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COWBIRD PARASITISM, HOST FITNESS, AND AGE OF THE HOST FEMALE IN AN ISLAND SONG SPARROW POPULATION

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ABSTRACT.—Mandarte Island, British Columbia, was colonized by Brown-headed Cowbirds (*Molothrus ater*) after an intensive study of the resident Song Sparrow (*Melospiza melodia*) population. I studied the Song Sparrow population from 1975 to 1979, when it was parasitized by one to three female cowbirds a year. Breeding success was lower than during the earlier study, but comparisons of breeding success before and after the arrival of cowbirds each year and after cowbird removal in 1977 suggested that cowbirds were not a major cause of the reduced breeding success. Parasitism depressed the breeding success of adult female Song Sparrows by 0.6 independent young per nest and that of yearling females by 0.5 independent young per nest. The costs of parasitism were almost entirely due to egg removal by female cowbirds. Parasitized nests of adult females contained 0.8 fewer eggs than unparasitized nests. The corresponding figure for yearling females was 0.5 eggs. Nests of adult females were parasitized twice as often as nests of yearling females. A behavioral explanation is proposed for this last difference. Song Sparrows with cowbird nest mates weighed less than control young, but survival of young from six days after hatching to independence did not decrease if there was a cowbird in the brood. Female Song Sparrows that were parasitized one or more times during a breeding season raised as many young to independence per year as females that were not parasitized. This was because parasitized females made more breeding attempts per year.

The Brown-headed Cowbird (*Molothrus ater*) is perhaps the best studied of all avian brood parasites (e.g., Friedmann 1963, Rothstein 1975a). Payne (1977) reviewed studies which show that cowbirds lower the reproductive success of their hosts. In the best series of studies, on the Kirtland's Warbler (*Dendroica kirtlandii*), the effects of cowbirds have been assessed experimentally (Mayfield 1975a, Shake and Mattson 1975, Walkinshaw and Faust 1975, Anderson and Storer 1976). The influences of cowbirds on the demography of host populations are, however, poorly known (Payne 1977). Three reasons for this are that: 1) the entire seasonal production of young by hosts usually is unknown, 2) the exact extent of parasitism is difficult to estimate, and 3) host survival is seldom followed after young leave the nest, when young cowbirds are still competing with young of the host.

The Song Sparrow (*Melospiza melodia*) was the subject of an early study of cowbird parasitism (Nice 1937). In my study, I examined the effects of cowbird parasitism on a Song Sparrow population inhabiting Mandarte Island, near Victoria, British Columbia, Canada. The cowbird is a recent immigrant to southwest British Columbia (first nesting records in the Victoria region are from the late 1920's). Cowbirds were absent from Mandarte Island during the study there of Song Sparrows by Tompa (1963, 1964), but they began to breed on the island in the late 1960's (R. H. Drent, pers. comm.). My study began in 1975 and was facilitated by the scarcity of alternative hosts for cowbirds, the isolation of the island, and its history as a study site. I concentrated on the following questions:

(1) Did colonization by cowbirds change the annual production of the Song Sparrow?

(2) Was the depression in Song Sparrow nesting success from cowbird parasitism followed by further differential survival of young from parasitized and unparasitized nests?

(3) Did parasitized females raise fewer young per season than unparasitized females?

I also examined the effect of age of the host female on cowbird parasitism. Female age is known to influence clutch size and breeding success in several passerines

(Klomp 1970, Perrins and Moss 1974, Middleton 1979), but has not previously been shown to influence brood parasitism.

METHODS

Mandarte Island lies about 7 km off the east coast of southern Vancouver Island in the Gulf (San Juan) Islands. The nearest land is the similar-sized Halibut Island, 1.3 km distant. Several larger islands lie within 5 km. Mandarte (6.3 ha) has three main vegetation zones: bare rock and cliffs; grassy meadows; and shrubs and small trees concentrated in a shallow trench extending the length of the island. The dominant shrubs, waxberry (*Symphoricarpos albus*) and rose (*Rosa sitkana*) provide nesting sites for the Song Sparrows. Song Sparrows also forage on the cliffs, meadows and rocky intertidal zone. The rugged terrain provides many natural vantage points, facilitating observation of the sparrows. A full description of the vegetation and location of the island is given by Tompa (1964).

The population was studied for nine years between 1960 and 1979. The breeding population varied from 30–69 pairs per year. I began color-banding Song Sparrows in 1974 and all breeding individuals were individually color-marked from 1975 to 1979. The breeding efforts of each female were followed each year. In 1975, two or three successful nests were not found, and one was not found in 1979. All successful nests were found from 1976–1978.

