supported by data from this site that demonstrates that most cowbirds eggs are laid during this interval (Sealy 1995). We determined the expected proportion of eggs that would be laid in nests of each host species if that female laid relative to host availability, by multiplying the proportion of the total nests that belonged to that species by the total eggs laid by the female. We used the subroutine STRUC in the program Genepop (Raymond & Rousset 1995), which uses the Markov chain method to estimate without bias the exact probabilities of all contingency tables. The significance level of all tests was corrected for multiple comparisons using the sequential Bonferroni method (Rice 1989).

This analysis assumed that all host nests included in the analysis were available for parasitism. It was possible to exclude host nests that were not appropriately timed with cowbird laying by keeping track of host nest initiation dates and knowing when the cowbirds laid. However, we did not know whether all nests we located were found by cowbirds. It has also been suggested (e.g. Hahn et al. 1999; Shonk 2001) that females have distinct laying ranges. We did not have behavioural data with which to estimate female laying ranges (and thus the host nests available within this range), so all nests on the central study area were included in the analysis. We assumed, therefore, that the overall relative availability of host nests was representative of what was actually available to females in their laying areas. If this is not a valid assumption, then it is possible that in some cases, where statistical testing indicates that a female used host nests relative to their availability, the result may be due to the inclusion of nests in the analysis that were not actually found by cowbirds. This influence would result in an underestimation of the number of individuals that laid selectively.

Fecundity

We used both direct and indirect methods to estimate female fecundity over a breeding season. The direct method involved totalling the number of eggs assigned to individual females via the genetic parentage analysis (Alderson et al. 1999b). Only 59 (34.5%) of the 171 females genotyped were assigned eggs or offspring sampled on the central study area. Another 10 females (5.8%) were assigned offspring found only outside the central area. These areas were not searched thoroughly for host nests; hence, our data do not accurately represent the reproductive output and laying behaviour of these 10 individuals, and they were not included in the analyses. Because the fecundity values were lower than expected, we compared the realized fecundity (the number of eggs

assigned to a female via the genetic parentage analysis) with potential fecundity estimates that we calculated using the indirect measures first proposed by Scott & Ankney (1980).

Estimates of potential fecundity can be obtained indirectly by sampling females in the population and determining the proportion of females that have eggs in their oviducts (Scott & Ankney 1980; Fleischer 1985; Fleischer et al. 1987). The percentage of females with an oviducal egg can be used as a measure of the population laying rate (Payne 1973; Scott & Ankney 1980). The potential number of eggs (potential fecundity) laid by females was then determined by multiplying the length of the interval (in days) over which a female laid eggs by the laying rate. These estimates will represent the upper limit of the potential fecundity of the population as a whole, because the analysis does not take into account potential individual variability in the onset of laying, laying rate or total number of eggs laid by individual females. Instead, it assumes that all females lay at the same rate throughout the entire breeding season.

We collected oviducal egg data in two ways. First, in 1995–1998, female cowbirds captured outside the study area were held in pens overnight to obtain eggs the following morning for use in other projects (e.g. McMaster 1997; Lorenzana 1999). Capture sites were more than 2 km from the central study area and birds from the central study site were rarely seen or captured at these locations. Twice when banded birds were captured they were released, not held overnight. Two large pens (2.5 × 0.975 × 0.975 m, raised 1.625 m above ground) were each subdivided into four individual 0.975 × 0.975 × 0.65-m holding cages (8 in total). Pens were constructed of 5 × 5-cm studs covered with 1.25 × 1.25-cm wire mesh. A minimum of three perches spanned each pen at different levels (following Rothstein 1977). A portion of the roof over each pen was covered with masonite to provide shade and other protection. Each evening, a funnel-shaped nylon mesh net was strung above the floor of each pen, into which the cowbird egg rolled the following morning and where the cowbird would be unable to reach the egg. The mesh was attached to one wall of the pen each morning to reduce visual contact between adjacent females. Cowbirds were fed white millet, a mix of Purina Gamebird Startena, Purina Hi-Pro Dog food, hard-boiled eggs and yeast, mealworms, crushed oyster shell and fresh water with vitamin supplement (Avi-con by Vet-a-mix). Food was provided in trays placed on the floor of each pen. Cowbirds were held for a maximum of 4 nights before being released at original site of capture.

