NEST PREDATION AND COWBIRD PARASITISM CREATE A DEMOGRAPHIC SINK IN WETLAND-BREEDING SONG SPARROWS[1]

CHRISTOPHER M. ROGERS[2], MARY J. TAITT, JAMES N. M. SMITH[3] AND GWEN JONGEJAN[4]
*Centre for Biodiversity Research, Department of Zoology, University of British Columbia,
6270 University Blvd., Vancouver, B.C., V6T 1Z4, Canada*

Abstract. We studied mechanisms underlying poor breeding performance in a color-banded population of Song Sparrows (*Melospiza melodia*) in coastal British Columbia for four years. Only 21% of sparrow nests produced fledglings. The main causes of nest failure were complete predation (42% of nests), and abandonment after parasitism by Brown-headed Cowbirds (*Molothrus ater*) coincided with partial predation (34%). Increasingly fewer sparrow young fledged as the number of cowbird eggs per nest increased, but nests with up to five cowbird eggs fledged cowbirds. Many nests produced only cowbird fledglings. Annual production of recruits was seven times below the annual rate of adult disappearance. Nevertheless, Song Sparrow numbers at the study site remained stable due to immigration. When reproductive success was estimated in the absence of cowbird parasitism, production of young remained poor. Thus, high levels of predation on nest contents explained the poor breeding performance. Experiments with dummy Song Sparrow eggs in Song Sparrow nests suggested that mice, shrews, and medium-sized birds were the principal egg predators, but these small mammals probably were not frequent predators on Song Sparrow eggs. Damage by bird predators coincided with the laying season of the cowbird, suggesting that cowbirds contributed to predation on sparrow nests. The study site is a population sink for Song Sparrows because of high rates of nest predation and brood parasitism. These ecological factors may be contributing to the significant long-term decline (1966–1994) of the Song Sparrow in British Columbia and throughout Canada.

Key words: Melospiza melodia, Molothrus ater, *source-sink population dynamics, metapopulations, predation on eggs and nestlings, brood parasitism, songbird population declines.*

INTRODUCTION

There has been much recent discussion of the existence and possible causes of population declines in North American songbirds (Robbins et al. 1989, Robinson et al. 1995, James et al. 1996). Where declines in songbird numbers are clear, they often have been blamed on poor breeding success due to: (1) high rates of predation on eggs and nestlings (Böhning-Gaese et al. 1993, Robinson et al. 1995), and (2) frequent brood parasitism by Brown-headed Cowbirds, *Molothrus ater* (Martin 1992, Robinson et al. 1995, 1996). We consider here if these two factors jointly cause poor breeding performance in a wetland population of Song Sparrows, *Melospiza melodia*.

We have explored the reproductive performance of Song Sparrows on islands of varying degrees of isolation off the southwest coast of British Columbia (B.C.), Canada (Arcese et al. 1992, Smith et al. 1996). Small offshore islands were population sources for Song Sparrows, where reproductive rates exceeded mortality rates. In contrast, near-shore Westham Island was a population sink, where fewer surviving young were produced than were needed to fill breeding vacancies arising from the deaths of adults (Krebs 1994). Levels of nest failure and cowbird parasitism were high on Westham Island, and both declined on islands with increasing degree of isolation from the mainland (Smith and Myers-Smith, in press). On the isolated Mandarte Island, the presence of breeding cowbirds was associated with increased nest failure rates in Song Sparrows (Arcese et al. 1992), perhaps because cowbirds acted as predators on sparrow eggs and young (Arcese et al. 1996). In this paper, we examine in detail the demographic features of the sink population of Song Sparrows on Westham Island. In particular, we focus on

how cowbird parasitism and nest predation cause poor nesting success and a subsequent major imbalance between annual adult mortality and annual recruitment. We also report the results of experiments using nests containing dummy Song Sparrow eggs, which we used to identify nest predators.

METHODS

STUDY SPECIES

Song Sparrows breed in moist, early-successional habitats in most of northern North America (Bent 1968). In coastal British Columbia, they are abundant in sea island scrub (Arcese et al. 1992) and dry forest (Smith et al. 1996) on small offshore islands. They also are common in wetland habitats in the Fraser Delta (Knapton and Krebs 1974). Song Sparrows in coastal British Columbia are resident year-round and highly territorial (Tompa 1964, Smith 1981). They have a long breeding season (Arcese et al. 1992), and are commonly parasitized by cowbirds (Smith 1981, Smith and Myers-Smith, in press). Song Sparrows can tolerate moderate levels of brood parasitism, because their early broods often fledge before cowbirds start to reproduce and because they can often rear cowbirds successfully together with their own young (Nice 1937, Smith 1981, Smith and Arcese 1994).

STUDY PERIOD AND AREAS

We studied Song Sparrows from March 1988 to August 1991, a period including four complete breeding seasons. We worked on two plots on Westham Island (12 km²), in the Fraser River Delta, British Columbia, Canada (123°18'W, 49°18'N). Westham is separated from the adjacent mainland and other nearby islands by 0.08–1.5-km wide tidal channels. Most of Westham Island is intensively farmed, but wetlands extend from northwestern Westham Island eastward along the south arm of the Fraser. The two plots were in the Reifel Waterfowl Refuge (50 ha, here termed "Reifel"), and the Alaksen National Wildlife Area (approximately 400 ha, here termed "Alaksen"). Both areas contained freshwater and brackish marshes, mud flats, upland dikes, wet meadows, ditches, and wooded swamps. Dike vegetation was dominated by scattered mature Douglas fir trees (*Pseudotsuga menziesii*), thickets of Himalayan blackberry (*Rubus procerus*), thistles (*Cirsium* sp.), and grasses. Dikes along the channels of the Fraser

River and beside drainage ditches were the principal breeding habitat of Song Sparrows. Two 60-m wide stretches of dike and surrounding vegetation were studied in detail. The plot at Reifel (650 m long, 3.9 ha) was bounded by wet meadows, sloughs, and shrub thickets; the Alaksen plot (1,450 m, 8.7 ha) was similar, but had smaller thickets of blackberry, and was partly bounded by brackish tidal marsh and planted fields. The Alaksen plot began 400 m north of the Reifel plot. We report data from these areas separately, mainly because sparrows at Reifel always had access to added food, which can influence Song Sparrow reproduction greatly (Arcese and Smith 1988). In 1988–1989, we supplied Reifel daily with added food (white millet) as part of a separate experiment (Rogers et al. 1991). Added food (millet and larger grains) also was supplied to birds by visitors to Reifel (but never to Alaksen) throughout the study. The positions and sizes of both study sites changed slightly from 1988 to 1989, but remained stable thereafter.