The ages of Song Sparrows were determined from knowledge of their year of hatching. In all, 177 birds were recruited to the breeding population and only six of these were not known to have hatched on the island. Five of the six 'immigrants' were females and four of the six arrived after the first study year, when some young were not banded in the nest. These four may, therefore, not have been genuine immigrants. I assume that the few birds of unknown origin were hatched in the summer prior to first capture.

I counted the numbers of cowbirds on the island each day. Three females were trapped and given standard metal bands and, in 1977, four females were removed from the population by trapping or shooting. Cowbird nestlings also were given standard metal bands.

Tompa (1963, 1964) collected breeding data on the Song Sparrow population by color-marking and following the activities of all breeding pairs, noting successful breeding by the presence of fledged young in each territory. He estimated fledgling production by following the fates of 56 nests distributed unevenly over four seasons and extrapolating his observed success figures to all breeding attempts known to have produced young. This method probably over-estimated fledging success per breeding attempt, as some nests were found late in the nesting cycle (Tompa, pers. comm.). Failure of early nests could thus have gone undetected.

I followed breeding in a similar way, but found during incubation almost all nests that later hatched young. In 1975, I found some early nests by searching along the shrubbery edge; this method was inefficient and may have disturbed some females. In late 1975 and after, I either followed incubating females to the nest after feeding trips, or observed them building, and visited the nest site after the female had incubated undisturbed for two or more days. Nests were checked every two to four days until the eggs hatched and then at least every two days until the nestlings were color-banded when about six days old. Nests containing older young were not visited consistently during 1975–1978, in case disturbance at this time might cause premature departure (Nice 1937). In 1979, nests were checked every two days until the young left; no premature departures were observed. After the young had left, the concealment of each nest was scored subjectively on a 0–6 ranked scale. Completely exposed nests scored 0 and very well concealed nests scored 6. The height of the nest rim above the ground also was measured.

Minimum numbers of young known to be alive after leaving the nest were counted from sightings of marked individual young up to the following ages: 4 weeks after hatching (when young Song Sparrows become independent of their parents), 10 weeks after hatching and 37–50 weeks after hatching (the beginning of the subsequent breeding season). The study was terminated when the last young left the nest in 1979. Estimates of postfledging survival in 1979 therefore were truncated, as only a portion of the young reaching independence could have been detected. I assume that no young left the island before independence. Survival estimates to this time would not then be influenced by young leaving the island. Later estimates of survival include both death and dispersal off the island. Most dispersal off the island occurs in September or October (Tompa 1964), but some transient unmarked young appeared on the island as early as mid-July. By Tompa's methods, these would have been judged to have been hatched on the island.

Mean values of all statistical measures are reported ±1 standard error, unless otherwise indicated.

RESULTS

COWBIRD POPULATIONS AND PARASITISM

Table 1 summarizes the breeding activities of female cowbirds each year. Cowbirds first arrived in late April or early May and were present for an average span of 63 days thereafter. Females and associated males (1–5) were not seen every day and spent only part of the day (usually in the morning) on the island. Banded individuals were seen repeatedly during the breeding season, particularly in 1979, when one female was seen at least 13 times between 2 May and 7 July. There was a lag of about 10 days from the first sighting each year to the detection of the first egg. The minimum number of Song Sparrow nests available was taken as the total number known to have been begun after the arrival of the first cowbird each year. This may overestimate the available nests slightly as some time may have been required for cowbirds to mature eggs after arrival. A female trapped on 24 April 1977 did not contain mature oocytes in the oviduct. On the other hand, some nests must have failed without my knowledge, thus causing an opposite bias. I doubt if either bias was a major source of error. The proportion of available nests parasitized varied from year to year, reaching 80% in 1976, when the average number of cowbirds sighted per day was greatest and the host population low. In 1975, one host nest contained two cowbird eggs and in 1976, five did so. This may indicate (Payne 1977) that

TABLE 1. Presence and breeding activity of female Brown-headed Cowbirds on Mandarte Island.

Year	Date of first sighting	Number of days sighted (censused)	Maximum number sighted per day	Average number sighted per sighting day	Date of first cowbird egg	Total nests parasitized	Eggs laid	Minimum number of host nests available	Number of young cowbirds banded
1975	April 29	17 (67)	2	1.24	May 8–10	16	17	29	13
1976	May 9	25 (80)	3	1.40	May 17–19	33	38	41	26
1977	April 23	19 (98)	2	1.05	—	0*	0	64	0
1978	May 2	32 (92)	2	1.06	May 13–17	22	22	70	13
1979	April 27	36 (87)	3	1.28	May 6–8	28	28	73	18

* Cowbird females removed in 1977.

more than one female cowbird was laying in these nests.