In 1998, we palpated the abdomens of females removed from traps after 1600 hours (Central Standard Time) to determine the presence or absence of an oviducal egg (Fleischer et al. 1987). The reliability of this technique was assessed by predicting the laying status of females held in cages overnight. We correctly assessed the laying status in 22 of 24 (92%) cases. Because accuracy was high and there were no significant differences in the laying rates determined by the different methods, data from

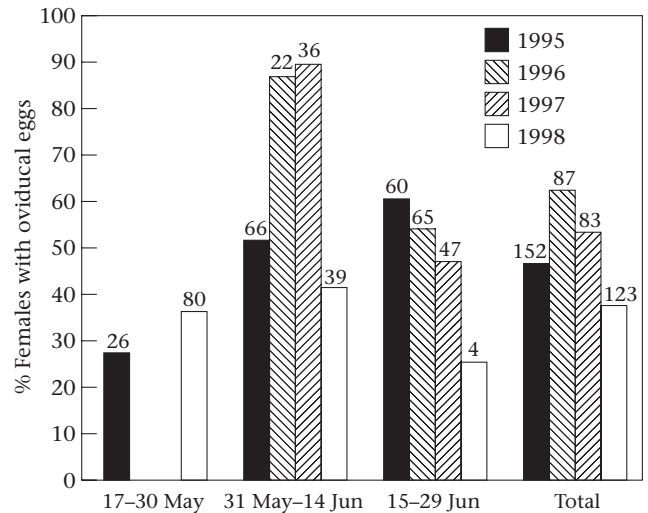


Figure 1. Proportion of females with oviducal eggs during the early, middle and late portions of the 1995–1998 cowbird breeding seasons at Delta Marsh, Manitoba. The 1995–1997 data were obtained from birds held in cages overnight. In 1998, data were obtained through abdominal palpation and holding birds overnight to determine laying rates. Sample sizes (female nights) are indicated on top of the bar corresponding to each interval.

the live-trapped and captive birds were pooled to determine the laying rate of the population in 1998. Because there may be seasonal and annual variation in laying rates (Scott & Ankney 1980; Fleischer 1985; Fleischer et al. 1987), rates were determined for three separate intervals in all years: 17–30 May, 31 May–14 June and 15–29 June.

Laying rates differed among intervals in 1995 ($G_{1,2}=88.9, P<0.001$), 1996 ($G_{1,2}=4.605, P<0.05$) and 1997 ($G_{1,2}=6.101, P<0.05$) but not in 1998 ($G_{1,2}=0.54, P>0.05$; Fig. 1). Therefore, we pooled the 1998 data, but not the 1995, 1996 and 1997 data, over the entire breeding season. Due to the lack of data, the laying rates for 17–30 May in 1996 and 1997 were estimated by pooling the laying rates over the intervals in which we had data. In 1996, the first cowbird egg was laid on 31 May, and in 1997 the first female held overnight in captivity was on 12 June. Based on trapping records, observations of marked birds (Woolfenden et al. 2001) and laying dates (determined from knowledge of the date an egg was laid in a host nest and the identity of the female that laid it), we determined the minimum length of time each breeding female was on the site. The lower bound on the number of eggs laid by each female (i.e. minimum potential fecundity) over the breeding season was estimated by multiplying the interval laying rate by the number of days a female was on the site during each interval. This estimate assumes that individuals did not remain on the site the entire breeding season. We also estimated the maximum potential fecundity for females by multiplying the interval-laying rate by the number of days in each interval. This estimate assumed that all females laid on the study site throughout the entire breeding season.

RESULTS

Parentage Assignments

We identified the genetic female parent for 201 (67.2%) of the 299 cowbird offspring samples that yielded DNA and 'virtual female' parents were assigned to an additional 34 offspring, which resulted in a maternal assignment of 78.6% to all genotyped offspring (Table 1).