DEMOGRAPHIC DATA

Demographic data were collected using methods reported in detail by Smith (1981) and Arcese et al. (1992). Nearly all territorial males and most breeding females were individually color-banded. Territories of males were mapped each spring using the locations of singing perches and of disputes between neighbors. Unpaired male Song Sparrows are readily recognized from paired males in spring because they sing about ten times as often (J. Smith, unpubl. data). Each spring and summer, we located each female every 2–7 days and followed her to her nest site if her nervous behavior and conspicuous calling indicated active breeding. Sparrow nestlings were color-banded at about six days after hatching. We checked nests just before and after the young were expected to fledge to assess nest success. Four territories at Reifel could not be monitored completely because they contained very large blackberry thickets along ditches. We monitored these territories for fledged young being fed by color-banded parents, and estimated their numbers using begging calls. A few very late broods of sparrow young were produced at the Reifel site each August, and we did not monitor the fates of these broods closely. Late broods of sparrows on nearby Mandarte Island typically generate few recruits (Hochachka

1990), but this result might not apply to Westham.

Juvenile survival. To estimate post-fledging survival of sparrow young, we followed all fledglings at Alaksen closely from the time they left the nest until they became independent from their parents (at about 30 days of age) in 1989 and 1990. However, few sparrow young were produced on Westham Island (see below), thus estimates of survival from independence to breeding age were supplemented with similar data from the long-term study of Song Sparrows on Mandarte Island, 52 km distant (Arcese et al. 1992). Our data do not distinguish juvenile mortality from juvenile dispersal, but this is not an important source of error here because juvenile recruitment averaged almost an order of magnitude below adult survival (see Results).

Adult survival. Annual survival of adults was defined as presence of a color-banded bird in the study area from April 30 in year t to April 30 in year t + 1. Whereas this definition potentially confounds survival with movement, Song Sparrows usually show strong breeding philopatry (Nice 1937, Johnston 1956, Tompa 1964, Arcese 1989), although Weatherhead and Boak (1986) demonstrated otherwise. No breeders moved between sites at Westham Island or in the nearby Gulf Islands (Smith et al. 1996), and searches of distant habitat on Westham Island failed to reveal any non-philopatric adults. Birds on both Mandarte and Westham Islands continued to breed on the same territories even when their nests failed up to six times in succession. Disappearance of a banded adult from the population was therefore assumed to indicate death. A few adult birds that moved slightly between years, but remained within 200 m of the territory occupied the previous year, were considered to have survived. On Mandarte Island, about 0.2% of females moved to neighboring territories during the breeding season over a 20-year period (J. Smith, unpubl. data).

BROOD PARASITISM

We noted the frequency of brood parasitism by Brown-headed Cowbirds (proportion of all nests found with eggs or young that contained parasitic eggs or young). We excluded from the total sample unparasitized nests that failed during the laying period, and nests found with an incomplete brood of one or two host nestlings. Intensity of brood parasitism was measured as number of cowbird eggs per parasitized nest. Cowbird eggs resemble Song Sparrow eggs closely (Rothstein 1975), but they can be distinguished by color, size, and spot pattern in coastal British Columbia (Smith and Arcese 1994). Because of the close resemblance, however, we undoubtedly made some recognition errors. However, our records indicate only a few cases of "sparrow" eggs that hatched into cowbirds (and vice versa), suggesting this error was rare. In one year (1991), as part of a separate study, most host and cowbird eggs were marked individually with patterns of dots applied with a fine black felt-tip pen to assess rates of egg turnover ($n = 23$ and 36 at Reifel and Alaksen, respectively).

RATES AND CAUSES OF NEST FAILURE

We used the Mayfield method (Mayfield 1975, Hensler and Nichols 1981) to assess daily probabilities of nests failing or surviving. Nests were scored as either successful (producing one or more Song Sparrow fledglings), or failing (producing no sparrow fledglings, or only cowbird fledglings). Five causes of nest failure were distinguished: (1) complete predation (all eggs or young disappeared from the nest before the expected hatching and fledging dates), (2) abandonment after partial predation (some but not all sparrow eggs [rarely nestlings] disappeared from the nest due to unknown agent[s]), (3) abandonment after partial predation in nests containing cowbird eggs, (4) brood parasitism alone (nest fledged only cowbird young), and (5) other (nests flooded by tides, that tipped over, or that failed during heavy rain).

IDENTIFICATION OF NEST PREDATORS

To study the identity of egg predators, in 1991 and 1992 we placed dummy eggs in recently-used and relocated Song Sparrow nests, or in nests of grass made by us to resemble sparrow nests. These nests were placed in blackberry thickets and grass clumps in locations resembling those of natural sparrow nests. Thirty of 248 trials (12%) were conducted at Reifel, and the remainder at Alaksen. Nests were each supplied with two Song Sparrow-sized wax or plasticene eggs. Wax eggs were marked with a brown permanent felt pen, and plasticene eggs were painted with pale green and brown acrylic paint to resemble Song Sparrow eggs. Plasticene eggs (mean weight = 4.2 g) were about 1 g heavier than Song Sparrow eggs (3.1 g), and

wax eggs (2.3 g) were just under a gram lighter. Wax eggs were used only up to the middle of 1991.

To test if cowbirds pecked dummy eggs, experimental nests were placed out at three times relative to the laying periods of cowbirds: before cowbirds began to lay (9–21 April, 1992 only), during the cowbird laying period (9 May–17 July), and after cowbirds had ceased laying (24 July–6 August). Nests were checked up to four times at 2-day intervals, and untouched nests were moved to a second location after 6 days. If the nest contents were "depredated," the predator responsible was assigned immediately when evidence was clear, otherwise damaged eggs were brought to the laboratory and checked for tooth or beak marks, using a hand lens or binocular microscope. Mouse (probably deer mice, *Peromyscus maniculatus*) damage was scored from marks of two prominent and grooved incisor teeth, shrew damage from many fine tooth marks and the removal of patches of painted egg surface from plasticene eggs. Larger mammals (probably raccoons *Procyon lotor* and mink *Mustela vison*) chewed and bit eggs, deforming them completely. Both raccoons and mink were seen regularly in the study area; a mink was observed to prey upon a brood of sparrow nestlings on the study site in 1996 (C. Wright, pers. comm.). Bird damage was either small puncture marks (attributed to Marsh Wren, *Cistothorus palustris,* Picman 1977) or larger beak imprints. To help identify predators, we imprinted sample eggs using the teeth and beaks (in skulls) of potential predators and compared them with eggs damaged in the experiments.