Four female cowbirds in all were removed from the island on 24 April, 1 May, 11 May and 10 June 1977. The female removed on 24 April had been banded in May 1975 and had been seen in 1976. The removals prevented cowbirds from breeding, as no cowbird eggs were found in 1977. Female cowbirds, however, continued to visit the island occasionally during the breeding season (Table 1). This suggests that not all birds seen on the island in other years actually bred.

The minimum number of females known to visit the island was two in 1975, three in 1976, five in 1977, two in 1978 and three in 1979. One of the two females present in 1975 was found dead on 1 June and only one female was seen thereafter. If we assume that each female laid an equal proportion of all eggs found, the minimum number of eggs laid on the island by each female was 4 and 13 in 1975; 13, 13 and 12 in 1976; 11 and 11 in 1978; and 9, 9 and 8 in 1979. As one female in 1979 accounted for 13 of 16 sightings where the legs could be clearly seen and identity established, it is unlikely that all females laid equally. Some females may therefore have laid considerably more eggs than these minimum estimates. Some cowbird eggs may have been laid in Fox Sparrow (*Passerella iliaca*) nests, but the three nests found were not parasitized.

Survival from cowbird eggs was 65% from laying to six days after hatching. Post fledging survival was very poor. Only 3 of the 70 cowbirds banded during the study were known to have reached independence from their foster parents. It is possible that some of them left the island, but most disappeared in the first week after leaving the nest. Fledgling cowbirds are not easily overlooked, because of their conspicuous behaviour (Smith and Merkt 1980).

SONG SPARROW BREEDING PERFORMANCE

Table 2 summarizes the breeding activities of Song Sparrows each year during 1960–1962 (Tompa 1964) and 1975–1979. Breeding in the eight years began in late March or early April, with an average of 29.6 ± 4.6 days passing (n = 5) before the arrival of the first female cowbird during 1975–1979. Most Song Sparrows thus raised their first brood of young free from disturbance by cowbirds. Total breeding success varied among years, but was not closely related to variation in density of Song Sparrows. Breeding success was higher overall when cowbirds were absent (mean number of young raised to six days after hatching per female per year = 6.18 ± 0.54, n = 4) than

TABLE 2. Estimates of total breeding output of Song Sparrows on Mandarte Island, British Columbia, during four years of Brown-headed Cowbird parasitism and four control years.

Year	Breeding female Song Sparrows	Date of first egg	Eggs per female per year	Young fledged* or banded per female per year	Cowbird status
1960	46–48	—	7.89	7.09*	Absent
1961	47	April 1–5	7.89	7.09*	Absent
1962	44	April 11–15	6.20	5.57*	Absent
1975	34	April 16	4.59	2.18	Present
1976	30	April 2	7.50	4.07	Present
1977	44	March 23	7.56	4.98	Removed (Absent)
1978	48	April 5	8.25	5.27	Present
1979	66	March 18	5.41	3.04	Present

TABLE 3. Yearly variation in survival of young Song Sparrows in relation to cowbird parasitism.

Category	Year	N	Average clutch size	Proportion surviving to 6 days after hatching	Proportion alive at 4 weeks after hatching	Proportion alive at 10 weeks after hatching	Proportion alive at 37–50 weeks after hatching
Parasitized	1975	16	2.63	0.50	0.29	0.10	0.10
	1976	33	2.48	0.61	0.48	0.45	0.32
	1978	21	2.95	0.61	0.44	0.21	0.11
	1979	28	2.64	0.65	0.20*	—	—
Unparasitized	1975	13	2.85	0.59	0.22	0.16	0.05
	1976	8	3.00	0.58	0.50	0.50	0.38
	1977	64	3.52	0.76	0.40	0.25	0.13
	1978	49	3.45	0.74	0.52	0.38	0.25
	1979	45	3.13	0.50	0.25*	—	—

* 1979 survival estimates to four weeks of age are incomplete, as the study was concluded at the end of this breeding season. No further survival estimates are available for 1979.

when they were present ($\bar{x} = 3.64 \pm 0.67$, n = 4). This comparison, however, depends critically on Tompa's data, which were extrapolated from a limited sample of nests. The breeding success in 1977, when female cowbirds were successfully removed, fell within the range of values when breeding cowbirds were present. It is possible, therefore, that the presence of cowbirds decreases overall production of Song Sparrows, but the data collected in this study alone do not support this conclusion, and Tompa's (1964) data and mine cannot be compared statistically because of differences in methods.