Individual Host Use Patterns

Within years, most females laid eggs in the nests of more than one host species, but a few used a single species of host (Fig. 2a). Specifically, (1) 77% (20/26) of females used more than one host species each year, (2) females using a single host species within a year switched host species from year to year, and (3) females that used multiple host species within one year used different hosts across years. For example, female 15912 laid 13 eggs in red-winged blackbird nests in 1994, but in 1995 parasitized both red-wing blackbirds ($N=3$) and song sparrows ($N=1$). Females 90816 and 15995 used multiple hosts in each year, but the species used and the frequencies at which they were parasitized varied between years (Fig. 2a).

Pooling data on host use by individual females across years (Fig. 2b) reinforces the idea that female cowbirds tend to use multiple hosts because, in addition to multiple host use in a single year, some females used different host species in different years. Overall, roughly two-thirds of all females (20/29) used more than one host, and the remaining third (9/29) used a single host (Fig. 3).

Incomplete sampling of a female's reproductive output within and across years could have underestimated the number of hosts used by a single female. Therefore, the number of females we determined not to be host specific was minimal. The possible effects of incomplete sampling were examined by regressing the number of eggs assigned to a female on the number of hosts used by that female in a given year. We found a significant relationship between these variables ($Y=0.97+1.78X$; $F_{1,85}=36.21$, $P<0.001$, $R^2=29.8\%$) when all females, including those assigned a single egg, were included in the analysis. We reran the analysis excluding females assigned only single eggs and found that the relationship between number of eggs and number of hosts was no longer significant ($Y=1.39+0.10X$; $F_{1,43}=3.41$, $P=0.072$, $R^2=7.3\%$). We suspected that the results of this analysis might have been unduly influenced by a single outlying point, a female (15912) assigned 14 eggs, all laid in red-winged blackbird nests. When this point was removed from the analysis there was a significant relationship between the number of eggs and hosts ($Y=0.95+0.24X$; $F_{1,42}=13.73$, $P<0.001$). Further analysis that excluded females with two eggs or less revealed no significant relationship between these variables when female 15912 was included ($Y=1.84+0.03X$; $F_{1,27}=0.15$, $P=0.704$) or was excluded ($Y=1.11+0.21X$; $F_{1,26}=4.125$, $P=0.052$). Thus, incomplete sampling may underestimate host use for females assigned one or two eggs, so only females assigned