AVIAN COMMUNITY CENSUS

We censused birds on both plots to identify potential avian nest predators and to estimate the relative abundances of hosts and cowbirds. We conducted 5-min point counts with a 50-m fixed radius at both sites three times each summer from 1989–1991. All censuses were done by JNMS.

RESULTS

THE AVIAN COMMUNITY

Based on point counts at Alaksen, the dominant songbird species in rank order of decreasing abundance were Marsh Wren, Song Sparrow, House Finch (*Carpodacus mexicanus*), American Robin (*Turdus migratorius),* and Red-winged Blackbird (*Agelaius phoeniceus*). At Reifel the order was Song Sparrow, House Finch, American Robin, Red-winged Blackbird, and Marsh Wren. Brown-headed Cowbirds were the sixth most abundant species at both sites. The ratios of the numbers of detections of cowbirds of both sexes to those of all suitable host individuals were 0.19 at Alaksen and 0.16 at Reifel. Suitable hosts were species that do not eject cowbird eggs, feed their nestlings insects, and do not nest in cavities.

The only common potential avian predator of eggs and young identified by the counts was the Marsh Wren. Rarer potential predators included Northwestern Crows (*Corvus caurinus*) and Bewick's Wrens (*Thryomanes bewickii*).

POPULATION DENSITY AND ADULT SURVIVAL

The mean density of breeding pairs at Reifel (5.6 pairs ha^{-1}) was over three times as high as at Alaksen (1.7 pairs ha^{-1}; Fig. 1A). Reifel had a markedly higher proportion (39% vs. 14%) of paired males over the four years pooled (Fig. 1B). Thus, numbers of territorial males differed less across sites than did numbers of breeding pairs. Annual survival of adult males was good for a small passerine at both sites, but was slightly higher on average at Reifel (mean over 3 years = 0.72) than at Alaksen (0.62). In contrast, adult female survival differed strongly among sites, being over three times as high at Reifel (0.57) as at Alaksen (0.17). The three high values (0.72, 0.62, and 0.57) are similar to slightly above median survival rates for Song Sparrows on Mandarte Island (Arcese et al. 1992). Survival in both sexes was poor for an unknown reason at Alaksen in 1990–1991. The weather in this winter was not extremely cold. Extreme cold is known to depress survival in Song Sparrows in southwestern British Columbia (Rogers et al. 1991). Only 37% of 30 males and none of 18 banded females survived.

Despite low return rates of adult females, the numbers of breeding birds in spring remained fairly stable over the four study years at both study sites. Whereas we cannot explain this synchrony, we suspect that it stems from annual changes in the size of the pool of dispersing yearlings.

HOST BREEDING AND CHRONOLOGY OF BROOD PARASITISM

We tested whether, as elsewhere on the B.C. coast, Song Sparrows have a period early in the
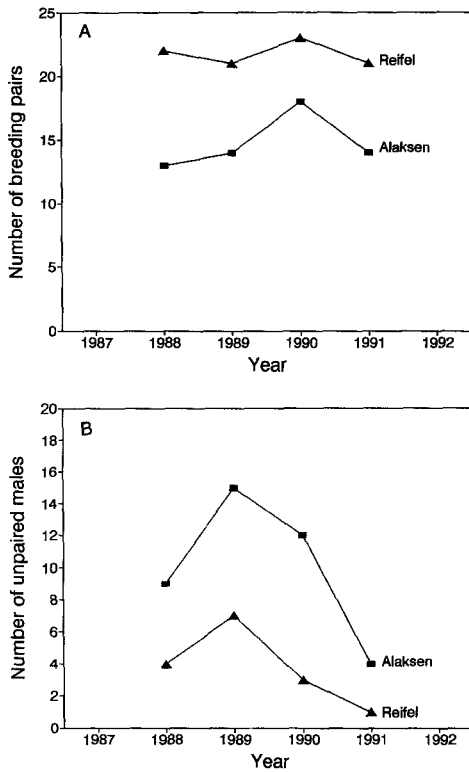
FIGURE 1. (A) Number of breeding pairs of Song Sparrows at Alaksen and Reifel during the four breeding seasons. (B) Number of unpaired male Song Sparrows at Alaksen and Reifel during the four breeding seasons.

season where they escape cowbird parasitism (Arcese et al. 1992, Smith and Arcese 1994). The first Song Sparrow eggs of the season were laid at about the same time at both sites, but last eggs were laid 14 days later on average at Reifel (Table 1). As a result, the sparrow breeding period averaged about 2 weeks longer at Reifel. Cowbirds began to lay about a week later on average than Song Sparrows at both plots, and the last cowbird eggs were laid a few days before the last sparrow eggs. As a result, the very earliest and latest Song Sparrow nests generally escaped parasitism (Fig. 2), but cowbird and sparrow laying seasons overlapped by over 90%.

Clutch sizes in unparasitized nests were similar at Reifel and Alaksen, averaging about 3 eggs per nest (Table 1). Parasitized nests had smaller clutch size (maximum number of eggs recorded in the incubation period) at both sites each year (by 0.37–0.67 eggs on average, Table 1) because of egg removal by female cowbirds. The frequency of parasitism was high in all years (0.48–0.73) and averaged over 0.60 at both sites (Table 1). The intensity of parasitism also was high at both sites, averaging about two cowbird eggs per parasitized nest (Table 1).