To examine the impact of cowbird parasitism on host nesting success, I considered only those nests known to be active after the arrival of the female cowbirds each year. In all, an average of 2.61 Song Sparrow eggs were found in 98 parasitized nests, while 115 unparasitized nests contained an average of 3.25 eggs. This difference is highly significant (t = 5.31, $P < 0.001$). This suggests that female cowbirds removed a Song Sparrow egg from a little over half of the nests they parasitized.

Table 3 presents my data on survival of young Song Sparrows in relation to year and parasitism. I tested for influences of these two factors on the proportion of Song Sparrow eggs surviving to (a) six days after hatching and (b) four weeks after hatching, by two-way analyses of variance. Both measures of breeding success were transformed by arcsin $\sqrt{P}$. Data from 1977 were excluded from this analysis. Contrary to expectation, neither measure of breeding success was influenced by parasitism ($P > 0.25$) and a similar proportion of sparrow eggs in parasitized (0.36) and unparasitized (0.37) nests produced independent young. Survival to six days of age did not vary significantly among years ($P = 0.42$), but survival to four weeks of age did vary significantly among years (F = 5.38, d.f. = 2,135; $P = 0.006$). In 1977, a higher proportion of Song Sparrow eggs laid after the arrival of cowbirds produced six-day old young than in other years combined ($\chi^2 = 19.59$, d.f. = 1, $P < 0.001$). Survival from six days of age to four weeks of age in 1977 did not, however, differ from other years ($\chi^2 = 3.66$, d.f. = 1, $P > 0.05$). There was no indication that later survival (or dispersal) of young from parasitized nests was poor compared to that from unparasitized nests (Table 3).

The failure of cowbirds to depress the average nesting success of sparrows suggested that further confounding factors might be present. Nest failures were the main cause of losses and I therefore examined patterns of nest success and failure more closely. I define nests raising at least one young of either species to banding age (six days) as successful and the remainder as failures. Nests failed for three reasons: starvation of young, desertion of eggs or young by the parents, and predation. Starvation was extremely rare and will be ignored. Table 4 presents the distribution of success and failure for all nests in all years. Nest failures were slightly commoner before the arrival of cowbirds (Table 4). I found therefore no strong evidence that cowbirds were a major cause of nest failure. Desertions were slightly more common before the arrival of cowbirds and also cannot be attributed to cowbird activity. Total nest failures were not distributed randomly among years ($\chi^2 = 13.80$, d.f. = 4, $P < 0.01$). There were many fewer failures in 1977, both before and after cowbird arrival. If 1977 is excluded, the proportion of nest failures did not differ significantly among years ($\chi^2 = 4.21$, d.f. = 3, $P > 0.50$). Nest failures in unparasitized late nests in all years except 1977 were nearly twice as common as in parasitized

TABLE 4. Nest success of Song Sparrows on Mandarte Island in relation to cowbird arrival and parasitism.

	Before cowbird arrival			After cowbird arrival							
				Parasitized			Not parasitized				
Year	Succeed	Fail	% Success	Succeed	Fail	% Success	Succeed	Fail	% Success	Total	% Success
1975	13	13 (7)	50	12	4	75	9	4 (2)	69	55	62
1976	22	9 (3)	71	27	6 (4)	82	5	3	63	72	75
1977	28	6	82	—	—	—	57	7	89	98	85
1978	29	13 (4)	69	17	4	81	39	10 (4)	80	112	76
1979	31	11 (2)	74	21	7 (1)	75	25	20 (1)	56	115	67
Total	123	52 (16)	70	77	21 (5)	79	135	44 (6)	75	452	74

In parentheses are the numbers of nests failing owing to desertion.

nests, though the difference was not significant ($\chi^2 = 3.08$, d.f. = 1, $P < 0.10$). The last result suggests that female cowbirds may have selected host nests which were likely to be more successful.

A simple basis for selection might be the concealment and position of the nest. My index of concealment did not, however, differ significantly between parasitized and unparasitized nests in any year ($P > 0.05$, Mann-Whitney U test). Parasitized nests tended to be slightly less well concealed, as claimed by Nice (1937). Parasitized nests also did not differ significantly from unparasitized nests in height. In addition, neither nest height nor nest concealment was closely related to nest success.

One variable known to be related to clutch size of Song Sparrows on Mandarte Island is the age of the female (Smith and Roff 1980). I therefore examined the patterns of parasitism and nest success in relation to female age. Females were classed as adult (older than one year) or yearling (one-year old) for all years after 1975. Female ages were not known in 1975 and these data were therefore omitted. The pattern of success and failure is shown in Table 5. Twenty percent of nesting attempts by adult females failed after the arrival of cowbirds, while 32% of nests of yearling females failed during this period ($\chi^2 = 3.87$, d.f. = 1, $P < 0.05$). Adult females were parasitized nearly twice as often (58%) as yearling females (30%, $\chi^2 = 14.68$, d.f. = 1, $P < 0.001$). However, yearling females that were parasitized did not differ in breeding success from parasitized adult females ($\chi^2 = 0.11$, d.f. = 1, $P > 0.90$). Among yearling females, parasitized nests were somewhat more successful, but the difference was not significant ($\chi^2 = 3.27$, d.f. = 1, $P > 0.05$).

