

DEMOGRAPHY OF BROWN-HEADED COWBIRDS AT DELTA MARSH, MANITOBA

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ABSTRACT.—Available estimates of demographic parameters for Brown-headed Cowbirds (*Molothrus ater*) vary geographically. However, few estimates are based on long-term studies of marked individuals. We conducted a mark–recapture study on the population of cowbirds at Delta Marsh, Manitoba during the 1993–1998 breeding seasons. We estimated annual survival, breeding site fidelity, and sex ratio, and compared those parameter estimates to other populations of Brown-headed Cowbirds. The Delta Marsh population had higher adult survival (male 90.1%; female 69.6%) and breeding site fidelity (males 66.9%, female 59.5%) than reported for other populations, and the sex ratio was significantly different from unity (1.9 males:1 female). We suggest that differences in survival and breeding-site fidelity between the Delta Marsh population and others may be due to differences in methods used to calculate parameter estimates. In contrast, variation in sex ratios is likely real and due to differences in the local ecological conditions. In our population, high survivorship and breeding-site fidelity may lead to low recruitment of new birds into the resident population and intense competition for limited breeding opportunities. The highly male biased sex ratio may result in strong sexual-selection pressure on males competing for the limited breeding opportunities. Those circumstances have implications for the social behavior and mating system of cowbirds. Received 8 September 1999, accepted 31 August 2000.

KNOWLEDGE OF A SPECIES' DEMOGRAPHY is essential for identifying the selective pressures that influence individual social and reproductive behaviors. For example, helping in cooperatively breeding birds may have evolved as a response to a lack of breeding opportunities caused by high survival of breeding adults and limited breeding habitat (Emlen 1982). Similarly, variation in sex ratio may intensify sexual-selection pressures acting on individuals of each sex through reproductive competition (Emlen and Oring 1977). Clearly, detailed data on key demographic variables such as survival, site fidelity, and sex ratio are essential for the interpretation of the ecological and evolutionary basis of observed social and reproductive behaviors.

Brown-headed Cowbirds (*Molothrus ater*) are obligate brood parasites. Females lay their eggs in nests of other passerine species (hosts) and relinquish all parental care to the hosts. Because Brown-headed Cowbirds (hereafter "cowbirds") are not limited by the energetic constraints of parental care, their social behav-

ior may be strongly influenced by local demographic conditions (Yokel 1986). Studies of geographically separate populations of cowbirds have led to contradictory descriptions of reproductive strategies and social behaviors, likely due to different resource distribution patterns and ecological variables (Ankney and Scott 1982, Rothstein et al. 1986, Yokel 1989a). Estimates of demographic parameters also vary across geographically separate cowbird populations and there is corresponding variation in descriptions of social mating systems. For example, in populations characterized by low cowbird density and high host-nest density, male mate guarding may result in socially monogamous mating relationships (Teather and Robertson 1986, Yokel 1989a). In contrast, high cowbird density may decrease organization within dominance hierarchies, which may result in a promiscuous social mating system (Yokel 1989a). However, most conclusive studies of color-marked birds (Darley 1971, 1982; Dufty 1982b, Teather and Robertson 1985, 1986; Yokel 1986, Alderson et al. 1999) generally indicate that cowbirds are nonterritorial and primarily socially monogamous (but see Elliott 1980).

Despite the potential for variation in cowbird demographic parameters and the potential val-

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ue of that information for interpreting cowbird social behavior, detailed demographic studies have not been reported. Most available demographic estimates are based on one or two years of data. Additionally, it is difficult to make comparisons between existing studies because of variability in methodologies used (mark-recapture vs. observation) and a lack of robust statistical analyses of the data collected.

Here we summarize the findings of a six-year investigation of the demography of a single population of individually marked cowbirds at Delta Marsh. We report estimates of site fidelity, survivorship, and longevity, plus descriptions of the sex and age structure of the population. Our findings suggest that cowbirds are relatively long lived and that recruitment into the breeding population is low. We discuss the implications of those results and suggest how population demography may have influenced cowbird social behavior.

METHODS

Study site and population.—We studied cowbirds at the University of Manitoba Field Station (Delta Marsh), located west of the Assiniboine River Diversion on the south shore of Lake Manitoba (98°23'W, 50°11'N). The study site (~60 ha) consisted of a 2 km strip of habitat running parallel to the lakeshore, composed of forested dune ridge (average width ~80 m) and an adjacent cattail (*Typha* sp.) marsh (~200 m wide). Detailed descriptions of the habitat are provided by MacKenzie et al. (1982) and Weatherhead (1989). Delta Marsh is known as an area of high productivity for breeding birds (MacKenzie et al. 1982, S. G. Sealy unpubl. data).