In 1991, we marked eggs individually in 59 Song Sparrow nests to assess rates of egg loss and turnover. Twelve of these nests failed by the first check after marking, and thus were discarded. Of the remaining 47 nests that were incubated, 18 (38%) maintained their original com-

TABLE 1. Mean values for reproductive performance of Song Sparrows at two sites on Westham Island, B.C. from 1988–1991. The first three values reported are simple arithmetic means ($\pm$ SE) for the four study years. All remaining values are means of annual site means ($n = 4$ years, $\pm$ SE). See text for definitions of some variables.

| Measure of performance	Alaksen	Reifel
Nests studied per year	46.5 $\pm$ 3.1	63.5 $\pm$ 5.6
Onset of laying	April 3 $\pm$ 2 days	April 6 $\pm$ 4 days
End of laying	July 18 $\pm$ 2 days	August 1 $\pm$ 3 days
Size of unparasitized clutches	3.07 $\pm$ 0.05	2.91 $\pm$ 0.05
Size of parasitized clutches	2.40 $\pm$ 0.14	2.54 $\pm$ 0.14
Proportion of nests parasitized	0.68 $\pm$ 0.03	0.60 $\pm$ 0.05
Cowbird eggs per parasitized nest	1.94 $\pm$ 0.12	2.02 $\pm$ 0.15
Proportion of nests succeeding	0.20 $\pm$ 0.03	0.22 $\pm$ 0.02
Proportion of nests failing (PF) from complete predation	0.33 $\pm$ 0.07	0.42 $\pm$ 0.02
PF from partial predation	0.07 $\pm$ 0.01	0.04 $\pm$ 0.02
PF from partial predation and brood parasitism	0.28 $\pm$ 0.06	0.24 $\pm$ 0.02
PF from brood parasitism	0.11 $\pm$ 0.02	0.05 $\pm$ 0.01
PF from other causes	0.04 $\pm$ 0.01	0.03 $\pm$ 0.01
Sparrows fledged per nest	0.33 $\pm$ 0.06	0.45 $\pm$ 0.07
Sparrows fledged per successful nest	1.73 $\pm$ 0.17	1.97 $\pm$ 0.14
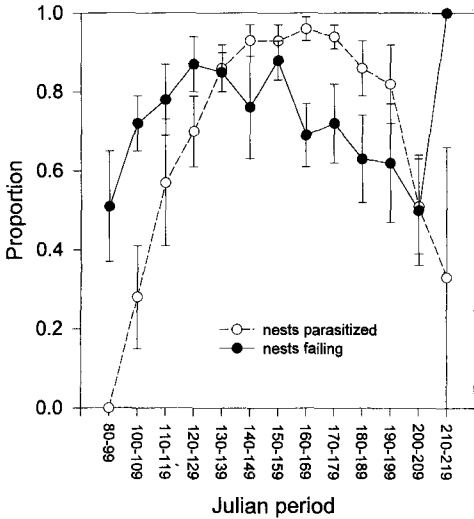
FIGURE 2.   Proportion of Song Sparrow nests failing, and proportion of Song Sparrow nests parasitized by Brown-headed Cowbirds, in 10-day intervals (Alaksen and Reifel pooled, years pooled). For example, all nests initiated (first egg laid) in the 10-day Julian interval of 100–109 (10–19 April) were classified as failed or succeeded, and as parasitized or unparasitized. The Julian interval of 80–99 is a 20-day interval when relatively few nests were initiated.

plement of eggs until they hatched or failed, 20 (43%) lost one or more marked eggs while remaining active, and 9 nests had a late cowbird egg added. Eggs were punctured in 5 of 47 of these active nests (11%). Thirty of the 117 marked sparrow eggs (26%) disappeared, and 9 of 72 cowbird eggs (13%) did so. Thus, over half of active nests suffered nonfatal disturbances during incubation that likely were caused by cowbirds. These rates of disturbance to eggs are much higher than on nearby Mandarte Island (Smith and Arcese 1994).

LOW NESTING SUCCESS AND CAUSES OF NEST FAILURE

The proportion of successful nests was consistently low each year for a small passerine (Martin 1992), ranging from a minimum of 12% at Alaksen in 1990, to a maximum of 28% at Reifel in 1991, with average values of about 20% at both sites (Table 1). The weekly nest failure rate varied within the season, with lower rates at the beginning and end of the year when the frequency of brood parasitism was reduced or zero (Fig. 2). Complete predation was the most frequent cause of nest failure in six of eight
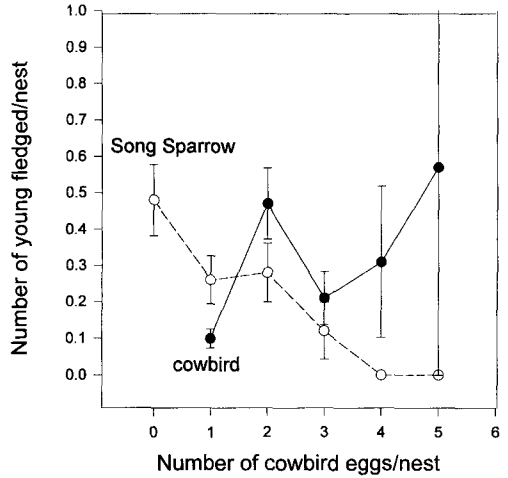

FIGURE 3.   Number of Song Sparrow and cowbird young fledged per nest in relation to number of cowbird eggs per nest (Alaksen and Reifel sites pooled).

year-site combinations, followed by partial predation combined with nest parasitism. Failure from parasitism alone was about twice as frequent at Alaksen as at Reifel (Table 1). We think this result is due to sampling error, as most other aspects of reproduction were very similar at the two sites. Alternatively, relatively higher intensity of parasitism at Alaksen was caused by similar cowbird numbers at the two sites combined with lower Song Sparrow (host) densities at Alaksen.

Increasing intensities of parasitism above three cowbird eggs per nest reduced fledgling success of Song Sparrows to zero (Fig. 3). In contrast, and to our surprise, the production of cowbird fledglings per nest did not decrease with additional cowbird eggs (Fig. 3). When complete predation, partial predation, and partial predation and brood parasitism were summed, nest predation was involved in the failure of 62–84% of nests per site and year. Similarly, brood parasitism was involved in 22–53% of all failures.