The foregoing analysis indicates that the effects of parasitism on yearling and adult female Song Sparrows must be assessed separately, as the slightly greater success of older females is confounded by their greater rate of parasitism. Table 6 summarizes the effects of parasitism on these two age groups. Parasitized nests of adult females contained an average of 0.79 fewer eggs than unparasitized nests (t = 4.55, d.f. = 100, $P < 0.001$). Female cowbirds therefore appear to have removed eggs from about four-fifths of these nests. Two-way analyses of variance, with years and parasitism as factors, showed that neither factor had a significant influence ($P > 0.35$) on the proportion of eggs laid (transformed by arcsin $\sqrt{P}$) by adult females that resulted in six-day old or four-week old young. The only effect of parasitism on adult females was the result of the reduction of average clutch size.

Parasitized nests of yearling females contained 0.51 fewer eggs on average than unparasitized nests (t = 2.65, d.f. = 82, $P < 0.01$). Eggs therefore were removed from nests of yearling females slightly less often than from nests of adults. Clutch sizes of unparasitized yearling females were significantly smaller than those of unparasitized adults (t = 2.03, d.f. = 100, $P < 0.05$) and the proportionate loss due to egg removal was similar in both age classes. Two-way analyses of variance, as carried out for adults, again failed to show a significant main effect of either parasitism or year on

TABLE 5. Success and failure of Song Sparrow nests on Mandarte Island in relation to cowbird parasitism and the age of the female Song Sparrow. Data are from 1976, 1978 and 1979 combined.

	Category	Succeeded	Failed	Total	% Success
Adult female	Parasitized	46	13	59	78
	Not parasitized	36	7	43	84
Yearling female	Parasitized	21	4	25	84
	Not parasitized	36	23	59	61
Total		139	47	186	74

TABLE 6. Survival of eggs and young of Song Sparrows in relation to cowbird parasitism and age of the host female. Survival to six days of age is based on data (N_1) from 1976, 1978 and 1979; later survival is based on data (N_2) from 1976 and 1978 only.

Category	N_1	Average clutch size ±SE	Proportion alive 6 days after hatching	N_2	Proportion alive 4 weeks after hatching	Proportion on island 10 weeks after hatching	Proportion on island 37–50 weeks after hatching
Adult female parasitized	59	2.68 ± 0.12	0.61	40	0.50	0.40	0.25
Adult female not parasitized	43	3.47 ± 0.12	0.72	27	0.55	0.44	0.27
Yearling female parasitized	25	2.60 ± 0.18	0.66	16	0.40	0.28	0.12
Yearling female not parasitized	59	3.14 ± 0.11	0.61	30	0.48	0.34	0.26

breeding success. There was, however, a significant interaction between parasitism and years and the proportion of eggs producing six-day-old young. In 1976 and 1978 survival was slightly better in unparasitized nests of yearling females, but it was much worse in 1979. The sample sizes for parasitism of yearling females are small. This final result should therefore be viewed with caution, but it is possible that yearling female Song Sparrows are more influenced by parasitism and/or year effects than adults.

Taken together, these two analyses show that the main cost from parasitism to sparrows is due to egg removal by cowbirds. Unparasitized adult females in 1976 and 1978 raised 1.93 independent young per nest compared to 1.33 for parasitized adults. The comparable figures for yearling females are 1.53 for unparasitized and 1.06 for parasitized birds.

I tested the direct effects of competition by cowbird nest mates on young Song Sparrows in two ways. I first compared the nestling weights of Song Sparrows in nests with and without cowbirds and then examined the post-fledging survival of Song Sparrows from nests that fledged a cowbird. I predicted that the larger cowbird nestlings would reduce the average weights of their Song Sparrow nest mates and lower their subsequent survival. Table 7 shows the weights of nestlings at banding age separated by parasitism and year. Two-way analysis of variance on data from 1976, 1978 and 1979 showed that both parasitism ($F = 16.048$, d.f. = 1,268, $P < 0.001$) and year ($F = 26.934$, d.f. = 2,268, $P < 0.001$) had significant effects. There was also a significant interaction between parasitism and years ($F = 3.038$, d.f. = 2,268, $P < 0.05$). Young were heaviest and the reduction in weight through parasitism was highest in 1976, when there were fewest breeding sparrows (Table 2). Brood size might be expected to correlate negatively with the average weight of young, but I found no significant correlation ($P > 0.25$, Spearman rank correlation) in any year.

