

# BROWN-HEADED COWBIRDS AND AN ISLAND POPULATION OF SONG SPARROWS: A 16-YEAR STUDY<sup>1</sup>

JAMES N. M. SMITH

*Center for Biodiversity, Department of Zoology, University of British Columbia,  
6270 University Boulevard, Vancouver, B.C. V6T 1Z4, Canada*

PETER ARCESE

*Department of Wildlife Ecology, 219 Russell Labs, 1630 Linden Drive, University of Wisconsin,  
Madison, WI 53706*

**Abstract.** We studied brood parasitism by Brown-headed Cowbirds (*Molothrus ater*) in a strongly fluctuating island population of Song Sparrows (*Melospiza melodia*). One to three cowbird females visited the island daily to search for host nests in 13 of 16 study years. Individual cowbirds visited on more days and laid more eggs at high sparrow densities, but some factor, perhaps aggression by territorial female cowbirds, limited cowbird numbers at high sparrow densities. Female cowbirds exhibited natal and breeding philopatry. Individual cowbirds laid about every other day on average, began to lay well after sparrows in most years, and avoided laying two eggs in the same nest. Cowbirds rarely laid after hosts had completed laying, and their eggs hatched as often as host eggs. Parasitism rates increased with host age, probably because of age-related differences in host behavior. Cowbirds removed a host egg from two-thirds of parasitized nests, and damaged two per cent of remaining host eggs. Parasitism reduced production of fledgling sparrows per nest by 0.79, but only by 0.27 fledglings in years when food was added experimentally to some territories. Nests failed more often during incubation in years with than without parasitism, supporting our earlier suggestion that cowbirds destroy eggs in host nests to enhance future laying opportunities. Colonization of Mandarte Island by cowbirds had little effect on sparrow numbers because of: (1) incomplete overlap in laying seasons; (2) multiple broods in sparrows; (3) functional and numerical responses of cowbirds to host density; (4) the sparrows' ability to rear their young with young cowbirds; and (5) density-dependent host reproductive success.

**Key words:** *Molothrus ater*; *Melospiza melodia*; reproduction; host-brood parasite interactions; population demography.

## INTRODUCTION

Two general topics have fascinated students of interspecific brood parasitism in birds: (1) how brood parasites affect the breeding success (e.g., Nice 1937, Nolan 1978, Walkinshaw 1983) and population dynamics of their hosts (May and Robinson 1985); and (2) parasitic adaptations (Lack 1968, Payne 1977, Davies and Brooke 1988) host defenses (Rothstein 1975a, Davies and Brooke 1988), and the costs and benefits of evolving these defenses (Rothstein 1990).

Intense interest in the first topic has been stimulated by the negative effects of brood parasites on rare or declining species (e.g., Walkinshaw 1983, Wiley 1988, Trail and Baptista 1993). There is therefore a need for detailed demographic studies of host/brood parasite interactions to bet-

ter understand them, and to help make management decisions about interactions between brood parasites and threatened populations of hosts. To date, only three of 29 recent long-term accounts of the lifetime reproductive success of birds (in volumes edited by Clutton-Brock 1988, and Newton 1989) discuss brood parasitism (Payne 1989, Orians and Beletsky 1989, Rowley and Russell 1989), and just one of these studies provides a detailed account of the effect of a brood parasite on host reproduction (Rowley and Russell 1989).

Even less is known about the population biology of the brood parasites themselves. There have been no long-term population studies of brood parasitic species because they are: often migratory; rare relative to their host populations or communities of hosts; difficult to band as nestlings due to their dispersed nesting habits; and highly mobile during the breeding period (Friedmann 1963, Rothstein et al. 1984). The popu-

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lation biology of brood parasites is easiest to study when only a few individual brood parasites interact with a single well-known host population. We encountered this situation in the Mandarte Island population of Song Sparrows (*Melospiza melodia*), where sparrows were parasitized by Brown-headed Cowbirds (*Molothrus ater*). This sparrow population has fluctuated strikingly in size from four to 72 breeding females (Arcese et al. 1992). This permitted us to examine cowbird activities under a range of host numbers from extreme abundance to great scarcity (the case met with endangered hosts), and in the near absence of alternative hosts.

In this paper, we first describe brood parasitism by cowbirds on Song Sparrows. Brown-headed Cowbirds are generalists that lay non-mimetic eggs in nests of a wide range of host species (Friedmann 1963, Friedmann et al. 1977). The Song Sparrow is one of the cowbird's most common hosts throughout their large sympatric range (Nice 1937, McGeen 1972, Friedmann 1963). We then focus on the cost of parasitism to host individuals, consider the cause of multiple parasitism of single nests by cowbirds, and demonstrate selective parasitism of older host females. Finally, we discuss the population biology of the parasite-host interaction over 16 years.

## STUDY AREA AND METHODS

Mandarte Island is a 6-ha rocky islet covered by open grassy meadows and rocky knolls intermixed with bands of 1.5–3 m tall shrubs (mostly *Symphoricarpos alba* and *Rosa nutkana*). The island is 1.3 km from the nearest land and about 10 km from the large land mass of Vancouver Island. The Song Sparrow is the most abundant host species present on the island (mean breeding density = 7.8 females/ha), and adults are resident and territorial year-round. The open terrain on Mandarte Island (low shrubs with many emergent perches) greatly facilitates observations of both sparrows and cowbirds. A population of 1–8 pairs of Fox Sparrows (*Passerella iliaca*) also inhabited the island each year, and 1–5 female Red-winged Blackbirds (*Agelaius phoeniceus*) bred in pairs, or trios of two females and a male, in 1981, 1982, 1985–1987 and 1991. Both these latter species are potential hosts for cowbirds, but we did not study their breeding biology in detail, nor did we ever find cowbird eggs or nestlings in 25–30 of their nests that we monitored.

We and our assistants lived on the island from

early April to late July each year from 1975–1991, except for 1980 and 1981. Four census visits were made to the island in the 1980 breeding season, and territorial Song Sparrows were counted. In 1981, the island was visited at least weekly, and breeding monitored normally. However, less frequent nest checks than usual were made in 1981.

All breeding adult Song Sparrows were marked with color-bands each year, and some adult cowbirds were captured in Potter traps or mist nets and banded with metal or celluloid color bands. The celluloid bands were provided by A. C. Hughes Ltd., (1 High St., Hampton Hill, Middlesex, TW12 1NA, U.K.). These bands only stayed on the cowbirds for about one year before they fell off, or the birds removed them. In seven years, however, some individual female cowbirds could be distinguished by distinctive plumage patterns, or by metal or color bands. Sparrow territories were mapped intensively each April, and the presence of breeders on territories was checked systematically every few days during the breeding season. Cowbird visits to the island were noted while we were observing sparrows, or looking for their nests from knolls or a 3 m ladder. Male and female cowbirds frequently perched together on dead emergent snags, where they could be seen from up to 200 m. Males often vocalized from these perches, and both sexes called in flight. These behaviors made their visits to the island fairly easy to detect, even when we were not conducting systematic observations of sparrows. We could not, however, always see cowbirds at close enough range to check for distinctive plumage patterns or leg bands. We recorded these visits routinely in daily log books, although with some variation in detail from year to year. Four adult female cowbirds were removed from the island by trapping or shooting soon after they arrived in 1977, to test the effect of cowbird exclusion on host reproductive success (Smith 1981).

We monitored the fates of 1,568 Song Sparrow nests. Most were found during incubation and then checked every 1–4 days. Cowbirds and Song Sparrows lay similar eggs (Rothstein 1975a), but we recognized cowbird eggs by their generally paler ground color, more compact shape, and more even spotting pattern. From 1986 to 1991, almost all eggs were removed briefly from nests for close inspection and for weighing on an electronic scale. Eggs in parasitized and unparasi-

tized clutches were handled equally. We color-banded nearly all nestling sparrows and most cowbirds (some were given metal bands only) 4–8 days after hatching. We did not band cowbird nestlings in 1976. After 1982, we checked nests carefully for the presence of surviving cowbird or sparrow young just before the expected time of fledging (10 days), and daily thereafter until all young left the nest. Similar, but less systematic checks were done before 1982. Our data analyses here focus closely on the sub-samples of sparrow nests active during periods when cowbirds were actively laying in Song Sparrow nests in the years 1976, 1978–1979, 1981, and 1983–1990.

The survival of young banded as nestlings was monitored by revisiting the territory, and locating begging fledglings. Cowbirds left the island soon after they became independent of their foster parents, but most young Song Sparrows remained on the island, where we re-sighted and trapped them in mist nests in late summer each year, save for 1979. Further details of methods are given in Smith (1981, 1988), in Arcese (1989), and in Arcese et al. (1992). Unlimited supplemental food (primarily moistened puppy chow) was supplied to about one third of Song Sparrow territories, and thus to cowbirds, in two years. In 1985, we provided a single feeder on each of 15 territories from 28 February to 24 July (Arcese and Smith 1988). In 1988, three feeders were provided on each of 15 territories from April 10 to 20 July (W. M. Hochachka, unpubl. data). Each feeding period spanned the entire cowbird laying season for that year, and adult cowbirds used the feeders regularly in both years.