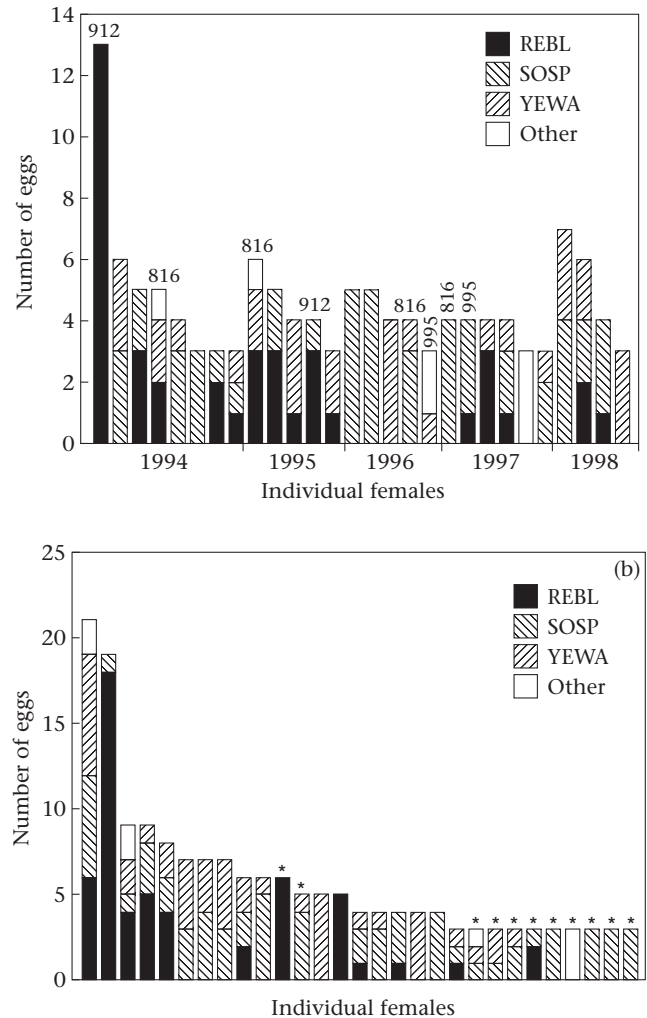


Figure 2. (a) Annual and (b) lifetime host use of individual females shown as the number of eggs laid in the nests of each host species (SOSP=song sparrow, YEWA=yellow warbler, REBL=red-winged blackbird). Each bar corresponds to a single female. Within years, individuals are sorted by the number of hosts used within years. (a) Includes only females assigned three or more eggs in each year and the last three digits of the band number are shown above the bar for females represented in more than one year. (b) Includes only females assigned three or more eggs over the course of the study (1993–1998) and data from females that did not appear in (a) are indicated by stars (★) above the bars.

three or more eggs were used in subsequent analyses of individual patterns of host use.

Host Use Patterns Relative to Host Availability

Analysis of individual host use relative to the availability of hosts demonstrates that 10 (59%) females parasitized hosts as expected based on their relative availability, but seven (41%) did not (Table 2). Specifically, of the females that did not distribute their eggs as predicted by the relative availability of host nests, five laid more eggs in song sparrow nests than predicted, one laid fewer eggs in yellow warbler nests than predicted and one laid

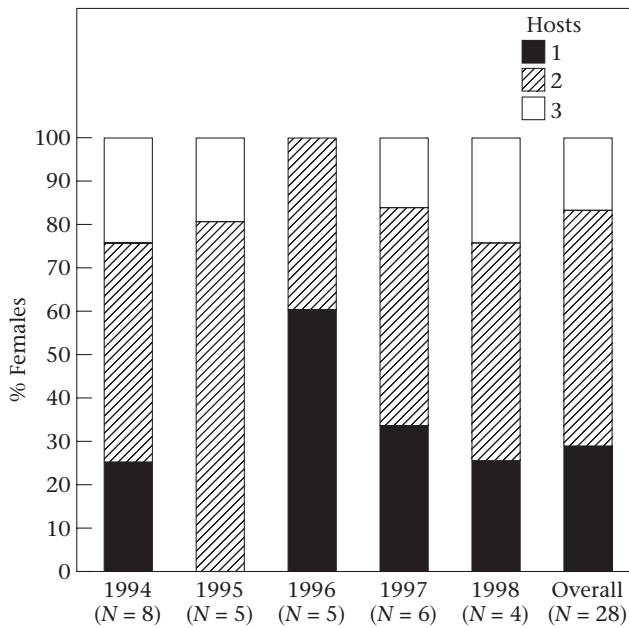


Figure 3. Annual host use patterns of females assigned three or more eggs per breeding season. The percentages of the total number of females that laid in the nests of one, two, three, or more different host species.

Table 2. Results of contingency table analysis (Markov chain method) to test for random host use by female cowbirds assigned four or more eggs

Female	Year	Nests (number available/ number parasitized)			P
		SOSP	REBL	YEWA	
15912	1994	0/20	13/114	3/36	≤0.05
	1995	1/7	3/35	0/110	≤0.05
15915	1994	2/10	3/68	0/25	NS
15917	1994	3/15	0/65	3/27	≤0.001
90827	1994	3/15	0/65	1/27	≤0.001
	1995	0/9	2/78	2/18	NS
90816	1995	0/6	2/34	2/96	NS
	1996	3/7	0/33	1/91	≤0.001
15936	1997	4/22	0/71	0/28	≤0.001
15936	1995	0/3	2/13	2/90	NS
15946	1996	5/10	0/34	0/19	≤0.001
15968	1996	0/0	0/4	4/64	NS
15848	1997	4/22	0/71	0/28	≤0.001
15995	1997	0/20	3/32	1/11	NS
90115	1998	4/7	0/43	2/77	≤0.001
VF10	1998	0/9	0/35	5/84	NS
90101	1998	2/15	2/65	2/72	NS

SOSP=Song sparrow, REBL=red-winged blackbird, YEWA=yellow warbler.