TABLE 7. Average weights (g) of young Song Sparrows at banding age (approximately six days after hatching) in relation to year and presence of cowbird nest mates.

Year	N	Parasitized	N	Not parasitized
1976	30	14.97 ± 0.52	24	17.54 ± 0.57
1977	—	—	143	15.20 ± 0.15
1978	20	13.58 ± 0.57	96	14.98 ± 0.25
1979	41	13.00 ± 0.35	64	13.60 ± 0.24

The survival of young Song Sparrows from nests with and without cowbird young in 1976 and 1978 is compared in Table 8. Only incomplete estimates of post-fledging survival were available in 1979 and host females could not be aged in 1975. Overall survival was better in 1976 (80%) than in 1978 (63%), but did not differ significantly in either year in relation to age of the Song Sparrow female or presence of cowbirds in the brood. Thus, the presence of cowbird nest mates caused Song Sparrow nestlings to be lighter, but it did not reduce survival from six days of age to independence from parental feeding (four weeks of age).

The above evidence indicates that cow-

TABLE 8. Survival of young Song Sparrows from six days after hatching to independence in relation to maternal age and presence or absence of cowbirds in the brood.

		Young of adult females		Young of yearling females	
Year	Parasitized?	Alive at 6 days age	Alive at independence (%)	Alive at 6 days age	Alive at independence (%)
1976	Yes	32	26 (81)	4	2 (50)
	No	24	21 (88)	5	3 (60)
1978	Yes	17	13 (76)	10	8 (80)
	No	63	46 (73)	73	48 (66)

TABLE 9. Total annual breeding effort by Song Sparrow females divided according to female age and parasitism. Data are from 1976, 1978 and 1979 combined. Females in the parasitized group were parasitized at least once during the breeding season. Statistical comparisons are between parasitized and unparasitized females in the same age class.

Female age	Status	Sample size	Number of breeding attempts per female	Number of successful breeding attempts per female	Total number of eggs laid per female	Total number of young banded per female	Total number of independent young raised per female
Adult	Parasitized	45	2.73 ± 0.12	1.96 ± 0.11	8.35 ± 0.41	4.64 ± 0.29	3.28 ± 0.30
	Not parasitized	26	2.15 ± 0.11	1.65 ± 0.11	6.73 ± 0.46	4.85 ± 0.33	3.27 ± 0.34
	'p' value (t test)		<0.005	<0.10	<0.01	>0.10	>0.10
One-year old	Parasitized	24	2.83 ± 0.19	1.42 ± 0.20	8.38 ± 0.71	3.75 ± 0.41	2.13 ± 0.41
	Not parasitized	32	2.22 ± 0.12	1.31 ± 0.14	6.56 ± 0.38	3.75 ± 0.42	2.06 ± 0.39
	'p' value		<0.01	>0.10	<0.025	>0.10	>0.10

bird parasitism depresses the reproductive success per nest in the latter part of the breeding season, particularly for adult females, which seem to be parasitized selectively. To assess the effects of parasitism on host fitness, we must consider the effects of parasitism over the whole breeding season, as Song Sparrows on Mandarte Island raise up to three broods of young per year (Smith and Roff 1980). I therefore calculated the total seasonal reproduction for all parasitized and unparasitized females followed during the entire breeding season on the island in 1976 and 1978–1979. Data from 1975 and 1977 were not used, as female ages were unknown in 1975 and cowbird parasitism was prevented in 1977.

Table 9 shows five measures of total annual breeding effort for Song Sparrow females divided by age and the occurrence of cowbird parasitism. The three years' data are pooled, as similar patterns were observed each year. The right-hand column of the table, the total number of young raised to independence, is the best measure of fitness and clearly shows that parasitized females were just as fit as their nonparasitized counterparts in each age group. Adult females raised over one-third more young to independence than yearling females regardless of parasitism. One explanation for this is that the "quality" of parasitized birds in each age group was higher than that of unparasitized birds. Table 9 shows that parasitized birds made significantly more breeding attempts per season in each age group and, as a result, laid significantly more eggs per season, despite losing some eggs from removal by cowbirds. The later reduction of total breeding success to the level of unparasitized birds could be due to the competitive cost incurred through parasitism by cowbirds. These data may indicate that the greater number of breeding attempts by parasitized females was a cause of the parasitism, because the greater the number of nests initiated, the greater will be the chance that at least one nest is parasitized. The opposite argument, that parasitism increased the number of nesting attempts, is unlikely, as most females were parasitized only once on the final nesting attempt of the year.