We analyzed our data with standard parametric statistical tests where they were approximately normally distributed. Non-parametric tests were used where sample sizes were small, or data were multimodal or categorical. Alpha was set at 0.05, and all statistical tests were 2-tailed. As 16 years of data were available for analysis, we sometimes pooled years for analysis, or combined subsets of years that were judged as being similar with respect to the mean reproductive output of individual female sparrows.

## RESULTS

### NUMBERS OF COWBIRDS AND SONG SPARROWS

Female cowbirds visited the island in every study year except 1982, when a male was seen only once. Cowbirds often spent several hours on the

island, particularly in the mornings, but also were seen to move on and off the island regularly. Small flocks of 2–30 cowbirds also visited the island at dusk to join a night roost of starlings (*Sturnus vulgaris*), particularly during June and July, when the roost contained several thousand birds.

The maximum daily number of females seen on the island during the breeding period was three in 1976 and 1979 (Table 1). Observations of roosting birds near dusk were excluded from this table, and from analyses based on it. No cowbirds were observed in 1982, despite intensive surveillance, or in 1980, when little time was spent on the island. Four females were removed sequentially in 1977. At least four different females (three of the banded) visited the island in 1986, and four females were shot in 1977. Although females continued to visit the island during 1977 (22 bird visits overall), no cowbird eggs were laid that year. In 1991, cowbirds visited the island occasionally, but no eggs were laid (Table 1).

Although at least two cowbird females were sighted on a single day in 11 of the 16 years, only a single female was sighted on 87% of 308 days with cowbird sightings. Multiple sightings in a single day were about three times as common in the first half of the cowbird laying season for both females (17.9% of 117 sightings vs. 5.9% of 102 sightings,  $G = 5.7$ ,  $P < 0.02$ ), and for males (18.9% of 95 sightings vs. 6.3% of 64 sightings,  $G = 7.8$ ,  $P = 0.006$ ). All years with a clearly-defined cowbird laying season were included in this analysis (i.e., 1990, with only a single case of parasitism, was excluded).

Individual female cowbirds visited the island repeatedly in all nine years when distinctively-marked birds could be recognized. One female banded as an adult in 1975 was re-trapped on the island in 1977, and metal-banded birds seen in successive years (1985–1986 and 1986–1987) may also have been the same individuals. Of 127 nestling cowbirds banded on the island, at least three females banded as nestlings (4.7%, assuming an equal sex ratio) were seen on the island as adults. Two of these were known to be yearlings by the color bands they bore when first sighted. These data suggest fairly strong natal and breeding philopatry among female cowbirds. At most, 25 breeding females used the island from 1976 to 1991 (sum of maximum daily totals per year, minus known banded birds returning). The

TABLE 1. Basic demographic variables for Brown-headed Cowbirds and Song Sparrows on Mandarte Island.

Year	Number of female sparrows	Number of female cowbird days (x per day)	Maximum daily number of female cowbirds	Percent of nests parasitized	Double parasitism (x/y cases)
1975	34	13 (1.13)	2	34	1/19
1976	30	36 (1.36)	3	46	6/35
1977*	45	22 (1.10)	(2)	0	—
1978	48	31 (1.03)	2	21	0/23
1979	65	41 (1.27)	3	22	1/28
1981	18	3 (1.00)	1	23	2/10
1982	26	0	—	0	—
1983	55	17 (1.24)	2	15	0/19
1984	53	4 (1.00)	1	18	2/24
1985	72	36 (1.13)	2	29	0/51
1986	61	30 (1.07)	2	20	1/31
1987	59	33 (1.03)	2	35	0/42
1988	55	36 (1.06)	2	30	0/39
1989	4	4 (1.25)	2	45	1/5
1990	9	3 (1.00)	1	3	1/1
1991	28	7 (1.17)	1	0	—

\* Four female cowbirds were removed soon after they appeared in 1977. Sightings of non-resident females, however, continued to occur this year.

true number was probably lower because some unbanded and metal-banded females may have returned in more than one year.

Although no quantitative data were gathered, male and female cowbirds were often seen together in pairs, sometimes in trios of two males and a female, or occasionally in larger groups. Chases between females were noted regularly in 1983, and rarely at other times. In 1983 a female cowbird struck a stuffed cowbird model placed in a sparrow territory to test sparrow responses to cowbird models (Smith et al. 1984).

The number of Song Sparrows was very unstable over the study because of two sharp population declines in the non-breeding seasons of 1979–1980 and 1988–1989 (Table 1; Rogers et al. 1991, Arcese et al. 1992). The duration of the laying period of cowbirds (Fig. 1a), and the number of eggs laid by cowbirds in nests of Song Sparrows (Fig. 1b), both increased with increasing host density. In contrast, neither the total proportion of sparrow nests that were parasitized, nor the mean or maximum number of cowbirds sighted on the island per day were significantly positively related to host density ( $r$ 's = 0.15, 0.17, and 0.42, respectively;  $n$  = 15 in all cases, and all  $P$ -values > 0.10). Thus, though female cowbirds showed a functional response

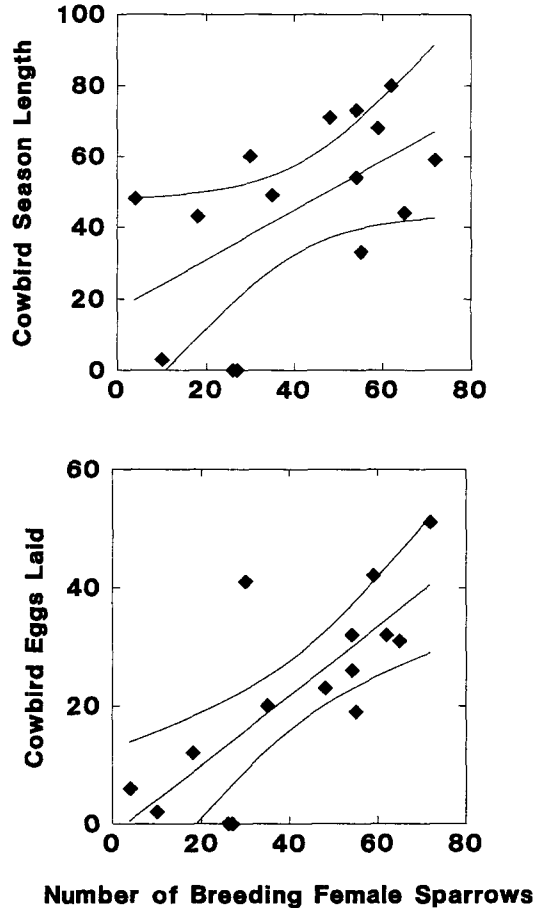


FIGURE 1. The length of the cowbird nesting season [date of first–last egg laid] (top), and the total number of cowbird eggs laid (bottom), each in relation to the number of breeding female Song Sparrows in 15 study years. The point for 1977 is excluded because of the experimental removal of cowbirds that year. Straight lines indicate the fit to the data by linear regression, curved lines indicate the 95% confidence bands on the slope (Season:  $b(SE) = 0.70 (0.28)$ ,  $F_{1,13} = 6.02, r^2 = 0.32, P = 0.029$ ; Eggs:  $b(SE) = 0.59 (0.13)$ ,  $F_{1,13} = 19.57, r^2 = 0.60, P < 0.001$ ).

to host density, there was little parallel numerical response (Holling 1965).

REPRODUCTION BY COWBIRDS

Cowbirds parasitized Song Sparrows in 13 of 15 years when cowbirds were not removed from the island (Tables 1 and 2). The pattern of laying by cowbirds was clearest at times when only one female was present for part or all of the breeding season (as judged by the presence of a lone band-

TABLE 2. Percent hatching success (N) of eggs laid by Song Sparrows and Brown-headed Cowbirds each year.

Year	Sparrows	Cowbirds
1975	69.5 (131)	83.3 (18)
1976	66.4 (229)	61.0 (41)
1977	82.3 (334)	—
1978	80.4 (378)	73.9 (23)
1979	65.3 (401)	67.7 (31)
1981	74.3 (144)	75.0 (12)
1982	72.1 (197)	—
1983	67.7 (427)	31.6 (19)
1984	64.4 (390)	57.7 (26)
1985	46.1 (479)	64.7 (51)
1986	45.9 (431)	59.4 (32)
1987	53.7 (395)	73.8 (42)
1988	52.7 (391)	53.1 (32)
1989	67.5 (40)	50.0 (6)
1990	71.7 (145)	100.0 (2)
1991	67.0 (221)	—

ed female, or if the mean number of females seen per day = 1.0). We estimated laying schedules of females at these times by back-dating from the age of nestlings when eggs hatched. When parasitized nests were found after the clutch was completed and subsequently failed before hatching, we assumed that the cowbird egg was laid seven days before the nest was first found. Because some additional cowbird eggs must have been laid in nests that failed before we found them (though probably <5% of all cases), we could only estimate the minimum number of eggs laid per female per period.