Data collection.—We collected mark-recapture and observational data throughout the 1993–1998 breeding seasons. Delta Marsh is located near the northern limit of the cowbird breeding range in Manitoba. Cowbirds arrived there later and the breeding season was shorter than reported at other areas (Lowther 1993). Generally, cowbirds returned to the study area in mid-May (Woolfenden 2000). In all years, the first cowbird egg was found on the study area in late May (range 18 May to 31 May; mean start date: 27 May), marking the beginning of the breeding season. Egg laying lasted for 31 (SD of ± 8) days, typically ending in late June or early July (range 19 June to 5 July; mean end date: 25 June) (Woolfenden 2000). We began trapping cowbirds prior to the egg-laying period (mean start date 15 May ± 3.7 days [SD]) and continued for 47 ± 8.7 days (SD) (mean end date 30 June ± 5.8 days [SD]). We began collecting observations of marked birds several days prior to trapping.

Adult cowbirds were trapped daily between 0600 and 2200 (CST) in tunnel traps. Traps (100 \times 60 \times 25 cm) were baited with cracked corn and placed on the ground throughout the study area at 14 trapping sites (hereafter "central trap sites"). Central trap sites were located in both ridge and marsh habitats, and number of sites and their locations remained consistent throughout the study. However, not all trap sites were operated simultaneously because we did not have enough traps. Traps were systematically rotated among trap sites to maximize chances that all cowbirds on the study site were trapped and marked. In 1993–1995, six traps were rotated among central sites throughout the trapping season. Trap effort was increased in 1996–1998 (Table 1) by increasing number of traps operated simultaneously rather than increasing number of central trap locations. Eight additional trap sites (referred to as "peripheral sites") were established outside the study site in 1997 and 1998 to increase number of adult cowbirds captured for a concurrent study of the genetic mating system.

At first capture, individual cowbirds were fitted with a unique combination of three plastic color bands and a numbered aluminum band issued by the U.S. Fish and Wildlife Service. Male cowbirds were aged as either second-year (SY, first calendar year after hatching) or after-second-year (ASY, at least two years post-hatching) on the basis of plumage characteristics (Selander and Giller 1960, Ortega et al. 1996). For all subsequent captures, we recorded band numbers, trap site, and time of capture. We recorded observations of marked birds while walking transects through the study site and also opportunistically while searching for nests and trapping. Observation effort varied among breeding seasons.

Population structure.—Data concerning presence of individual cowbirds were collected in the central traps and from observations of marked individuals on the study area. That information was summarized for each year to estimate minimum length of time that each cowbird was present on the study site. We used the within-year capture sighting summaries to distinguish between residents and nonresidents (birds that move through the area during migration or while seeking breeding opportunities but do not remain to breed). Individuals estimated to be on the study area for five or more days within a single breeding season were categorized as residents (Darley 1971, Yokel 1989a). All other individuals were considered nonresidents. Data collected in peripheral traps were not used to determine residency because birds trapped there may not have been part of the resident population. However, trap records did indicate that many resident birds used both central and peripheral traps, indicating that activity ranges of some residents were not wholly contained within the study area.

TABLE 1. Numbers of cowbirds trapped and trap effort at Delta Marsh, 1993–1998. Table includes data from both central and peripheral traps. Trap effort is the number of traps operating multiplied by the number of hours operated. Totals of each sex trapped include both unbanded (not previously trapped on the study site) and banded birds (returned birds trapped in previous years). Percentages of unbanded birds of each sex are presented as the percentage of all birds trapped in a given breeding season.

Year	Trap effort (trap hours)	Number of traps	Females trapped		Males trapped	
			Total ^a	Unbanded	Total ^a	Unbanded
1993	500	6	50	N/A	102	N/A
1994	528	6	31	19 (61%)	69	31 (45%)
1995	801	6	63	40 (63%)	114	74 (65%)
1996	2538	12	64	44 (69%)	101	64 (63%)
1997	2904	20	101	69 (69%)	179	115 (65%)
1998	2557	20	85	68 (80%)	152	86 (57%)
Mean ± SD	1638 ± 1138.9		65.7 ± 24.8	48.0 ± 21.0 (73.1%)	119.5 ± 39.6	74.0 ± 30.7 (61.9%)

^a Totals do not include birds that were observed on study site but not trapped; total numbers of birds captured and sighted are given in Tables 2, 3, and 4.