Larger reproductive costs may reduce subsequent adult survival in birds (Askenmo 1979, Bryant 1979). I therefore tested whether parasitism by cowbirds influenced survival of breeding female Song Sparrows. Survival of parasitized females until the next breeding season was 70%, somewhat higher than that of unparasitized females (56%), and was not influenced by female age.

In summary, when age of the host female was considered, cowbirds reduced the nesting success of adult female Song Sparrows by about 0.6 independent young per nest and that of yearling females by about 0.5 independent young per nest. The latter result is less certain, because fewer one-year-old females were parasitized than expected by chance. Over the whole breeding season, parasitized females in each age group were just as fit as unparasitized females, because the effects of parasitism were counteracted by a greater number of nesting attempts per parasitized female. Survival of parasitized females until the subsequent breeding season was slightly better than for unparasitized females, despite the costs of parasitism.

DISCUSSION

I first consider information on the cowbird population. Mandarte seemed to be visited by one to three females. When three females were removed in late April and early May 1977, there was no immediate replacement. The female removed on 10 June may not have been a potential breeder on the island, as she was shot in the evening and may have been visiting the island to join a communal roost of Starlings (*Sturnus vulgaris*). In the cowbird control operation carried out on Kirtland's Warblers, most captures also were made at the beginning of the breeding season (Shake and Mattson 1975). The females laying on Mandarte therefore probably had restricted breeding areas which were regularly patrolled. It is not known if other nearby islands were also included in these ranges, but this seems possible judged by the many days (Table 1) when no cowbirds were seen on the island. Other nearby islands are inhabited by less dense populations of Song Sparrows and also by other suitable hosts (Tompa 1964). The diurnal pattern of cowbird appearances on the island suggests that the afternoons were spent on feeding grounds, possibly on southern Vancouver Island. Cowbirds occasionally joined roosts of Starlings on the island in June and July.

The arrival of cowbirds on the island averaged nearly a month after the onset of breeding by Song Sparrows. This ensured that early Song Sparrow nests escaped parasitism. It would seem advantageous for cowbirds to arrive earlier or to reside in the area, as the mild winters of southwest British Columbia allow several potential hosts to begin breeding by early April (B.C. nest record scheme).

My rough estimates of minimum egg production per female per season on the island (8–13) are similar to estimates from other studies (Payne 1977).

Brown-headed Cowbirds most often remove a single egg from parasitized nests (Rothstein 1975b), but Nice (1937) estimated that eggs were removed on only about one-third of the occasions that Song Sparrow nests were parasitized. Egg removal rates in this study were below 1 egg/nest but above 0.33 eggs per nest. Clutch sizes of parasitized females averaged about 0.8 eggs less than unparasitized clutches for adults and about 0.5 eggs less for yearlings.

Survival of cowbirds in the nest was similar to that of Song Sparrows, but later survival was very much poorer. Fledgling cowbirds remain less hidden than fledglings of Song Sparrows and have more conspicuous food begging calls (Smith and Merkt 1980). I suggest that the poor survival of fledgling cowbirds is due mainly to predation by crows (*Corvus caurinus*), which kill many Song Sparrow fledglings. Banded sparrow legs were often found below crow feeding perches. It is also possible that some young cowbirds reached independence and immediately left the island without being seen.

I now consider the effects of parasitism on reproduction of Song Sparrows. Tompa's (1964) estimates of Song Sparrow breeding success were much higher than those found in the present study. The removal of cowbirds in 1977 did not raise annual Song Sparrow production to the level reported by Tompa, and Song Sparrow production was lower in 1977, when cowbirds were prevented from breeding, than in 1978 when cowbirds bred successfully (Table 2). Further, the Song Sparrow population increased sharply in two years (1977 and 1979) following cowbird success, but increased only slightly in a year (1978) following cowbird exclusion. I therefore conclude that the effects of cowbird colonization on annual production of young by Song Sparrows were slight, and had no influence on the breeding population size. This contrasts with the severe decline in populations of the Yellow-shouldered Blackbird (*Agelaius xanthomus*) that followed colonization of Puerto Rico by the Shiny Cowbird (*Molothrus bonariensis*; Post and Wiley 1976).

Before considering the exact impact of cowbirds on Song Sparrow breeding success, I consider the issue of bias in the nesting records. Nests found late in the nesting cycle are less exposed to subsequent failure, and their success can over-estimate the actual value (Mayfield 1975b). I found some evidence for this bias in that nests of adult females, which were more successful, were found on average slightly, but significantly, later in incubation than nests of young females ($P < 0.05$, Mann-Whitney U test). Since mortality rates of nests/day were low in this study, the effect of this bias probably is slight.