Estimated laying dates of female cowbirds in years with few multiple sightings of female cowbirds were not strongly clustered. Figure 2 displays the data for the four years when multiple sightings of females were rare, and there was no double parasitism (Table 1). Females appeared to lay almost continuously in 1978, 1987 and 1988. Only in 1981 was there any hint of eggs appearing in clutches.

We estimated rates of egg production by individual cowbirds as follows. We examined the records of cowbird visits to the island, and selected all periods within the cowbird laying season that met the following criteria: (1) only one female was sighted per day within a period of five or more days, (2) no sighting of two females occurred on any day within three days of either end of the above period, and (3) no period contained a gap in sightings of female cowbirds of

more than six days. There were ten such periods during the study, two each in 1978, 1985, 1986 and 1988, and one each in 1983 and 1987. We assume that only one female visited the island to lay during these periods, and that the number of eggs appearing per day is thus a reliable estimate of the minimum egg-laying rate per female. The mean rate of laying in these ten periods was  $0.50 \pm 0.07$  (SE) eggs per day, with high values of 17 eggs in 21 days from May 14 to June 3 1985, and 6 eggs in 7 days from May 1 to 7, 1986. During four of the ten periods, cowbirds had access to supplemental food on the island, but the mean laying rate at these times ( $0.56 \pm 0.09$ ) was similar to the laying rate during periods without supplemental food ( $0.47 \pm 0.10$ ).

#### BREEDING PHENOLOGY OF HOST AND PARASITE

The onset of breeding by Song Sparrows varied greatly, with the earliest first egg on February 24 and the latest on 19 April (Fig. 3). Laying by sparrows began earliest when host density was low and spring temperature was high (Arcese et al. 1992). The onset of laying by cowbirds was quite variable (Fig. 3), and averaged much later than that of sparrows. As a result of these patterns, 50 percent of all female sparrows ( $SE = 12\%$ ,  $n = 12$  years) successfully hatched their first clutches before cowbirds began to lay. Some females even fledged their first brood, and hatched young from a second clutch before cowbirds began to lay.

In two years, cowbirds laid their first eggs before being seen on the island, but in 11 years there was an average gap of 9 days (range = 1–27) before laying began. The onset of laying by cowbirds was uncorrelated with the median date of the first Song Sparrow egg each year ( $r = 0.04$ ,  $n = 13$  years when parasitism occurred,  $P > 0.50$ ; Fig. 3). Once parasitism occurred, cowbirds continued to lay until the end of the sparrow laying season in most years (Fig. 3).

#### MULTIPLE PARASITISM BY FEMALE COWBIRDS

Multiple parasitism (>1 cowbird egg/nest) was rare in our study (15 of 309 cases, 4.9%; Fig. 4) and was unrelated to the number of female cowbirds visiting the island (Table 1). More than two cowbird eggs were never found in one nest. To test if cowbirds laid randomly in all available nests, we pooled all data from the 12 years with

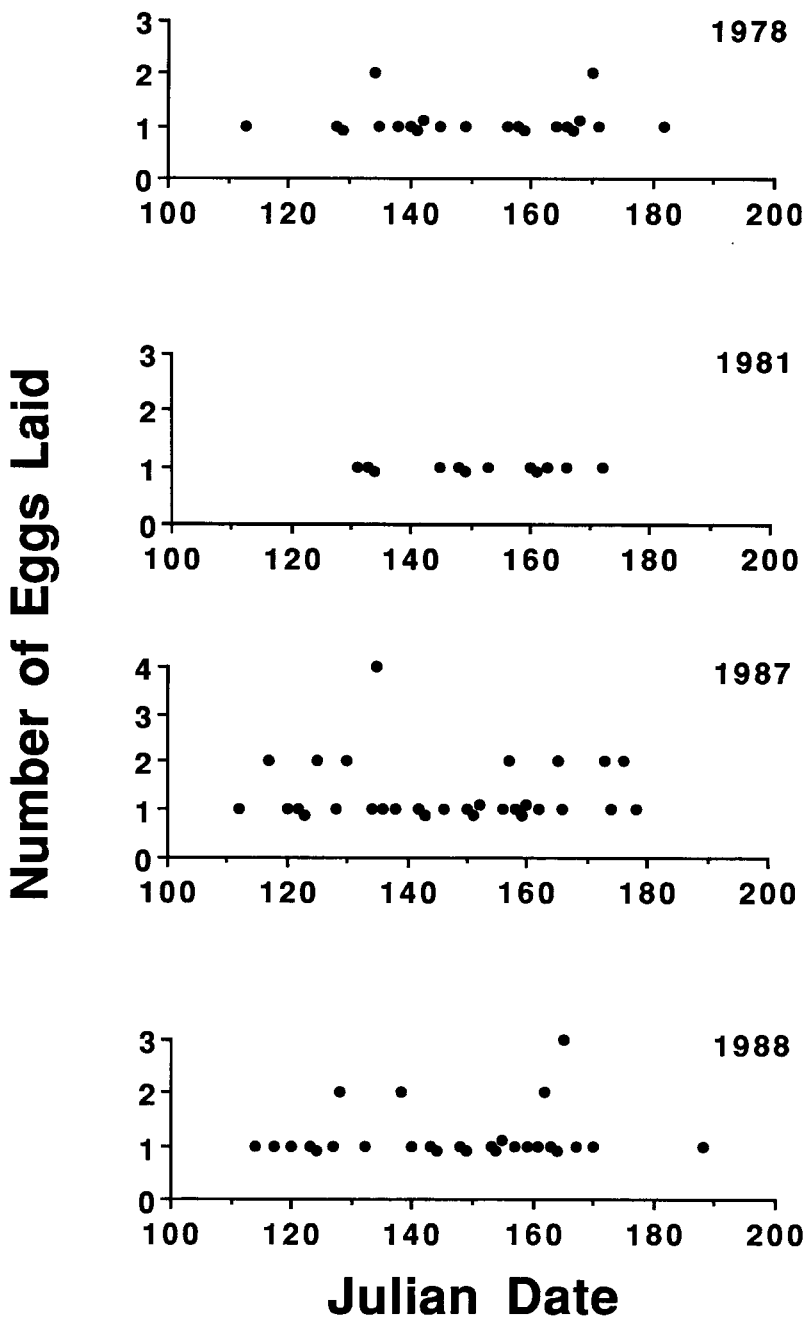


FIGURE 2. Phenology of egg-laying by cowbirds in four years in which a single cowbird female probably laid most cowbird eggs (Julian dates: March 1 = 60; April 1 = 91; May 1 = 121; June 1 = 152; July 1 = 182).

extended cowbird laying seasons. The distribution of eggs per nest during the cowbird laying period differed significantly from a truncated Poisson distribution (Orlans et al. 1989), with

there being more nests with a single egg and fewer nests with more than two eggs than expected ( $G = 24.13$ ,  $df = 2$ ,  $P < 0.001$ ). That is, cowbirds avoided laying in previously parasitized nests.

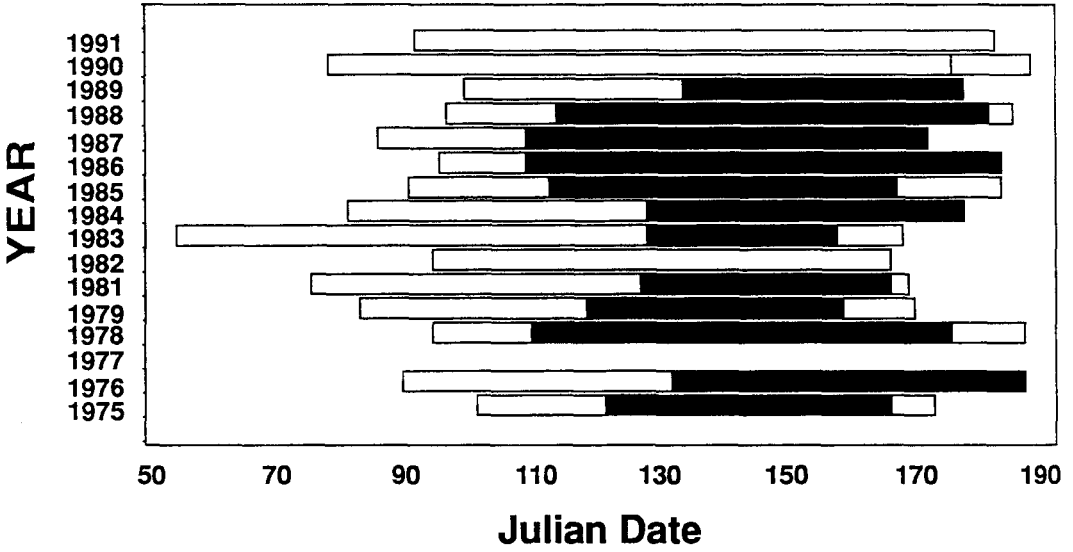


FIGURE 3. Breeding phenology of Song Sparrows and Brown-headed Cowbirds on Mandarte Island by year. Open bars represent breeding periods of sparrows and filled bars those of cowbirds. The narrow vertical line in 1990 indicates a single case of parasitism (dates same as for Fig. 2).