The number of cowbird eggs laid in nests of each species of host and the number of host nests available each year.

Significance level of all tests was corrected for multiple comparisons using the sequential Bonferroni method.

fewer eggs in red-winged blackbird nests. In summary, females that did not use hosts proportionately to their availability either parasitized the less abundant song

sparrows more frequently than expected based on their availability or parasitized the more abundant yellow warbler and red-winged blackbird less frequently than expected.

Female Fecundity

We estimated annual and overall (pooled over the 6 years of the study) realized fecundity, defined as eggs laid in host nests that could potentially fledge cowbird young (Alderson et al. 1999a), based on the number of eggs assigned to each individual within and between years. In general, realized fecundity was low but varied both between females and across years (Table 3). Mean annual realized fecundity ranged from 1.3 eggs/female in 1993 to 3.0 eggs/female in 1994. Many of the females were assigned only one egg (55% in 1993, 44% in 1994, 57% in 1995, 50% in 1996, 65% in 1997, 66% in 1998). The highest annual realized fecundity documented was 13 eggs (one female in 1994). One female was assigned seven eggs in 1998, four were assigned six eggs each (one in 1994, one in 1995 and two in 1998) and five females were assigned five eggs (two in 1994, one in 1995, two in 1996).

Twenty (33.9%) of the 59 individually identified females (excluding virtual females) were assigned eggs in 2 or more years. The mean \pm SD number of years in which a female was assigned eggs was 1.6 ± 0.9 (range 1–5 years). One female was assigned eggs in 5 consecutive years, another in 4 different years, each of four females were assigned eggs in 3 consecutive years and the remaining 14 were assigned eggs in 2 years.

Estimates of the number of eggs assigned to females in 1996–1998 were much lower than estimates of potential fecundity based on population laying rates (Fig. 1). Estimates of minimum individual potential fecundity based on the population laying rates were 8.8 ± 3.1 eggs in 1995, 14.0 ± 4 eggs in 1996, 16.0 ± 3.0 in 1997 and 4.8 ± 4.1 in 1998 (Appendix). Thus, the total numbers of eggs predicted to be laid in each season based on the laying rate data of the available population were as follows: 70 (1995), 150 (1996), 165 (1997) and 82 (1998). In all years, the number of cowbird eggs found in the central study area (32 in 1995, 37 in 1996, 42 in 1997, 66 in 1998; Table 1) and individual realized fecundity (2.5 ± 1.6 in 1995, 2.6 ± 1.7 in 1996, 2.1 ± 1.4 in 1997; 2.2 ± 1.8 in 1998; Table 3) were lower than that predicted by minimum potential fecundity estimates, and the differences between realized fecundity and maximum potential fecundity were even larger (Appendix).

DISCUSSION

Most studies documenting population-level patterns of cowbird parasitism agree that cowbirds, as a species, are host generalists (e.g. McGeen 1972; Friedmann & Kiff 1985; Lowther 1993), but there is a general lack of information on the laying behaviour of individual females (but see Dufty 1983; Fleischer 1985; Gibbs et al. 1997; Alderson et al. 1999a; Hahn et al. 1999). Our results, based on an individual-level genetic analysis,

Table 3. Estimates of mean realized annual fecundity for female brown-headed cowbirds based on the number of eggs, nestlings and fledglings assigned to each individual female based on exclusion analysis. Included are data from females that laid at least one egg within the study area