Rothstein (1975b) calculated from Nice's (1937) Ohio data that cowbird parasitism reduced the average number of Song Sparrows leaving the nest by 1.38. In this study, I found that parasitized adult females raised 0.86 fewer young to banding (six days after hatching) than unparasitized adults (Table 6). The only year that I had full information on further losses in the nest was 1979. I found no evidence that parasitized adult females suffered greater losses of young between banding and leaving the nest (about 11 days after hatching) in 1979. Adult females therefore suffered lower nest losses from parasitism than all birds in Nice's study. For yearling females, the number of Song Sparrows raised to banding age per nest was similar in parasitized (1.72) and unparasitized (1.92) nests. The smaller effect for this group was because slightly fewer eggs were removed from the nests of young birds (Table 6) and because success rates of parasitized nests were slightly higher than for unparasitized nests of young females (Table 5). Thus, the overall depression of host production (0.46 young/nest up to six days of age) was considerably less than found by Nice. Several differences between the Ohio and Mandarte populations could have influenced parasitism. Song Sparrows on Mandarte are slightly larger (Smith and Zach 1979), have smaller clutches and the population is much more dense. The cowbird population in Ohio (Nice 1937) was larger and the overlap between the breeding seasons of cowbirds and sparrows was greater. Adult survival on Mandarte was higher and the age distribution consequently more biased towards old birds than in Ohio.

Unlike most other studies of parasitism, I was also able to estimate survival of young hosts after departure from the nest. I found no indication (Table 8) of higher mortality of host young from nests containing cowbirds at this time. Cowbird nestlings reduced the weights of Song Sparrow nest mates (Table 7) and required more food as fledglings (Smith and Merkt 1980). One might therefore expect them to be serious competitors as fledglings, but this was not the case, perhaps because cowbird fledglings survived poorly compared to sparrows. Lowered nestling weights did not therefore result in poor subsequent survival, as found for Great Tits (*Parus major*) by Perrins (1965). In this study, host survival in the nest adequately predicted the effects of cowbird parasitism beyond departure from the nest. This last result, however, should not be applied uncritically to other populations.

The two most unusual findings in this study are: (1) that parasitism was highly selective on nests of adult hosts, and (2) that parasitized female Song Sparrows raised as many young to independence as unparasitized birds of the same age.

The selective parasitism of nests of adult females did not seem to be closely related to the concealment or position of the nest. I offer a behavioral hypothesis to explain this result. Song Sparrows behave aggressively toward both live and stuffed cowbirds (Nice 1937, Robertson and Norman 1976, 1977). Further, Robertson and Norman (1977) found that those host species that were more frequently parasitized showed stronger responses to freeze-dried cowbirds presented near nests. I therefore propose that adult female Song Sparrows (which tend to be paired to old males) respond more strongly to passing cowbirds and therefore cause their nests to be discovered more often than those of young females. I have no evidence for this "nest-cue" hypothesis (Robertson and Norman 1977), but it is readily testable. Unfortunately, the Mandarte population crashed to seven pairs of sparrows in 1980. It will therefore be some time before this hypothesis can be tested there.

If the nest-cue hypothesis is correct, it raises the question of why Song Sparrows respond aggressively to cowbirds at all. One possible answer is that aggressiveness to all intruders to the nest area (e.g., predators such as deer mice, *Peromyscus maniculatus*; conspecifics) is advantageous and that aggressiveness toward cowbirds is an expression of a greater general aggressiveness by adult females. Huntingford (1976) has shown that male sticklebacks (*Gasterosteus aculeatus*) that are more aggressive towards conspecifics are also more aggressive toward predators at a later stage in the nesting cycle.

The apparent lack of difference in fitness between parasitized and unparasitized female Song Sparrows must also be a consequence of selective parasitism. Females that were parasitized made more breeding attempts per year and could therefore withstand the losses of eggs, and perhaps small nestlings, caused by cowbirds. The simplest explanation of this selective parasitism is that birds breeding more often were at greater risk of parasitism, but it is also possible that cowbirds responded to some other index of the "quality" of the host individuals. Host aggressiveness could again be a possible cue, and habitat features might also have provided an index of host quality to cowbirds.

Based upon this study, estimates of the effects of parasitism on host populations should be viewed with caution (e.g., Rothstein 1975b, Payne 1977), if they are based on the assumption that parasitized nests are a random sample of the host nests available. Experimental tests of the idea that cowbirds select better than average nests are required.

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