Almost half the cases of double parasitism ( $n = 7$ ) occurred in 1976 and 1989. These were two of the three years with the highest mean daily sighting rate of female cowbirds (Table 1), and thus were also years when independent laying in the same nest by two females was likely.

The proportion of cowbird eggs that survived to banding age (ca. 6 days after hatching) in doubly-parasitized nests (13 of 30 eggs, 43%) did not differ significantly from that in singly parasitized nests (156 of 294 eggs, 53%;  $G = 0.46$ ,  $df = 1$ ,  $P = 0.50$ ).

Nine of 15 (60%) doubly-parasitized nests occurred during the last 14 days of the annual cowbird laying period (Fig. 4), when the availability of host nests was declining sharply (Fig. 4). This suggests that a shortage of host nests was a cause of multiple parasitism. We tested this idea by comparing the mean number of unparasitized sparrow nests available in weeks with only single and with double parasitism. As predicted, many fewer unparasitized nests were available in weeks with double parasitism ( $\bar{x} = 1.64 \pm 0.98$  [SE],  $n = 11$ ) than in weeks with only single parasitism ( $\bar{x} = 5.18 \pm 0.45$ ,  $n = 91$ ), and this difference was significant ( $t = 2.633$ ,  $df = 100$ ,  $P = 0.005$ , one-tailed t-test).

Supplemental feeding did not increase the frequency of doubly-parasitized nests. There were

15 cases of double parasitism in years without supplemental food and no cases in 1985 or 1988, when supplemental food was provided for the entire cowbird laying period. Supplemental feeding advanced the onset of laying by sparrows by 18 days on average in 1985, when food was available from mid-March onward (Arcese and Smith 1988). However, supplemental feeding had little effect on the onset of laying by cowbirds in either 1985 or 1988 (Fig. 3).

PARASITISM AND HOST NESTING SUCCESS

Smith (1981) showed that calculations of the impact of nest parasitism on individual Song Sparrows were potentially confounded by the fact that cowbirds parasitized adults more often than yearlings, and also that adults produced more offspring than yearlings on average (see also Smith et al. 1984, Nol and Smith 1987). We therefore divided our data by host age when considering clutch size and the survival of eggs to hatching, banding, fledging and independence.

The mean yearly clutch size of parasitized nests was smaller than in unparasitized nests in 10 of 11 years for adult Song Sparrows, and in all 10 years for which comparisons could be made for yearlings (Fig. 5). The mean difference in egg number between parasitized and unparasitized

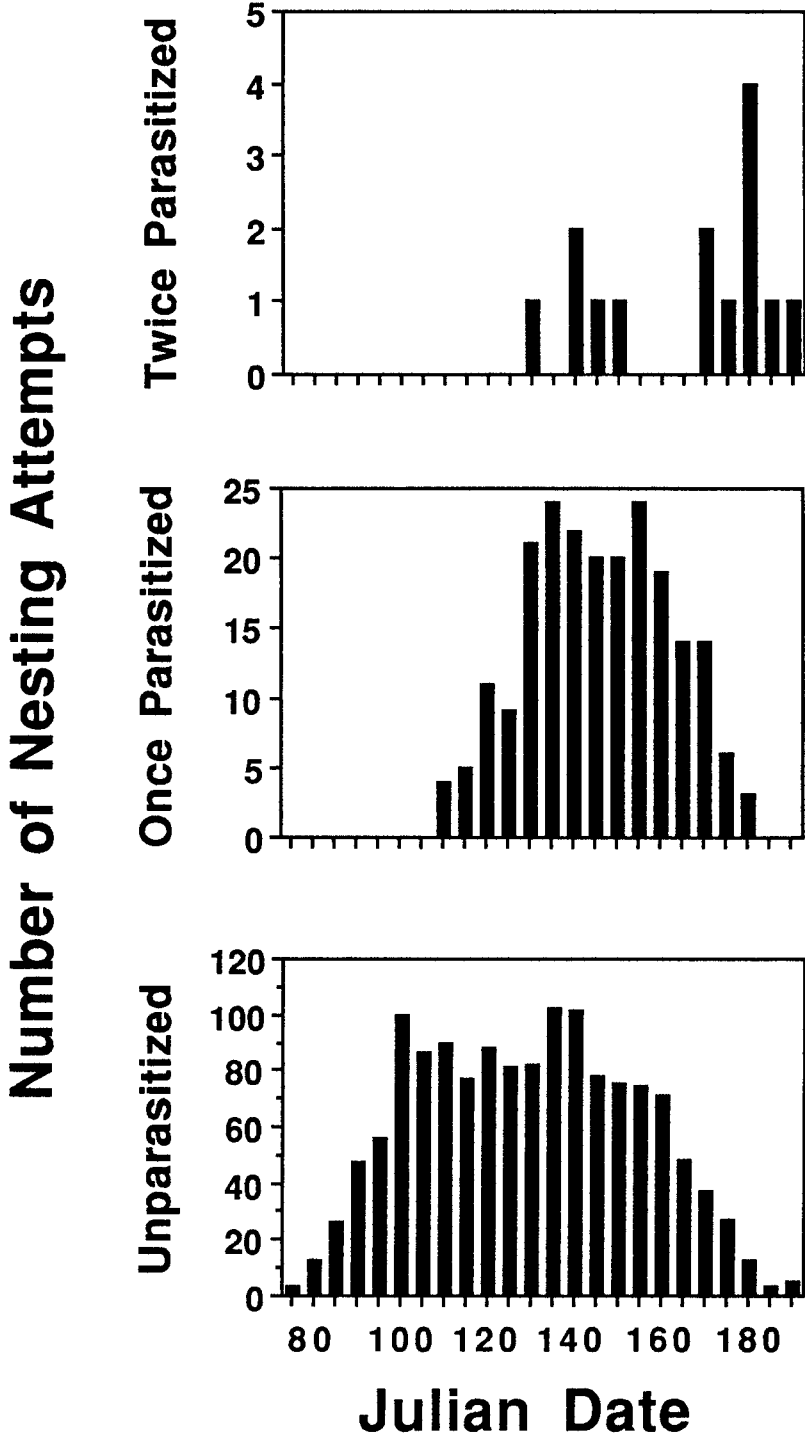


FIGURE 4. The frequency distributions of clutch initiation dates for: all unparasitized Song Sparrow nests (1975–1990); for sparrow nests that received one cowbird egg; and for sparrow nests that received two cowbird eggs (dates same as for Fig. 2).



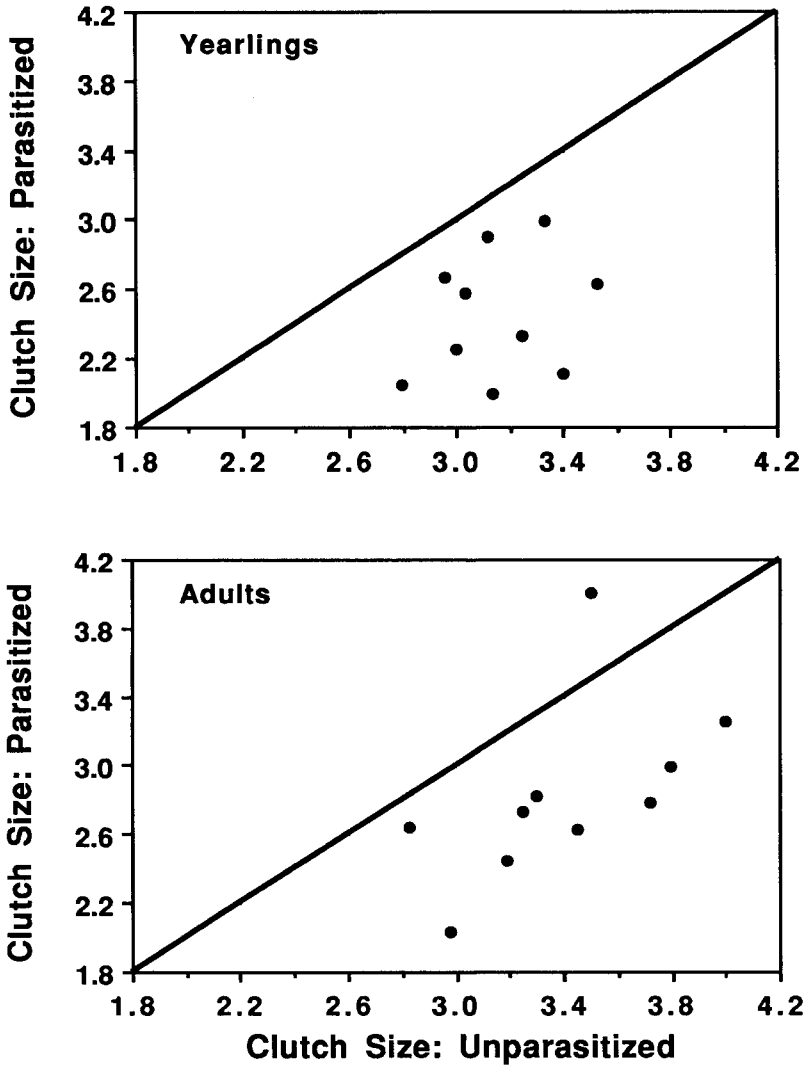


FIGURE 5. Clutch sizes in parasitized and unparasitized nests for adult and yearling Song Sparrows. The sloping line is  $x = y$ ; i.e., the expectation if no eggs were removed by cowbirds from parasitized clutches. Each point indicates the mean clutch size for one year.

nests was 0.65 for adults and 0.70 for yearlings (0.67 overall), and it did not differ significantly between age-groups ( $t = 0.53$ ,  $df = 20$ ,  $P > 0.50$ ). This difference suggests that cowbirds removed a host egg from about two thirds of parasitized nests, regardless of host age.