As bait and other birds in the traps likely attract cowbirds, we were concerned that individuals from outside the study area might have been attracted to traps on the study area, possibly to access the supplemental food or potential mates. If those individuals were actually breeding off-site, but frequented traps on a regular basis, we may have incorrectly categorized them as residents. To investigate that possibility, we observed and trapped cowbirds outside the study area periodically during breeding seasons to assess number of banded birds found off-site. Cowbirds were trapped at two locations, one approximately 8 km east of the eastern edge and the second approximately 800 m west of the western most edge of the study area (G. McMaster, J. C. Lorenzana, and S. G. Sealy unpubl. data) in 1995 to 1998. Trapping took place several times a week for 2–3 weeks during the cowbird laying season. Only 1–2 already banded, resident birds per year were detected outside the study area. Those anecdotal data suggest that central traps were used by two types of cowbirds. Residents, whose activity areas were largely contained within the study site, and transients, who moved through the area during migration.

By limiting the residency criteria to birds captured or sighted on the study area for a minimum of five days, and excluding birds that were only captured or sighted on the periphery of the study area, we attempted to limit the effects of nonresident birds on our estimates of demographic parameters. Inclusion of nonresident birds in our resident data set would have inflated estimates of population size, biased estimates of return rates, and possibly skewed sex ratios. Therefore, all results reported in this paper are based on analyses of resident birds only, unless otherwise stated. Results are presented as mean ± SD, unless otherwise indicated. Significance is at the $P = 0.05$ level and table-wide significance is tested using the sequential Bonferroni correction (Rice 1989).

Age and sex structure.—We estimated breeding-site fidelity of the population by determining percentage of the resident population that was previously banded. Because male birds can be accurately aged in the year following hatching (Selander and Giller 1960), we were also able to determine age structure of the resident male population. That analysis was not done for females because it is difficult to distinguish SY and ASY females accurately (but see Darley 1971).

Number of individuals in each sex and male-age class in resident and the nonresident populations were determined for each year. Contingency table analyses were used to determine whether (1) the age ratios (ASY vs. SY) of resident and nonresident males were significantly different; (2) the sex ratio of the resident and nonresident populations differed from unity; and (3) the sex ratio of the resident population was significantly different from the nonresident population.

TABLE 2. Summary of the total (resident + nonresident) and resident populations over the 6 years of the study. These data are derived from both central traps and observations. It shows the total number of birds present annually, the number of resident birds present annually, and the mean \pm SD number of days a resident bird was present on the study site (based on the dates of first and last capture or sighting). Return percentages indicate the percentage of the resident population in a given year that is made up of returning birds.

Year	Total population size ^a (proportion of nonresidents)	No. of resident birds ^a	Mean no. days residents were on study site	No. of days residents were on study site (range)	Return percentages (no. of returned birds)
Males					
1993	102 (0.44)	57	22.5 \pm 13.2	5–52	N/A
1994	82 (0.34)	54	23.8 \pm 15.8	5–54	75.9% (41)
1995	196 (0.55)	88	24.8 \pm 14.9	5–52	60.2% (53)
1996	121 (0.63)	45	22.5 \pm 13.2	5–49	68.9% (31)
1997	197 (0.58)	82	22.2 \pm 12.3	5–47	45.1% (37)
1998	187 (0.64)	68	30.6 \pm 15.2	5–52	76.5% (52)
Mean \pm SD	138.7 \pm 46.7	65.7 \pm 16.7	24.4 \pm 3.2		65.6% (42.8)
Females					
1993	50 (0.44)	28	24 \pm 11.8	5–43	N/A
1994	39 (0.36)	25	28 \pm 15.2	5–52	48.0% (12)
1995	75 (0.44)	42	24 \pm 12.8	5–50	57.1% (24)
1996	68 (0.53)	32	25 \pm 14.6	5–51	56.3% (18)
1997	101 (0.62)	38	21 \pm 11.0	5–46	40.5% (15)
1998	88 (0.58)	37	24 \pm 15.3	5–50	27.0% (10)
Mean \pm SD	69.7 \pm 23.2	33.6 \pm 6.5	24.3 \pm 2.1		46.6% (15.6)

^a These values are based on both capture and sighting data.