Daily rates of nest survival fluctuated closely together at Reifel and Alaksen, with low values in 1990 and a modest peak in 1991 (Fig. 4). 1990 also was the year with the lowest intensity of cowbird parasitism across both sites (1.66 cowbird eggs per nest, compared to over 1.93 eggs per nest in other years). This pattern is opposite to that expected if high levels of cowbird activity cause frequent nest failure (Arcese et al.
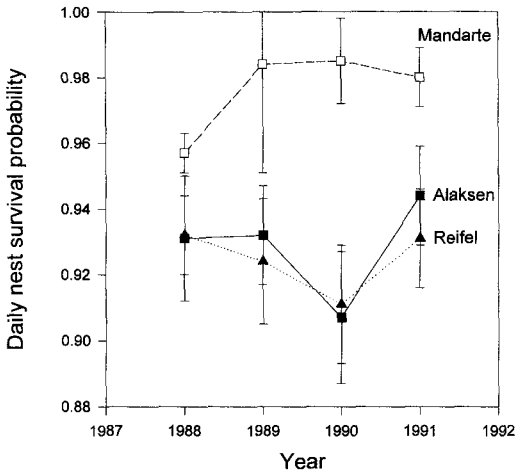
FIGURE 4. Daily nest survival rate for Song Sparrow nests in the four breeding seasons for Alaksen, Reifel, and Mandarte Island.

TABLE 2. Frequency of different nest predators attacking dummy eggs placed at different times in 272 previously-used Song Sparrow nests. Data for 1991 and 1992 are given separately. Early = before laying period of cowbird, middle = during cowbird laying, late = after cowbird laying ended (dates in text). The percentage is the proportion of all nests with a particular fate.

Identity of predator	Early		Middle		Late		Percent
	1991	1992	1991	1992	1991	1992	
Mouse	—	21	30	22	15	15	37.9
Shrew	—	2	12	11	12	11	17.6
Large mammal	—	1	2	2	3	2	3.7
Marsh Wren	—	4	0	3	0	0	2.6
Other avian	—	0	25	8	0	1	12.5
Unknown	—	1	4	9	1	10	9.2
Untouched	—	14	11	7	7	6	16.5
Total	—	43	84	62	38	45	100.0

1992, 1996). Nest survival rates at both sites always were well below the values seen on Mandarte Island (Fig. 4). In 1988, nests failed 1.6 times more often at Reifel and Alaksen than on Mandarte, and the difference was about three- to six-fold in other years. Mayfield estimates for nest survival for the entire nest period (26 days) for each site were 0.153 for Reifel, 0.159 for Alaksen and 0.442 for Mandarte Island for the four years combined.

We tested for an association between cowbird parasitism and high rates of nest failure. Nest failure was equally frequent in parasitized and unparasitized nests: 24 of 101 (24%) unparasitized nests produced sparrow or cowbird young, whereas 55 of 243 parasitized nests (23%) did so. Within parasitized nests, we did not find a strong relationship between nest failure and the number of cowbird eggs laid. In fact, nests with a single cowbird egg failed more often (108 of 126 nests, 86%) than nests with two or more cowbird eggs (90 of 127 nests, 71%). The poor success of singly-parasitized nests was caused by a high frequency of early nest failures (43% of singly-parasitized nests failed within 5 days compared to only 24% of multiply-parasitized nests). The simplest interpretation of this result is that many singly-parasitized nests received only one cowbird egg because they did not survive long enough to be parasitized more often. In summary, we found no evidence that preda-

tors, perhaps female cowbirds, selectively destroyed unparasitized clutches.

Most experimental nests (83.6%) were depredated within 6 days. The identity of nest predators, as judged from marks on damaged artificial eggs, is summarized in Table 2. Results for wax and plasticene eggs were very similar, and we pooled data for both types. Mice (probably mainly deer mice) damaged over a third of all eggs, and shrews caused the second greatest amount of damage. Both mice and shrews were consistent predators on experimental nests throughout the five study periods. Although other small rodents also occur on Westham Island, none are as arboreal or as omnivorous as the deer mouse. One of us (CMR) observed a deer mouse visiting a Song Sparrow nest at night; the nest failed from predation shortly thereafter. In contrast to these small mammals, birds caused nest failures of experimental nests only during the laying period of the cowbird (33 of 34 cases). In one case of puncture damage, a cowbird egg was laid in the experimental nest. Several clear beak imprints were left on plasticene eggs, and all but one of these were made by a medium-sized bird such as a cowbird or Redwinged Blackbird. The remaining mark was made by a larger crow-sized bird.

PRODUCTION OF FLEDGLINGS, INDEPENDENT YOUNG AND YEARLINGS

We now ask if this level of reproductive output is sufficient to replace losses to the population through adult mortality. We estimated directly the seasonal production of independent young at

TABLE 3. Production and survival of independent juvenile Song Sparrows in relation to numbers of adults disappearing at Reifel and Alaksen, 1988–1991. See text for estimation procedures.

Year/site	Estimated number of independent young reared	Number surviving to breed (max.)	Number surviving to breed (mean)	Number of adults disappearing in next year
1988 Alaksen	5.85	4.15	2.14	17
1988 Reifel	6.75	4.79	2.47	18
1989 Alaksen	8.00*	5.68	2.93	16
1989 Reifel	11.70	8.31	4.28	13
1990 Alaksen	2.00*	1.42	0.73	37
1990 Reifel	7.65	5.43	2.80	19
1991 Alaksen	5.85	4.15	2.14	No Data
1991 Reifel	9.00	6.39	3.29	No Data

* Actual number reared.

Alaksen in 1989 and 1990. In 1989, 14 female Song Sparrows produced 15 sparrow fledglings, 8 of which survived to independence, an average of 0.57 per female. In 1990, 18 females produced 7 fledglings and two independent young sparrows, an average of 0.11 per female. In addition to the 10 sparrows reared to independence (45% of those fledged), these same females also reared 20 cowbird fledglings over the two years, 9 of which survived to independence (45%).

To estimate annual production of independent young at Reifel, and in other years at Alaksen, we multiplied the average number of young fledged per site per year by 0.45, the average value observed at Alaksen in 1989–1990. We also estimated the probability that these independent young would survive to breeding age, using the maximum (0.710) and the mean (0.366) values for survival from independence to breeding age from 15 years of data from Mandarte Island (Arcese et al. 1992). These results are given in Table 3, along with the numbers of adult Song Sparrows disappearing at each site each year. Fledgling production alone fell below replacement levels in all periods, and estimates of the numbers of young surviving to breeding age were on average 7.0 (range 1.6 to 20.1) times less than the number of adults disappearing, using the maximum value for survival to one year of age. The shortfall in young production was approximately twice as great when we used the mean estimate of survival from independence to breeding age (Table 3). A small number of additional late-season young may have been reared at Reifel (see above), but even

if these had survived exceptionally well, they could not have accounted for more than 3–4% of the shortfall. Only nine locally-banded young actually gained breeding territories on the study sites, compared to over a hundred vacancies available. Thus, Song Sparrows at Westham Island reproduced at far below the rate required to replace themselves by local recruitment. Reproductive success of Song Sparrows generally is much higher (Nice 1937, Johnston 1956, Arcese et al. 1992). Song Sparrows at Westham also reproduced more poorly than did almost all Neotropical migrant species reviewed by Martin (1992).