The overall hatching success of Song Sparrow and cowbird eggs was similar in most years, save for 1983, when only about half as many cowbird eggs hatched (Table 2). Most cases of hatching failure were due to predation at the egg stage, but the low hatching success of cowbird eggs in 1983

was probably due to infertility, as eight of 14 cowbird eggs failed to hatch in nests that produced sparrow hatchlings.

A second cause of hatching failure was egg damage. In 1985–1991, when eggs were weighed, we noted small puncture marks or cracks in 32 of 1560 (2.0%) of Song Sparrow eggs in nests started during cowbird laying periods. In contrast, only two of 435 sparrow eggs were damaged outside cowbird laying periods in 1985–1991 ( $G = 6.33$ ,  $df = 1$ ,  $P < 0.02$ ), and none were punctured. Twenty-one of the 32 damaged eggs were

in parasitized nests, and only one egg was damaged per nest in 26 of the 28 nests with damaged eggs. Egg damage by cowbirds was probably slightly more frequent than this estimate suggests. Puncture marks were often so small as to be easily overlooked, even when an egg was handled, and 11 additional broken sparrow eggs were also noted during cowbird laying periods.

To explore the relationships between age of the host female, brood parasitism and reproductive success, we divided our data into three sets of similar years: (1) seven "good" years with brood parasitism and above average survival of host young (1976, 1978, 1981, 1983–1984, 1989, 1990); five "bad" years with parasitism and below average survival (1979, 1985–1988); and three years without parasitism (1977, 1982 and 1991). For each set of years we further divided reproductive attempts into four stages: (1) survival of eggs from laying to hatching; (2) survival of hatchlings to banding age (about 6 days old); (3) survival of banded nestlings to fledging (about 11 days old); and (4) survival of fledglings to independence (about 30 days old). We only considered the subsets of nests begun at or after the start of laying by cowbirds in years with parasitism. And in years without parasitism, we controlled for seasonal effects by considering only the subset of nests initiated after the median date of laying by cowbirds over all years (May 1). We did not have reliable measures of the survival of cowbirds in stage 4.

Although an analysis of the survivorship curves of young in parasitized and unparasitized nests might seem appropriate here, we used the above approach because the age structure of breeding female sparrows was closely linked to population size (Smith and Arcese, unpubl. data) and also to the probability of parasitism (see below). Population size fluctuates widely on Mandarte Island, and it affects several aspects of reproductive performance (Arcese et al. 1992). As a result, we were unable to satisfactorily control for non-independence of female age, parasitism, population size, and nestling survival without partitioning the data as described above.

Survival of sparrow eggs and young varied strongly with stage, to a lesser degree with parasitism, and only slightly with female age. Survival was generally high (75% or more) in stages 2 and 3, but lower (55–80%) in the longer stages 1 and 4. Total nest failure (mostly predation) was the main cause of losses at stage 1. The identity

of the main nest predators on Mandarte is unconfirmed, but deer mice (*Peromyscus maniculatus*) are the main nest predators of Song Sparrows on the nearby mainland (J.N.M. Smith and G. Jongejan, unpubl. data), and this species is abundant on Mandarte. We therefore suspect deer mice were responsible for most losses of eggs and small nestlings. Northwestern Crows, *Corvus caurinus*, preyed regularly on fledgling sparrows, and probably also took broods of older nestlings.

In good years (Fig. 6), eggs in parasitized nests survived about 15 to 20% better to hatching than in unparasitized nests of all sparrow age classes. No such difference existed in bad years (Fig. 7). Subsequent survival of sparrow nestlings and fledglings did not vary strongly with either age or parasitism in either good (Fig. 6) or bad years (Fig. 7). Survival of sparrow eggs, but not nestlings, was very high in years without parasitism (Fig. 8).

Survival of cowbird eggs and young was high overall up to the end of stage 3, and was similar in hosts of differing age at all stages (Fig. 9). Interestingly, cowbirds survived better in stages 2 and 3 in bad years than in good years. Although we did not monitor survival of fledgling cowbirds to independence systematically, it may have been poor. Several fledgling cowbirds were preyed on by crows, and others apparently disappeared before 25 days of age, the minimum age at which fledgling sparrows gained independence.

An estimate of the overall cost of parasitism to sparrows was calculated for 1981–1988, the set of six years with the best estimates of host survival in relation to parasitism to the end of stage 3. We only began to check fledging success systematically in 1982, and there was almost no parasitism after the sparrow population decline in early 1989. Two of these were good and four were bad years for sparrow reproduction. We consider the two years with added food (1985 and 1988, both bad years) separately, because feeding reduced the frequency of parasitism in pairs with access to additional food in 1985 (Arcese and Smith 1988). The results are shown in Table 3.

Parasitized nests fledged an average (mean of annual mean differences) of  $0.79 + 0.17$  (SE,  $n = 4$ ) young fewer than unparasitized nests in years without added food. This difference, however, was much smaller in two years with added food ( $0.27 + 0.06$ ). Only about 50% of sparrow eggs laid on Mandarte result in fledglings (unpubl.

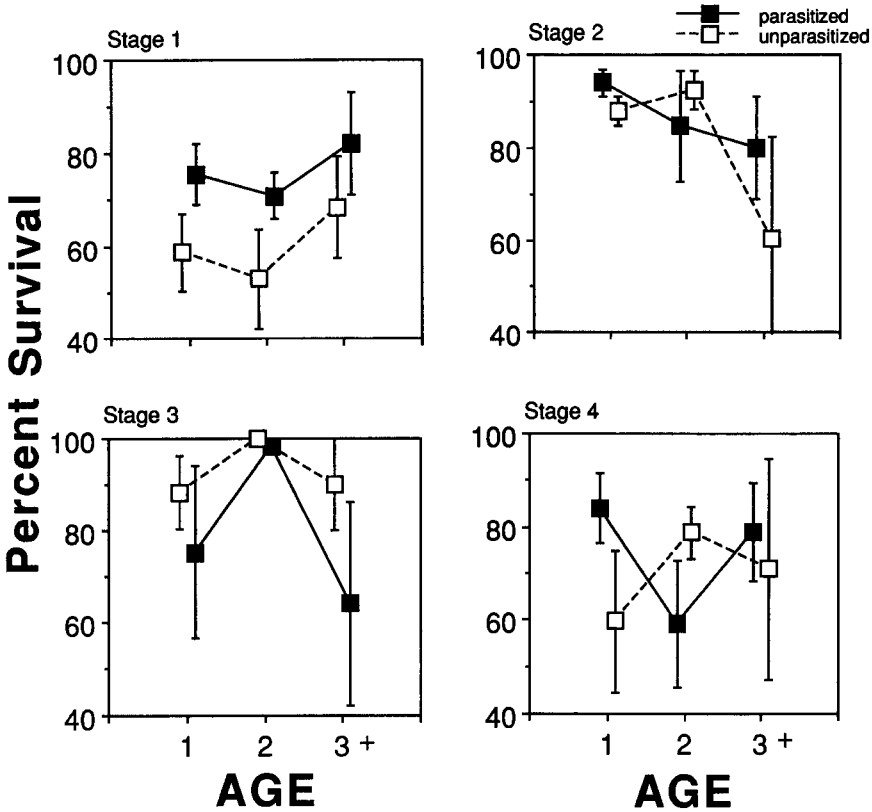


FIGURE 6. Survival of Song Sparrow eggs and young in good years (see text for definition) for sparrow reproduction in relation to parental age, cowbird parasitism, and stage of the reproductive cycle. Stage 1 = before hatching; stage 2 = nestlings 0–6 days in age; stage 3 = nestlings 6 days of age to fledging; stage 4 = fledging to independence. Bars display one standard error. No comparison of survival by female age was statistically significant for any stage in parasitized or unparasitized nests ( $n = 7$  yrs, all  $P_s > 0.10$ ; one-way ANOVAs on data transformed by  $\log_{10}$ ).

data). Because of this mortality in the nest, the initial average difference in clutch size between parasitized and unparasitized clutches (0.67 eggs) should translate into a difference of about 0.33 fledglings. The calculated cost of 0.79 fledglings therefore implies an additional loss of about 0.46 fledglings per parasitized nest, beyond the losses caused by female cowbirds removing eggs.