	1993	1994	1995	1996	1997	1998	Annual $\bar{X} \pm \text{SD}$
Offspring assigned female parents	16	56	30	33	30	49	35±14.9
Females breeding	12	19	12	13	14	22	15±4.6
Eggs per female							
$\bar{X} \pm \text{SD}$	1.3±0.5	3.0±2.9	2.5±1.6	2.6±1.7	2.1±1.4	2.2±1.8	
Range	1–2	1–13	1–6	1–5	1–4	1–7	

Two females were assigned eggs both inside and outside the study area in a single year. Annual fecundity estimates include data from virtual females (see Methods).

confirm that most females parasitized more than one host species, but a few specialized on one host species. We also provide evidence of nonrandom host use by some females in the population and low realized fecundity. In general, our findings suggest that the laying behaviour of individual females falls somewhere between the two extremes described by the 'host selection' and 'shotgun' hypotheses.

This is the first study to document individual female patterns over several years, and our findings reveal that female laying behaviour is flexible, with discrimination by some individuals between host species in relation to their availability and/or quality. We have demonstrated that some females parasitize host species relative to their availability, but others appear to discriminate between them by laying more often in nests of rare hosts and less often in those of abundant hosts. Our findings also demonstrate flexibility in female laying behaviour across years (Fig. 2b). Therefore, documenting female host use over only a single year may underestimate multiple host use by some females, especially if the availability of host species varies from year to year.

Host Use

Despite intensive nest-searching effort, the number of eggs per female and the number of females for whom we had more than 1 year of data were small. Although we believe that we located most potential host nests (Alderson et al. 1999a; Woolfenden 2000), the possible effects of sampling error on our findings are addressed here because it is possible that the number of host species used by individuals depended on the number of eggs assigned to that female. Regression analysis indicates that incomplete sampling of female reproductive output might result in an overestimation of the number of females that use a single host species when a female was assigned fewer than two eggs; therefore, we limited our analysis to females with three or more eggs. Our results demonstrate that it is possible to detect multiple host use in females assigned only three eggs, as 50% ($N=10$; Fig. 2b) of females in this category were recorded using more than one host species.

However, due to differences in the relative availability of the three main host species (Woolfenden 2000), the sampling effects of the number of eggs assigned on host use patterns may not be as straightforward as the regres-

sion analysis suggests. If individual cowbirds selected hosts at random, most of their eggs would have been laid in red-winged blackbird or yellow warbler nests simply by chance, because the relative availability of nests of these species is much higher each year than that of song sparrows nests (Woolfenden 2000). Therefore, host use would apparently be limited to one or two hosts even if females did not actively select hosts. Because realized fecundity was low (Table 3), we would expect females laying only a few eggs to parasitize the most abundant host species, but this was not what we observed. Most individuals that laid two or three eggs laid them in the nests of more than one host species, and song sparrows were often one of the hosts used despite their relatively low availability. This result supports our assertion that we can detect nonrandom host use by individual females despite the small number of eggs assigned to individual females.

Simple descriptions of the patterns of individual host use provide limited insights into the laying behaviour of individual females. Tests of hypotheses explaining how females distribute their eggs between available host nests also require information about host nest availability. This is the first study to combine both of these components in a single analysis, and our results document nonrandom host use by some females. In general, some females parasitized hosts in proportion to their availability, others avoided parasitising yellow warblers or red-winged blackbirds, and others parasitized song sparrows more frequently (Table 2). We interpret the behaviour of females that parasitize hosts nonrandomly as a type of discriminate laying, wherein individuals parasitize some hosts more or less frequently than expected based on their relative availability. We showed previously that cowbirds at Delta Marsh parasitize song sparrows more often than expected based on their availability (Alderson et al. 1999b; Woolfenden 2000), possibly because they are better hosts (based on the likelihood of successfully fledging a cowbird) than either yellow warblers or red-winged blackbirds (Norris 1947; Berger 1951; Weatherhead 1989; Smith & Arcese 1994; Sealy 1995). Nonrandom host use may be the result of females selecting hosts to maximize the success of each egg.