Survival.—Encounter histories for all individuals were summarized over 6 breeding seasons. Because not all individuals were captured every year, it was necessary to use capture–recapture methodologies (Cormack 1964, Jolly 1965, Seber 1965, Lebreton et al. 1992) to estimate probability of survival and return to the study area. Capture–recapture analyses provide separate estimates of survival probability (ϕ , the probability that an individual survives from one year to the next regardless of whether or not it is recaptured or resighted) and recapture–resighting probability (p , the probability that a bird will be recaptured or resighted given that it is alive). That approach accounts for surviving individuals that are not recaptured or resighted in every year.

Data analysis followed the basic mark–recapture methodology outlined by Lebreton et al. (1992). Briefly, a general model that considers all factors suspected to affect survival and recapture–resighting is constructed. The model is verified and then progressively simpler (less parameterized) models are fit to the data. Selection of the best-fit (most parsimonious) model is based on minimization of Akaike's Information Criteria (AIC, Akaike 1985, Lebreton et al. 1992), and that model is then used to estimate survival and recapture probabilities. Finally, likelihood ratio (LR) tests can be used to test effects of specific factors (e.g. sex, relative age, and year) on survival and recapture probabilities. Those analyses were

conducted with the program MARK (G. C. White unpubl.). Model notation follows Lebreton et al. (1992), where each parameter (ϕ = survival, p = recapture–resighting) included in the model is listed with the corresponding effects on that parameter indicated by subscripts (a = relative age; s = sex; t = year). Bootstrap goodness-of-fit testing (GOF) was used to test the fit of the data to the global (most parameterized) model.

RESULTS

Population structure.—A summary of the total number of individuals trapped annually and trap effort is shown in Table 1. Over six breeding seasons, 469 males and 290 females were banded during 9,828 h of trapping. On average, about 50% of all males and 50% of all females that were captured or sighted on the study site in any breeding season were residents (Table 2). Total number of birds captured or sighted (residents + nonresidents) was consistently greater in the last four years of the study, likely due to greater trap effort in those years. Number of residents also fluctuated, but not consistently with respect to trap effort (Tables 1 and 2). For example, numbers of male and female

TABLE 3. Numbers and proportions (indicated in parentheses) of males in each age category (ASY = at least two calendar years after hatch; SY = first year after hatch) for the resident and nonresident populations.

	Resident population ^a		Nonresident population ^a		χ^2 -value	P-value ^b
	ASY	SY	ASY	SY		
1993	49 (0.86)	8 (0.14)	23 (0.51)	22 (0.49)	14.71	0.0001
1994	50 (0.93)	4 (0.07)	22 (0.79)	6 (0.21)	3.39	0.066
1995	73 (0.83)	15 (0.17)	84 (0.78)	24 (0.22)	0.82	0.366
1996	38 (0.84)	7 (0.16)	48 (0.63)	28 (0.37)	6.23	0.012
1997	57 (0.70)	25 (0.30)	58 (0.50)	57 (0.50)	7.17	0.007
1998	60 (0.88)	8 (0.12)	76 (0.64)	43 (0.36)	12.96	0.0003
Mean	53.4 (0.83)	11.2 (0.17)	51.8 (0.64)	30.0 (0.36)		

^a These values are based on both capture and sighting data.

^b Contingency table analyses of the ratios of ASY and SY males in the resident and nonresident populations.

residents decreased in 1996 despite increased trap effort. However, as number of traps increased, proportion of the male and female populations made up of nonresidents tended to increase (Table 2). Those trends suggested that increased effort increased detection of nonresidents. The time elapsed between an individual's first and last sighting was 24.4 ± 3.2 days for males and 24.3 ± 2.1 days for females (Table 2), which is much higher than the minimum duration of five days designated by our criterion.

On average, 65.6% of resident males and 46.6% of resident females were banded in previous years (returns) (Table 2). Male returns were lowest (45%) in 1997 and female returns were low in 1997 (40.5%) and 1998 (27.0%). Using data from Tables 1 and 2, we estimated the number of new birds recruited into the resident population in a typical year. For each sex, the average number of returned birds (Table 2) over all years of the study was subtracted from the average number of resident birds (Table 2) to estimate the number of new birds recruited into the resident population annually. Using that calculated value, we determined percentage of the total number of new birds on average (Table 1) that were recruited into the resident population. That estimate suggests that typically only 30% of the new males and 38% of the new females detected will be recruited into the resident population.

Age and sex structure.—ASY males constituted most of the resident male population in all years (mean = 83%) (Table 3). Tests of observed numbers of ASY and SY males in resident and nonresident populations indicated that age ratios of males between the two populations were significantly different in all but two of the six

years tested (Table 3). In the other four years (1993, 1996–1998), the ratio of SY to ASY males was significantly lower in the resident population (Table 3).