Finally, we also examined the body mass of host young in parasitized nests compared to contemporaneous controls. Contrary to our earliest results (Smith 1981), but in agreement with a more recent comparison (Smith and Arcese 1988), Song Sparrow young were no lighter when raised with cowbirds as nest-mates than when raised alone (two-way ANOVA on masses of five- and six-day-old young corrected for age, data from

1983–1989;  $P = 0.80$  for the effects of both parasitism [ $F_{1,468} = 0.05$ ] and year [ $F_{6,463} = 0.52$ ]; interaction term,  $F_{6,463} = 1.42$ ,  $P = 0.20$ ).

AGE-SELECTIVE PARASITISM:  
ADAPTATION, MALADAPTION OR  
CHANCE?

In earlier studies (Smith 1981, Smith et al. 1984), we noted that cowbirds preferentially parasitized older female Song Sparrows over yearlings. In this section, we explore the extent of host selection by age, and we examine two hypotheses for why the phenomenon occurs among Song Sparrows on Mandarte Island.

First, since two-year-old and older Song Sparrows raise more offspring than yearlings do on average (Nol and Smith 1987), the selection of

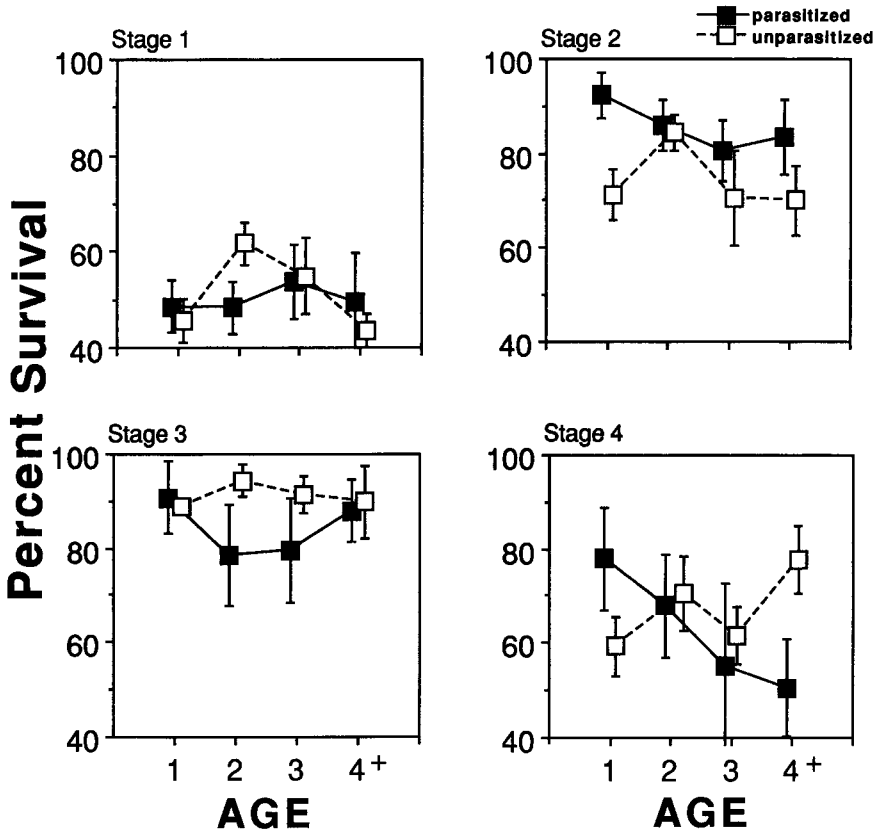


FIGURE 7. As Figure 6, but data from bad years for sparrow reproduction ( $n = 5$  yrs, all  $P_s > 0.10$ ; analyses same as for Figure 6).

older hosts might represent an evolved mechanism in cowbirds for obtaining hosts that are more likely to also raise parasites successfully (Smith et al. 1984). By the "best host" hypotheses, we assume that the ability of a parent to rear sparrow young is a reliable index of its ability to rear cowbird young; and we predict that the rate of parasitism and average female reproduc-

tive success will be positively correlated across age-classes of hosts.

The percent of nests parasitized annually increased almost exponentially with increasing host age (Fig. 10). However, two-year-old females produced the most sparrow young in the population on average (Nol and Smith 1987; Figs 6, 7). Three- and four-year-old sparrows suffered

TABLE 3. Numbers of Song Sparrows fledged from parasitized and unparasitized nests [ $\pm$  SE (N)] initiated during the cowbird laying period from 1983-1988.

Year	Type of year	Parasitized nests	Unparasitized nests
1983	Good	0.632 $\pm$ 0.191 (19)	1.767 $\pm$ 0.207 (30)
1984	Good	0.917 $\pm$ 0.208 (24)	1.919 $\pm$ 0.230 (37)
1985*	Bad	0.780 $\pm$ 0.149 (50)	0.989 $\pm$ 0.128 (93)
1986	Bad	0.581 $\pm$ 0.137 (31)	1.053 $\pm$ 0.129 (94)
1987	Bad	0.488 $\pm$ 0.131 (43)	1.039 $\pm$ 0.175 (51)
1988*	Bad	0.667 $\pm$ 0.172 (33)	0.967 $\pm$ 0.146 (60)

\* Years with experimental food addition.

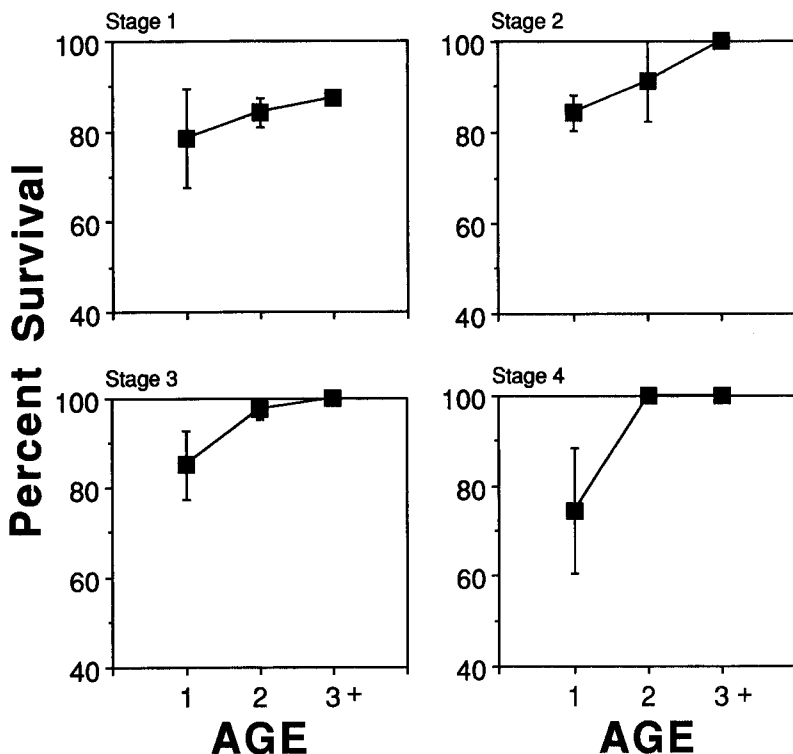


FIGURE 8. As Figure 6, but data from 3 years without parasitism by cowbirds. Too few data were available for statistical tests of significance.

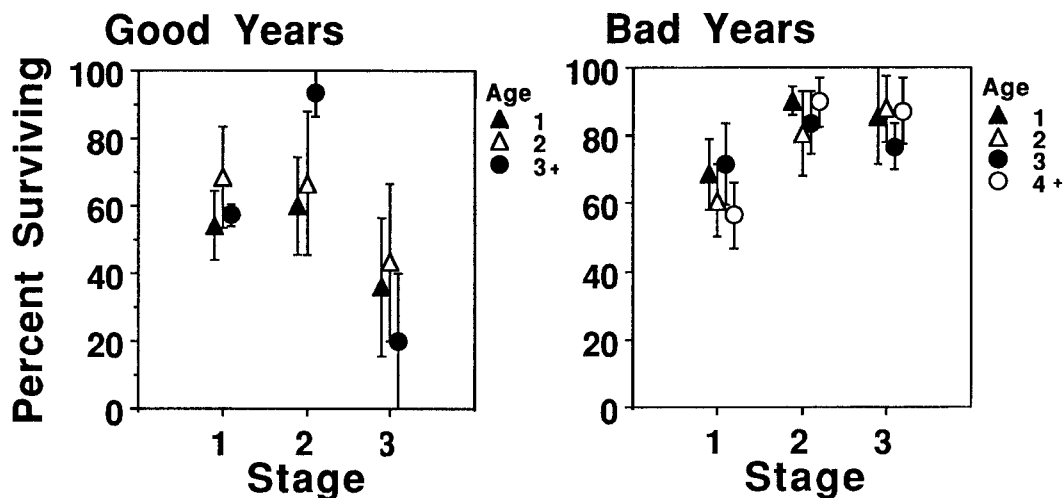


FIGURE 9. As Figure 6, but data for survival of cowbirds in host nests tended by females of different age. The survival of cowbirds was not monitored in stage 4. No comparisons of survival by host age were statistically significant for any stage in either good or bad years for Song Sparrow reproduction (all  $P_s > 0.40$ ; one-way ANOVAs on data transformed by  $\log_{10}$ ).

the most parasitism, but they were no better at rearing either sparrows (Figs. 6, 7) or cowbirds (Fig. 9) than yearling or two-year-old birds. Thus, the main prediction of the best-host hypothesis was not supported.