Female Fecundity

This study represents the first time that both realized and potential fecundity have been measured in the same

geographical region. Comparisons of our estimates of fecundity to previous studies yield several important findings. First, the potential fecundity in cowbirds at Delta Marsh is lower than that reported in other populations (Payne 1973; Scott & Ankney 1980; Fleischer 1985; but see Hahn et al. 1999), which suggests that geographical variability in fecundity is an important consideration when making comparisons between populations. These differences may be driven by intraspecific competition for host nests. Where cowbird-to-host ratios are high, as at Delta Marsh, intraspecific competition between females might be high due to limited host nest availability and, therefore, females may lay fewer eggs. By contrast, where competition for host nests is low, females may respond by increasing the number of eggs laid. The average female cowbird-to-host ratio (Robinson et al. 2000) for the host community at Delta Marsh was 0.2 ± 0.05 (1994=0.14; 1995=0.23; 1996=0.22; 1997=0.24; 1998=0.15), which is much higher than those reported for other areas (Robinson 1999). This difference suggests that competition for host nests at Delta Marsh is intense. Additional support for host limitation in this system is provided by the high frequencies of multiple parasitism documented in this study (see also McLaren et al. 2003).

Another important point is that the realized fecundity was low, relative to the potential fecundity in this population of cowbirds. This eliminates geographical biases that may have influenced estimates and therefore provides the only estimates of the relationship between these parameters collected to date. Finally, our measures of potential fecundity suggest that laying rates vary both seasonally and annually. Laying rates for breeding season intervals ranged from 0.24 to 0.9 eggs per day, with estimates of 0.37 and 0.53 eggs per day throughout the season. Previous estimates have ranged from 0.73 to 0.77 eggs per day (Payne 1976; Scott & Ankney 1980; Fleischer 1986; Rothstein et al. 1986; Fleischer et al. 1987; Holford & Roby 1993), which suggest that laying by female cowbirds may be more flexible temporally, spatially and individually than previously appreciated.

Flexibility in reproductive output would allow females to respond to variability in food resources, host nest availability and other cowbirds. Females could produce fewer eggs when resources are scarce or competition for available resources is high, because female cowbirds are relatively long-lived. Robust demographic analysis of this population revealed that annual female survival is almost 70%, and females may live at least 6 years (Woolfenden et al. 2001). Taken together, these observations suggest that individuals possibly trade-off current against future reproductive success. An alternative interpretation is that female host use behaviours may be learned and can change as individuals grow older and gain experience. Because we did not age AHY female cowbirds we could not directly test predictions of this hypothesis (but see Hahn et al. 1999). However, our data demonstrate that individuals used different hosts in different years (Results; Fig. 2b). Without information on female ages and the quality of individual hosts (measured as differences in cowbird survival among individual host nests), it is

impossible to know whether the differences in host use are due to learning, experience or the result of annual variation in host availability.

The discrepancy between realized fecundity and potential fecundity raises the possibility that realized fecundity is higher than our estimates suggest. Alderson et al. (1999a) and Hahn et al. (1999) reviewed possible explanations for discrepancies in the realized and potential fecundity of female cowbirds. Based on data from this study population, Alderson et al. (1999a) considered the possibility that females laid some eggs off-site. Our findings support this conclusion, but because of the few females involved, the impact on our results should be minimal. We determined that 10 of the 69 females (14%) were assigned eggs from nests found only outside the central study area, and two females (3%) laid in nests located both inside and outside the area. More eggs from these females and eggs laid by at least some of the females not assigned eggs, may have been laid in nests in areas that were not searched thoroughly. Determination of the extent to which this may bias estimates of realized fecundity can be done only by collecting detailed behavioural observations of individual females to document laying behaviour, using for example, radiotelemetry techniques. Preliminary results from a telemetry study of the Delta Marsh population indicate that female cowbirds seldom moved off-site during the breeding season (Shonk 2001).