REPRODUCTIVE SUCCESS IN THE ABSENCE OF BROOD PARASITISM

Cowbirds are recent immigrants to southwestern British Columbia, having arrived about 1955 (Rothstein 1994). It is therefore of interest to ask what the production of young Song Sparrows at Westham Island would be in the absence of cowbird parasitism (Table 3). For each year and site, we computed the value

$$RP = N_f \times A \times S_T \times F_{SN} \times S_{f-i} \times S_{i-b}$$

where:

RP is the production of potential breeding recruits in year X + 1

N_f is the number of breeding females per site in year X

A is the mean number of breeding attempts per female at that site in year X

S_T is the Mayfield estimator of total nest survival for unparasitized nests at the site in all 4 years (0.2312 at Reifel, 0.1737 at Alaksen)

F_{SN} is the mean number of fledglings reared from successful unparasitized nests over all 4 years (2.308 at Reifel, 1.833 at Alaksen)

S_{f-i} is the estimate of survival of fledglings from leaving the nest to independence from parental care used in Table 3 (0.45)

S_{i-b} is the maximum estimate of survival of independent young from independence to breeding age used in ·Table 3 (0.71)

According to these estimates of young production, about 40% more locally born young sparrows would have survived to breeding age in the absence of cowbird parasitism (a mean of 7.11 vs. 5.04 site^{-1} year^{-1}, $n = 8$). However, the estimated production of local recruits still averaged 58.5 $\pm$ 10.7% ($n = 6$ site-year combina-

tions) below the numbers required to fill local breeding vacancies. This calculation is strongly influenced by the low values of total nest success. If low nest success was partly due to predation on eggs and nestlings by cowbirds (see below), our estimates of young production in the absence of cowbirds may be too low, and the Song Sparrow population at Westham could really be self-sustaining in the absence of cowbirds. Only a cowbird removal experiment will resolve this issue.

We recognize a second possible source of error. A, the mean number of breeding attempts per female (for a given site and year), is probably not independent of the intensity of brood parasitism. To illustrate, if brood parasitism were especially high at a site in one year and nests that failed early in the nesting cycle (due to parasitism in whole or part) were quickly followed by renests, the contribution of that site/year combination to A would inflate its value and lead to an overestimate of annual productivity. We thus regard these productivity estimates as upper bounds.

DISCUSSION

CAUSES OF POOR REPRODUCTIVE SUCCESS IN SONG SPARROWS

We consider five possible causes of the poor reproductive success of Song Sparrows at Westham Island.

(1) High population density. High population density in Song Sparrows on Mandarte Island depresses reproductive success (Arcese et al. 1992) and creates a pool of nonbreeding male "floaters" (Smith and Arcese 1989). Sparrow population densities on Westham Island, however, fell below mean values found on nearby Mandarte Island by Arcese et al. (1992), and no nonbreeding floaters were detected. Furthermore, reproduction on Mandarte in 1988, a high density year, was much more successful than on Westham Island in any of the four study years. Within Westham Island, female densities were over three times as high at Reifel as at Alaksen, yet reproductive success was similarly low at both sites. In sum, whereas habitats on Westham differ from those on Mandarte, and effects of population density doubtless vary with resource abundance, we found little reason to believe that the poor reproductive performance of Song Sparrows at Westham Island was due to intraspecific competition for scarce resources.

(2) Insufficient food supply. The poor reproduction at both sites, and the poor female survival at Alaksen were unlikely to have been caused by insufficient food. The year-round addition of ad libitum food at Reifel did not lead to greater per-capita reproductive success there, and no breeding adults moved from Alaksen to Reifel, only 400–1,500 m distant. The few Song Sparrow nests that escaped predation and brood parasitism produced about two sparrow fledglings on average at both sites, about the mean value found on the nearby Mandarte Island at times of moderate breeding density (Arcese et al. 1992, 1996).

(3) Nest predation. Predation rates at both sites were extremely high, averaging 68% (sum of total predation plus partial predation and consequent desertion). This exceeds all values summarized for 36 species of Neotropical migrant passerines by Martin (1992). Daily nest predation rates in heavily-parasitized songbird populations in Illinois (Robinson 1992, Robinson et al. 1995) were similar to those noted here. In our experiments, deer mice, and to a lesser degree shrews and birds, were the principal predators on dummy eggs. We were surprised to find shrews playing such a large role as predators. Up to six species of shrew occur at Alaksen. On Mandarte Island, where daily nest failure rates were much lower (Fig. 4), there are no shrews. Deer mice also are abundant on Mandarte Island, but they have many alternative food sources to sparrow nest contents in the large seabird colonies there. Shrews and mice probably have trouble breaking Song Sparrow eggshells, and their role at Westham Island may have been overestimated by the experiments with dummy nests because plasticene and wax eggs can be easily gripped by mammals with small jaws. Song Sparrows also may be large enough to fight off predation attempts by these small mammals. Whether these small mammal species commonly prey on real Song Sparrow nests remains uncertain (see also Haskell 1995).

The identity of the larger avian predators could not be inferred directly from egg damage on real Song Sparrow nests, but point censuses showed cowbirds and Red-winged Blackbirds were common locally, and may have caused beak imprints of similar size to those seen on dummy eggs. Both cowbirds and red-wings are much less abundant on Mandarte Island.

The temporal association of egg damage by

birds with the cowbird laying period suggests that cowbirds caused some nest failures directly. We know from parasitic laying in one experimental nest, that cowbirds visited dummy nests. Also, variation in parasitic activity by cowbirds among years on Mandarte Island correlates positively with nest failure rates in Song Sparrows, and sparrow eggs and young on Mandarte survived better in parasitized nests than in unparasitized nests (Arcese et al. 1996). Arcese et al. (1992, 1996) hypothesized that female cowbirds prey on host nests that are too far advanced to parasitize successfully, in order to create future laying opportunities for themselves, and that predation by cowbirds contributes to low nesting success in songbird populations. We did not find support for a key prediction of this hypothesis, i.e., better survival of eggs and young in parasitized sparrow nests. In further disagreement with the hypothesis, we found a drop in nest failure rates in the year of lowest cowbird activity. We did, however, find evidence of scramble competition among female cowbirds (frequent removal and turnover of host and parasite eggs in sparrow nests). Thus, a high rate of intraspecific competition for host nest space in some years may swamp any future benefits gained by preying selectively on late host nests.