A second explanation for why parasitism may vary by host age arises if we assume that female cowbirds select hosts at random, but that female hosts of different age produce nests in a non-random manner (the "random selection" hypothesis). For example, we have shown elsewhere that older Song Sparrows initiate more nests each year than do yearlings (Smith 1981, Nol and Smith 1987). Thus, if one assumes that the probability of parasitism is equal for each nest initiated during the cowbird laying period, then females that nest more often will have a higher cumulative probability of being parasitized.

In support of the idea that parasitism is dictated in part by host availability, we found that adult and yearling females which were parasitized at least once had indeed made more nesting attempts during the cowbird laying period than those which had not been parasitized. The mean number of nesting attempts during the cowbird laying period by two-year-old or older adult females ranged from 1.22–2.60 nests for those parasitized, and from 1.11–2.07 for those not parasitized. Overall, the number of nests begun by older parasitized females exceeded that by older unparasitized females by an average of 0.53 nests (compared on a yearly basis to control for variation in nesting frequency;  $t = 3.57$ ,  $df = 9$ ,  $P = 0.007$ , paired  $t$ -test). For yearlings, the corresponding values were 1.00–2.25 for unparasitized females, and 1.25–2.30 nests per period for parasitized females. In this case, the number of nesting attempts by parasitized females exceeded that by unparasitized females by 0.38 nests on average (compared as above;  $t = 4.02$ ,  $df = 8$ ,  $P = 0.004$ , paired  $t$ -test).

These results show that females which initiated nests more frequently were also more likely to be parasitized at least once. However, among females that were parasitized, yearling and older females did not differ markedly in the number of nesting attempts made during the cowbird laying period (compared on a yearly basis as above; mean difference = 0.05,  $t = 0.38$ ,  $df = 10$ ,  $P = 0.71$ , paired  $t$ -test). We also found no difference in the frequency of nest initiation among yearling and older females that were not parasitized (com-

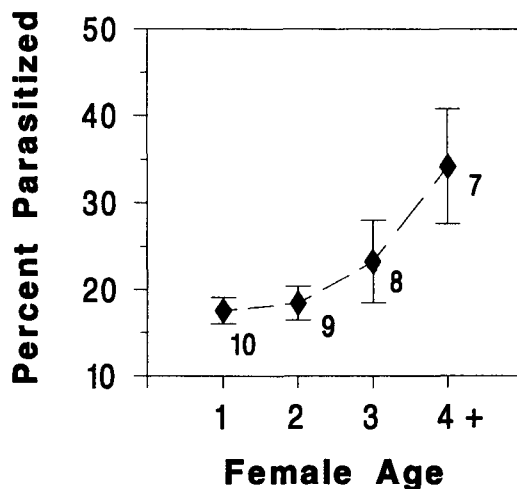


FIGURE 10. Mean yearly percent of sparrow nests parasitized in relation to host female age. The vertical bars indicate  $\pm 1$  SE, and sample sizes beside each point indicate the number of years that age class was represented. Data were analyzed by weighted (by the square root of the number of nests,  $F_{3,30} = 4.48$ ,  $P = 0.01$ ) and unweighted ( $F_{3,30} = 3.74$ ,  $P = 0.022$ ) ANOVAs after normalizing the data by  $\log_{10}$  transformation.

pared as above; mean difference =  $-0.09$ ,  $t = 0.88$ ,  $df = 8$ ,  $P = 0.41$ , paired  $t$ -test). Moreover, it is clear from Figure 10, which presents the rate of parasitism on a per nest basis, that parasitism occurred non-randomly with respect to host age. Overall, therefore, our results show that the number of nesting attempts made during the period of cowbird activity may explain why some individuals within each age-class are parasitized while others are not (i.e., some females produce more nests available for parasitism). However, this difference in the frequency of nest initiation does not explain differences in the rate of parasitism of females of different age.

#### IMPACT OF PARASITISM ON HOST NUMBERS

The demographic effect of a brood parasite on a multi-brooded host is the product of the probability of being parasitized, the number of breeding attempts per season, and the decrement in host production per parasitized attempt (May and Robinson 1985). In our study, 25% of 1,313 nests were parasitized in all 13 years with parasitism, and the average Song Sparrow made 2.42 breeding attempts per year. We estimated the cost of parasitism to be about 0.79 host young lost per parasitized nest. Since about 65% of

TABLE 4. A comparison of the reproductive performance of Song Sparrows in relation to parasitism by Brown-headed Cowbirds on Mandarte Island (this study) and in Columbus, Ohio (Nice 1937).

Measure of performance	Ohio	Mandarte
Median onset of laying: sparrows	17 April	2 April
Median onset of laying: cowbirds	25 April	1 May
Mean egg weight: sparrows, g (N)	2.28 (44)	3.12 (387)
Mean egg weight: cowbirds, g (N)	3.17 (24)	2.55 (102)
Mean size, unparasitized clutches	4.12	3.45
Percent egg damage	2.0	2.0
Percent of nests parasitized	43.9	24.9
Percent of multiply parasitized nests	29.5	4.6
Number of eggs removed per parasitized nest	0.36	0.67
Sparrow young fledged per unparasitized nest	3.41	1.34*
Sparrow young fledged per parasitized nest	2.03	0.64*
Percent parasitized nests failing	0.65	0.43

\* Data from all nests during cowbird laying periods, 1983-1989.

fledging young reached independence, the average yearly cost per parasitized individual was thus  $0.25 \times 2.42 \times 0.79 \times 0.65 = 0.31$  independent young. Females in the population reared an average of 3.0 independent young per year. From the perspective of the population, about fifteen young sparrows ( $0.31 \times 46.8$ , the mean number of breeding females) are lost from the population on average as a result of parasitism by cowbirds, a minor impact in the average year. In addition, most parasitism takes place in the latter part of the year, when young sparrows are less likely to survive locally to breeding age than are sparrows hatched earlier in the season (Arcese and Smith 1985, Hochachka 1990).

## DISCUSSION

Our study spanned 16 years, a long-term dimension lacking in most previous studies of brood parasitism (but see Rowley and Russell 1989). Our results, however, should be generalized with caution because of the isolated study site, the simple host community, and the very sparse "population" of brood parasites involved; i.e., the very elements that facilitated our analysis.

## COSTS OF BROOD PARASITISM TO SONG SPARROWS

Nice (1937, Rothstein 1975b) studied the effects of cowbirds on Song Sparrow reproduction in rural/suburban habitat in Columbus, Ohio from 1930 to 1936. There are several interesting differences between Nice's data and ours (Table 4). Sparrows began to lay about two weeks earlier on Mandarte, but cowbirds laid about a week earlier in Ohio. Thus, the breeding seasons of host and parasite overlapped considerably less on Mandarte, and the frequency of parasitism there was lower (25% vs. 44%).

Cowbirds on Mandarte laid small eggs relative to cowbirds in Ohio, and the reverse was true for sparrows. The small cowbird eggs on Mandarte, and the yellow gape markings of nestlings there (S. I. Rothstein, pers. comm.), suggest that the small cowbird race *M. ater obscurus* parasitized the large sparrow race *Melospiza melodia morphna* on Mandarte. In contrast, a larger cowbird race *ater* parasitized a smaller sparrow race *euphonia* in Ohio.

Parasitism in Ohio caused the loss of fewer eggs, but the impact of parasitism on host fledging success was about twice as great. Three factors that might explain the greater cost of parasitism in Ohio are: (1) the greater size differential between host and parasite; (2) the higher frequency of multiple parasitism; and (3) the generally poor level of sparrow breeding success in years when the data on costs were available from Mandarte Island.

Both Nice's study and ours agree that the Song Sparrow, unlike smaller hosts (Walkinshaw 1983, Grzybowski et al. 1986), can rear most of its own young successfully when parasitized. Perhaps the moderate costs of parasitism, and the difficulties of egg recognition (Davies and Brooke 1988), explain why Song Sparrows have yet to evolve egg rejection as a defense against parasitism. Desertion of parasitized nests was also not used by sparrows in our study, as expected from experiments on the conditions causing desertion in passerines (Rothstein 1982). Surprisingly, our results failed to show any weight loss in sparrow young with cowbird nest mates, or any decrement in post-fledging survival. Song Sparrow foster parents on Mandarte seemingly have the excess foraging capacity to rear cowbird young, without obvious fitness loss in their own young.