Female Laying Behaviour

'Selective host use' and 'shotgun' laying behaviours represent two extremes of the possible gradient of laying behaviours shown by cowbirds. The results of this study do not provide definitive support for female cowbirds having a single laying 'strategy' at either end of the continuum. Rather, some females parasitize hosts at random, others parasitize only a single host species, and yet others use multiple host species but not in relation to their availability. This apparent flexibility in host use over time may be an adaptation to the temporal and local variability of host nests. Temporal variation has been documented (Woolfenden 2000) in the availability of host nests in this population. In environments such as Delta Marsh, where individuals cannot predict the future availability of a resource, behavioural flexibility and the ability to discriminate between resources of varying quality should be adaptive. Some workers have suggested that cowbirds may be able to assess individual host quality (Smith 1981; Smith & Arcese 1994; Sedgwick & Iko 1999; Grant & Sealy 2002) and/or prefer one host species over others in a host community. If the availability of high-quality hosts varies, then flexible laying will permit individuals to exploit locally and temporally variable host nest resources. Individual flexibility in laying rates would afford individuals another way to respond to variability in resources. A thorough understanding of the cues that cowbirds use to choose host nests and resource availability thresholds that result in behavioural changes will require extensive study of the responses of individual

cowbirds to variations in host availability over many years.

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Appendix

Table A1. Estimates of minimum (calculated for time individual was known to be on study site based on trap, observation and laying data), maximum (calculated for entire breeding season), and realized (number of eggs assigned) fecundity for all individuals that laid eggs on the central study area*

Year	Band number	Days on central study area			Potential fecundity		Realized fecundity
		Early season	Mid season	Late season	Minimum	Maximum	
1995	15912	3	7	0	5	17	4
	15915	8	11	0	8	17	1
	15936	5	15	4	12	17	5
	15941	3	3	0	3	17	3
	15946	5	15	5	12	17	1
	90811	8	15	3	12	17	1
	90816	4	9	0	6	17	6
	90832	7	15	4	12	17	2
	Total				70	144	23
$\bar{X} \pm SD$				8.8 ± 3.7		2.9 ± 2.0	
1996	15995		15	10	18	18	1
	15927		11	0	9	18	2
	15936		15	4	15	18	5
	15946		8	0	7	18	5
	15967		15	7	17	18	4
	15968		15	0	13	18	1
	15981		13	4	13	18	3
	90147		13	1	12	18	4
	90816		15	10	18	18	4
	90822		15	10	18	18	3
	90827		12	0	10	18	1
	Total				150	198	33
	$\bar{X} \pm SD$				14.0 ± 4.0		3.0 ± 2.0
1997	15805	3	15	9	20	20	4
	15806	3	10	0	11	20	2
	15816	3	15	6	18	20	1
	15848	3	15	6	18	20	4
	90114	0	1	0	1	20	1
	15849	3	15	2	16	20	3
	15918	0	1	0	1	20	1
	15972	0	0	1	1	20	1
	15927	3	15	6	18	20	2
	15968	3	12	0	13	20	1
	15995	3	11	0	12	20	4
	79841	0	1	0	1	20	1
	90816	3	15	10	20	20	1
	90822	3	15	10	20	20	1
	Total				170	280	27
	$\bar{X} \pm SD$				12.1 ± 7.9		1.9 ± 1.3
	1998	15811	7	0	0	3	13
15816		8	15	8	12	13	1
15855		8	11	0	7	13	1
15869		8	15	10	13	13	1
15914		8	11	0	7	13	1
15929		0	1	0	1	13	1
15936		0	1	0	1	13	1
15975		0	1	0	1	13	1
15976		1	0	0	1	13	1
15981		2	0	0	1	13	3
15989		1	0	0	1	13	1
15995		7	10	0	7	13	2
90101		8	3	0	4	13	6
90115		8	15	8	12	13	7
90125		0	13	10	9	13	1
90132		0	6	0	3	13	2
90813		1	8	0	4	13	1
Total					87	221	32
$\bar{X} \pm SD$					5.1 ± 4.3		1.9 ± 1.8

*All values have been rounded up to the next whole egg.