(4) *Brood parasitism by cowbirds.* Cowbird parasitism of natural nests was frequent (mean frequency, 64%) and intense (mean of about 2 cowbird eggs per nest). These levels are both high compared to those reported previously in Song Sparrows (Nice 1937, Arcese et al. 1992) and also high relative to rates in nests of most Neotropical migrants (Martin 1992). About 8% of all sparrow nests producing fledglings reared only cowbird young. Other nests contained up to five cowbird eggs, and these were frequently deserted or preyed upon. Increasingly intense parasitism reduced nestling survival of Song Sparrows to zero above three cowbird eggs per nest, but had surprisingly little effect on nesting success of cowbirds. Even nests containing four to five cowbird eggs fledged an average of 0.4 cowbirds, almost as many sparrows (0.48) as were fledged from unparasitized nests.

Cowbird:host ratios were in the 15–20% range on Westham Island. Levels of this ratio above 0.10 are associated with high rates of parasitism in host communities elsewhere (Donovan et al., in press, Thompson et al., in press). On Westham Island, we found a high frequency of parasitism combined with frequent predation on eggs and nestlings. When we estimated the contribution of brood parasitism alone to reproductive failure, it was weak compared to the effect of predation.

SONG SPARROWS ON WESTHAM ISLAND: A POPULATION SINK?

Song Sparrows have been common on the study area for over 20 years (Knapton and Krebs 1974). Although local production of sparrow young on the territories we studied was inadequate to replace annual disappearance of adults, enough sparrows joined the population each year to keep numbers stable (Fig. 1). All but nine recruits (8%) were unbanded birds of unknown origin. In contrast, on nearby Mandarte Island, over 95% of recruits hatched locally (Arcese et al. 1992). The unbanded recruits at Alaksen could have come from nearby or more distant sites. We studied other territories at Reifel and Alaksen, and found very low levels of nesting success (unpubl. data). Thus we think it likely that the immigrants came from distant sites.

Westham Island is apparently a population "sink" (Pulliam 1988), where landscape-level effects have rendered a protected reserve habitat almost irrelevant to the regional population dynamics of one of the two most common songbirds there. Song Sparrows at the Alaksen National Wildlife Area apparently can only persist there because of immigration from "source" habitats. Indeed, Westham Island may always have been a sink for Song Sparrows, but historical data are lacking. Such a metapopulation viewpoint (Fahrig and Merriam 1994) also has proven useful in studies of forest songbirds (Villard et al. 1992, Brawn and Robinson 1996).

In our study, we assumed that disappearing adults had died, because we detected no breeding dispersal beyond a few local (< 200 m) shifts of territories by females. If adults that experienced nest failures frequently dispersed to breed elsewhere in the same summer, as found in eastern Song Sparrows by Weatherhead and Boak (1986), our estimates of survival might be low. However, the fact that female sparrows renested locally despite repeated failures suggests that dispersal within seasons was uncommon. We cannot dismiss the possibility of between-year movements. Whereas no breeding dispersal was detected between years, only short movements would have been detected by our meth-

ods. Even if frequent adult dispersal did occur between years, this does not alter the conclusion that Westham Island acts as a population sink, as adult loss rates greatly exceeded local recruitment of juveniles, and Song Sparrows, like most small passerines, are so short-lived that their lifetime fitness is greatly reduced by a single unsuccessful breeding season (Newton 1989).

High rates of nest predation and brood parasitism may partly underlie the nation-wide, long-term population decline of the Song Sparrow in Canada. Breeding Bird Survey of Canada data (reported by permission of the Canadian Wildlife Service [CWS]) indicate that the Song Sparrow has declined over the long-term (1966–1994) in Canada as a whole (% change/year = −1.50, $P < 0.01$ in linear regression), as well as in each of the four main physiographic regions of Canada recognized by the CWS. We demonstrated that nest predation and brood parasitism reduced recruitment well below annual mortality at two sites only; further data on Song Sparrows from other geographic regions are necessary to test this hypothesis more completely.

ACKNOWLEDGMENTS

LITERATURE CITED

ARCESE, P. 1989. Territory acquisition and loss in male Song Sparrows. Anim. Behav. 37:45–55.

ARCESE, P., AND J. N. M. SMITH. 1988. The effects of population density and supplemental food on reproduction in Song Sparrows. J. Anim. Ecol. 56:119–136.

ARCESE, P., J. N. M. SMITH, AND M. I. HATCH. 1996. Nest predation by cowbirds and its consequences for passerine demography. Proc. Natl. Acad. Sci. 93:4608–4611.

ARCESE, P., J. N. M. SMITH, W. M. HOCHACHKA, C. M. ROGERS, AND D. LUDWIG. 1992. Stability, regulation and the determination of abundance in an insular Song Sparrow population. Ecology 73:805–822.

BENT, A. C. 1968. Life histories of North American cardinals grosbeaks, buntings, towhees, finches, sparrows, and allies. U.S. Natl. Mus. Bull., Washington, DC. Reprinted by Dover Press, New York.

BÖHNING-GAESE, K., M. L. TAPER, AND J. H. BROWN. 1993. Are declines in North American insectivorous landbirds due to causes on the breeding range? Conserv. Biol. 7:76–86.

BRAWN, J. D., AND S. K. ROBINSON. 1996. Source-sink census data may complicate the interpretation of long-term census data. Ecology 77:3–12.

DONOVAN, T. M., F. R. THOMPSON III, AND J. FAABORG. In press. Ecological trade-offs and the influence of scale on Brown-headed Cowbird distribution. In T. Cook, S. K. Robinson, S. I. Rothstein, S. G. Sealy, and J. N. M. Smith [eds.], Ecology and management of cowbirds. Univ. Texas Press, Austin, TX.

FAHRIG, L., AND G. MERRIAM. 1994. Conservation of fragmented populations. Conserv. Biol. 8:50–59.

HASKELL, D. G. 1995. A reevaluation of the effects of forest fragmentation on rates of bird-nest predation. Conserv. Biol. 9:1316–1318.