We identified two additional costs associated with cowbird activity in our study. The first was

egg damage, which affected about two percent of sparrow eggs. Since about two-thirds of this damage was in parasitized nests, and we found little such damage in nests outside cowbird laying periods, female cowbirds were the likely culprits. Cowbirds may damage host eggs while trying to remove them from nests, or while laying their own egg, or host females may damage their own eggs while resisting such attempts. The second additional cost we found was a higher rate of total nest failure during years and periods of cowbird activity. We have discussed elsewhere why cowbirds might act as nest predators (Arcese et al. 1992), and we present a full analysis of this hypothesis in another paper (Arcese and Smith, unpubl. ms).

#### COWBIRD SUCCESS AND PARASITIC TACTICS OF FEMALE COWBIRDS

Cowbirds reproduced very successfully in the nests of Song Sparrows in our study. Nice (1937), also found high success rates for cowbird eggs in Song Sparrow nests. In contrast, Nolan (1978) found that only 5% of cowbird eggs laid in Prairie Warbler (*Dendroica discolor*) nests produced fledglings because of poor laying synchrony and high rates of nest failure.

The number of cowbird eggs laid per host nest varies considerably among accounts in the literature, but multiple parasitism is common. For example, Weatherhead (1989) reported multiple parasitism by Brown-headed Cowbirds in 12% of Yellow Warbler (*Dendroica petechia*) nests, and in 30% of Red-winged Blackbird nests. In an extreme case, Post et al. (1990) noted an average of 3.74 Shiny Cowbird, *Molothrus bonariensis*, eggs in 100 nests of the Yellow-shouldered Blackbird, *Agelaius xanthomus*, in Puerto Rico. Multiple parasitism could result from repeated laying in the same nest by an individual cowbird, or as is perhaps more likely (Fleischer 1985), from laying by several cowbirds.

Female Brown-headed Cowbirds avoided multiple brood parasitism on Mandarte Island, and they never laid more than two eggs per nest. Two parasitic eggs were laid in the same sparrow nest much less often than expected by chance, suggesting that individual females avoided re-laying in nests they had parasitized previously. Double parasitism took place when there were few or no unparasitized host nests available. Other studies (Mayfield 1965, review in Orians et al. 1989) show either that eggs are laid at random,

or in a clumped pattern. We suggest that individual female cowbirds avoid multiple parasitism because they are aware of which nests they have parasitized. And further, that they do not return to these nests either to avoid ejecting their own eggs or because cowbird young survive better in singly-parasitized nests. While our data did not support this last point, our sample size of multiple parasitized nests was small and this precluded a powerful test. Alternatively, avoidance of multiple parasitism might only be strongly selected against in smaller hosts like warblers and vireos (Nolan 1978, Grzybowski et al. 1986), which cannot raise cowbirds in doubly-parasitized nests.

In contrast to our results for Mandarte, multiple parasitism by cowbirds occurs frequently in Song Sparrow populations in man-modified habitats on the British Columbia mainland (C.M. Rogers, M.J. Taitt, J.N.M. Smith and G. Jongejan, unpubl. data), and multiple parasitism was also frequent in Nice's (1937) study (Table 4). We suggest that the special conditions on Mandarte Island (usually only one laying cowbird present) explain the rarity of multiple parasitism there. In disturbed habitats, cowbirds can feed near their breeding areas, maintain higher densities, and probably cannot often monopolize access to host populations.

The age-selective parasitism we found was not due to adaptive selection of better, older host individuals; nor was it caused by age-related differences in the rate of nest initiation. However, in a previous study (Smith et al. 1984) we showed that age-related differences in host behavior, stemming from differential experience with cowbirds, did provide a plausible mechanistic explanation for this pattern; i.e., that cowbirds follow a gradient of mobbing responses to the place where hosts show most alarm or defensive behavior, and that older, more experienced hosts show the strongest mobbing response near their nest. While mobbing a cowbird seems maladaptive to the Song Sparrow in this case, mobbing may be an effective deterrent against other enemies at the nest (Smith et al. 1984).

#### COWBIRD FECUNDITY

We estimated that individual female cowbirds laid an egg about every two days. Cowbird laying seasons lasted up to 80 days, suggesting at least 40 eggs may be laid by an individual. This estimate is higher than those reviewed by Payne



(1977), or those found for captive yearling cowbirds by Jackson and Roby (1992). It is, however, close to those of Scott and Ankney (1980, 1983), and of those of Holford and Roby (1993) for two-year-old captive cowbirds. In shorter periods, production of eggs by individual females approached an egg per day over periods of up to three weeks. Our estimate of an average laying rate of an egg every two days is probably conservative. Cowbirds that laid eggs on Mandarte may also have laid eggs in nests of other host species on Mandarte, or in nests of Song Sparrows or other species on other islands near Mandarte. Thus, cowbirds may indeed act like "passerine chickens" (Scott and Ankney 1983). Supplemental food did not markedly increase laying rates by cowbirds in two years, although it was associated with an improved ability of sparrows to avoid parasitism (Arcese and Smith 1988).

#### COWBIRD-HOST DYNAMICS

The population biology of the Song Sparrow was first studied on Mandarte Island by Tompa (1964), when cowbirds were absent and the mean number of breeding females equalled 50.8 (range = 47–62,  $n = 4$  years). Cowbirds first colonized the island in the late 1960s (R. H. Drent, pers. comm.). However, the arrival of cowbirds appears to have had little effect on the average number of breeding female sparrows, though the population fluctuates so much that numbers are often far from the mean of 44.7 (range = 4–72,  $n = 15$  years; Arcese et al. 1992).

Since 1975, cowbirds and Song Sparrows on Mandarte Island have interacted in a predictable and density-dependent manner. We noted a strong functional response by cowbirds to host abundance (Fig. 1). Cowbirds tended to visit the island irregularly, and to lay only sparingly, during years with very low sparrow numbers. We therefore suggest that individual cowbirds behaved like foraging animals seeking prey. When hosts (prey) were locally scarce, cowbirds ranged over a wider area than Mandarte Island, seeking other opportunities for laying. When hosts were numerous, cowbirds increased their use of the island, and some probably laid eggs exclusively on Mandarte.

Despite the strong functional response by cowbirds, there was only a weak numerical response. This suggests that cowbird numbers were limited at higher host numbers, perhaps by the aggres-

sive behavior of females to one another. In our study, the most common pattern of cowbird abundance was for up to three females to be seen early in spring, but for only a single female to be present later in the summer. In 1983, two individually-identified females appeared to occupy different parts of the island. Chases were observed between these individuals, and the bird that was consistently chased was also the one least often observed overall. These patterns, along with the rarity of multiple parasitism on Mandarte, suggest to us that aggression among females limited the number of laying cowbirds on the island. Female territorial behavior or site-related dominance (Dufty 1982; Darley 1983; Rothstein et al. 1984, 1986; Yokel 1989) have been reported frequently in cowbirds elsewhere. However, studies using radio-telemetry have shown that while characteristic ranges are used for egg laying by individual cowbirds, these are not usually exclusive to a single female (Dufty 1982; Darley 1983; Rothstein et al. 1984, 1986; Fleischer 1985). Such ranges can be far from (Rothstein et al. 1984), or adjacent to communal feeding areas (D. Ward and J. Smith unpubl. data). Further work is needed to test if, or under what conditions, aggression plays a role in female spacing among cowbirds.

While brood parasitism had only a minor impact at the population level on Mandarte, it may have had a much greater effect on Song Sparrows elsewhere. In Columbus, Nice's study population declined by 62% from 1930 to 1936, as parasitism rose from 25 to 75%. Habitat destruction, however, also contributed to this decline (Nice 1943). We have found much higher rates of parasitism in other Song Sparrow populations in British Columbia, and in association, very poor production of sparrow fledglings (C. M. Rogers, M. J. Taitt, J. Smith and G. Jongejan, unpubl. data).

In a related sparrow, Trail and Baptista (1993) have recently suggested that increasing parasitism by cowbirds has caused population declines in White-crowned Sparrows (*Zonotrichia leucophrys*) in the San Francisco Bay area. Trail and Baptista's argument is based on a simple density-independent population model, that does not apply to Song Sparrows on Mandarte. Sparrow reproductive success on Mandarte was high at low densities, even when cowbirds were present, but cowbirds tended to avoid the site altogether at low host numbers. When bird populations are

endangered, they usually also face other perils, such as habitat loss and fragmentation, in addition to cowbird parasitism. Experience with the Kirtland's Warbler (*Dendroica kirtlandii*) and Black-capped Vireo (*Vireo atricapillus*), however, has shown that cowbird parasitism can be a major cause of endangerment in a host species with large losses of young per parasitized nest (Walkinshaw 1983, Grzybowski et al. 1986).

In conclusion, the colonization of Mandarte Island by cowbirds appears to have had little effect on the average number of Song Sparrows breeding there. The reasons for this included: limited cowbird numbers and hence only moderate levels of parasitism and a rarity of multiply parasitized nests; incomplete overlap in the breeding seasons of host and parasite; only slight to moderate losses of host young in parasitized nests; and lastly, density dependence in both host reproductive success and in the egg-laying behavior of cowbirds.

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