HENSLER, G. L., AND J. D. NICHOLS. 1981. The Mayfield method of estimating nesting success: a model, estimators and simulation results. Wilson Bull. 93:42–53.

HOCHACHKA, W. M. 1990. Seasonal decline in reproductive success of the Song Sparrow. Ecology 71:1279–1288.

JAMES, F. C., C. E. MCCULLOUGH, AND D. E. WIEDENFELD. 1996. New approaches to the analysis of population trends in landbirds. Ecology 77:13–27.

JOHNSTON, D. W., AND J. M. HAGAN III. 1992. An analysis of long-term breeding bird censuses from eastern deciduous forests, p. 75–84. In J. M. Hagan III and D. W. Johnston [eds.], Ecology and conservation of Neotropical migrant landbirds. Smithson. Inst. Press, Washington, DC.

JOHNSTON, R. F. 1956. Population structure in salt marsh Song Sparrows. Part 2. Density, age structure and maintenance. Condor 58:254–272.

KNAPTON, R. W., AND J. R. KREBS. 1974. Settlement patterns, territory size and breeding density in the Song Sparrow (Melospiza melodia). Can. J. Zool. 52:1413–1420.

KREBS, C. J. 1994. Ecology: the experimental analysis of distribution and abundance. 4th ed. Harper and Row, New York.

MARTIN, T. E. 1992. Breeding productivity considerations: What are the appropriate features for management?, p. 455–473. In J. M. Hagan III and D. W. Johnston [eds.], Ecology and conservation of Neotropical migrant landbirds. Smithson. Inst. Press, Washington, DC.

MAYFIELD, H. 1975. Suggestions for calculating nest success. Wilson Bull. 87:456-466.

MÖLLER, A. P. 1991. Clutch size, nest predation, and distribution of avian unequal competitors in a patchy environment. Ecology 72:1336–1349.

NEWTON, I. [ed.] Lifetime reproduction in birds. Academic Press, London.

NICE, M. M. 1937. Studies in the life history of the

Song Sparrow. Part I. Trans. Linn. Soc. New York 4:1–247.

PICMAN, J. 1977. Destruction of eggs by the Long-billed Marsh Wren (Telmatodytes palustris palustrus). Can. J. Zool. 55:1914–1920.

PULLIAM, H. R. 1988. Sources, sinks and population regulation. Am. Nat. 132:652–661.

ROBBINS, C. S., J. R. SAUER, R. S. GREENBERG, AND S. DROEGE. 1989. Population declines in North American birds that migrate to the Neotropics. Proc. Natl. Acad. Sci. 86:7658–7662.

ROBINSON, S. K. 1992. Population dynamics of breeding Neotropical migrants in a fragmented Illinois landscape, p. 408–418. In J. M. Hagan III and D. W. Johnston [eds.], Ecology and conservation of Neotropical migrant landbirds. Smithson. Inst. Press, Washington, DC.

ROBINSON, S. K., S. I. ROTHSTEIN, M. C. BRITTINGHAM, L. J. PETIT, AND J. A. GRZYBOWSKI. 1996. Ecology and behavior of cowbirds and their impact on host populations, p. 438–460. In T. E. Martin and D. M. Finch [eds.], Ecology and management of Neotropical migratory birds. Oxford Univ. Press, New York.

ROBINSON, S. K., F. R. THOMPSON III, T. M. DONOVAN, D. R. WHITEHEAD, AND J. FAABORG. 1995. Regional forest fragmentation and the nesting success of migratory birds. Science 267:1987–1990.

ROGERS, C. M., J. N. M. SMITH, W. M. HOCHACHKA, A. L. E. V. CASSIDY, P. ARCESE, AND D. SCHLUTER. 1991. Spatial variation in winter survival of Song Sparrows. Ornis Scand. 22:387–395.

ROTHSTEIN, S. I. 1975. An experimental and teleonomic investigation of avian brood parasitism. Condor 77:250–271.

ROTHSTEIN, S. I. 1994. The cowbird's invasion of the far west: history, causes, and consequences experienced by host species. Stud. Avian Biol. 15:301–315.

SMITH, J. N. M. 1981. Cowbird parasitism, host fitness and age of the host female in an island population of Song Sparrows. Condor 83:152–161.

SMITH, J. N. M., AND P. ARCESE. 1989. How fit are floaters? Consequences of alternative territorial behaviors in a non-migratory sparrow. Am. Nat. 133:830–845.

SMITH, J. N. M., AND P. ARCESE. 1994. Brown-headed Cowbirds and an island population of Song Sparrows: a 16-year study. Condor 96:916–934.

SMITH, J. N. M., AND I. H. MYERS-SMITH. In press. Spatial variation in parasitism of Song Sparrows by Brown-headed Cowbirds. In S. I. Rothstein and S. K. Robinson [eds.], Brood parasites and their hosts. Essays in memory of Herbert Friedmann. Oxford Univ. Press, Oxford.

SMITH, J. N. M., M. J. TAITT, C. M. ROGERS, L. KELLER, P. ARCESE, A. L. E.V. CASSIDY, AND W. M. HOCHACHKA. 1996. A metapopulation approach to the population biology of the Song Sparrow Melospiza melodia. Ibis 138:120–128.

THOMPSON, F. R. III, S. K. ROBINSON, T. M. DONOVAN, J. FAABORG, AND D. R. WHITEHEAD. In press. Biogeographic, landscape, and local factors affecting cowbird abundance and host parasitism levels. In Robinson, S. I. Rothstein, S. G. Sealy, and J. N. M. Smith [eds.], Ecology and management of cowbirds. Univ. Texas Press, Austin, TX.

TOMPA, F. S. 1964. Factors determining the numbers of Song Sparrows Melospiza melodia (Wilson) on Mandarte Island, B.C. Canada. Act. Zool. Fenn. 109:3–73.

VILLARD, M-A., K. FREEMARK, AND G. MERRIAM. 1992. Metapopulation theory and Neotropical migrant birds in temperate forests: an empirical investigation, p. 474–482. In J. M. Hagan III and D. W. Johnston [eds.], Ecology and conservation of Neotropical migrant landbirds. Smithson. Inst. Press, Washington, DC.

WEATHERHEAD, P. J., AND K. A. BOAK. 1986. Site infidelity in Song Sparrows. Anim. Behav. 34:1299–1310.