In all years, both resident and nonresident populations were male-biased. The resident sex ratio was significantly different from unity in all years except 1996 (Table 4). The difference in 1996 was because of fewer males in both resident and nonresident populations (Table 4). The sex ratio of the nonresident population was significantly different from unity in 1996 through 1998 (Table 4), but there were no significant differences in sex ratios of resident and nonresident populations in any year.

Survival.—We tested the fit of the global (most parameterized) model ($\phi_{[a^*s^*t]}p_{[a^*s^*t]}$) with the bootstrap GOF testing procedure (program MARK, G. C. White unpubl.). The model was rejected ($P = 0.001$) but further investigation, including an examination of the plot of the residuals, suggested that the lack of fit was due to overdispersion of the data. Overdispersion (or extra binomial variation) (Burnham et al. 1987, Anderson et al. 1994) results when the empirical sampling variance is larger than the theoretical variance and reflects a lack of independence or heterogeneity among the fates of individuals in a population. Overdispersion is indicated when there is a biological suspicion of overdispersion and the value of \hat{c} (variance inflation factor) is $1 < \hat{c} < 3$. We suspect that the fates of individual cowbirds were not independent for the following reasons (1) it has been documented that social pairs (male and female) are more often seen together than with other individuals (Teather and Robertson 1986, Yokel 1986, 1989a), possibly a result of mate

TABLE 4. Sex ratio of the resident and nonresident populations.

Year	Female ^a	Male ^a	Sex ratio	χ^2 -value	<i>P</i> -value
Resident population					
1993	28	57	2.0	9.89	0.002 ^b
1994	25	54	2.1	10.65	0.001 ^b
1995	42	88	2.1	16.28	0.000 ^b
1996	32	45	1.4	2.20	0.138
1997	38	82	2.2	16.13	0.000 ^b
1998	37	68	1.8	9.15	0.002 ^b
Mean	33.7 ± 6.5	65.7 ± 16.8	1.9		
Nonresident population					
1993	22	45	2.0	5.38	0.02
1994	14	28	2.0	2.40	0.12
1995	33	108	1.8	3.23	0.07
1996	36	76	2.1	7.38	0.007 ^b
1997	63	115	1.8	7.82	0.005 ^b
1998	51	119	2.3	14.17	0.0002 ^b
Mean	36.5 ± 18.1	81.8 ± 38.6	2.0		

^a These values are based on both capture and resighting data.

^b Indicates sex ratio is significantly different from unity ($P \leq 0.05$) after Bonferroni correction.

guarding; (2) males are often observed and trapped in small groups on our study site (B. Woolfenden pers. obs.); and (3) presence of birds in traps may increase the probability of catching other individuals. This biological reasoning, combined with a \hat{c} value of 1.808 for the global model and no obvious pattern in the plot of the residuals, suggested that the global model $\varphi_{(a^*s^*t)}p_{(a^*s^*t)}$ was structurally adequate despite the lack of fit.

The overdispersion in the data set was corrected by inflating both the estimated sampling variance and covariance by multiplying them

TABLE 5. Summary of some of the models fitted to the capture–recapture data and their corresponding QAICc^a scores. The parameter structure indicates whether survival (φ) or recapture–resighting (p) was dependent on year (t), sex (s), or relative age (a).

Model	No. parameters	Deviance	QAICc ^a
$\varphi_{(a^*s)}p_{(t)}$	5	240.343	1023.590
$\varphi_{(a^*s^*t)}p_{(a^*s^*t)}$ ^b	33	111.181	1010.454
$\varphi_{(a)}p_{(t)}$	7	182.048	995.401
$\varphi_{(s)}p_{(t)}$	7	171.329	989.472
$\varphi_{(a^*s)}p_{(t)}$ ^c	9	163.326	989.116

^a Quasi-Akaike’s Information Criterion (QAICc) is simply the AIC (Akaike’s Information Criterion) corrected for overdispersion in the data and sample size.

^b Global model.

^c Selected model based on lowest QAICc value, which indicates the best fit (most parsimonious) model and was subsequently used to estimate survival and recapture–resighting parameters (Table 6).

by \hat{c} (for a complete explanation of the approach, see Burnham et al. 1987 and Anderson et al. 1994). The program MARK automates that adjustment. Final model selection was based on the QAICc (Quasi-Akaike Information Criterion) which is simply the AIC corrected for overdispersion in the data and sample size (E. Cooch and G. C. White unpubl.).

Model selection procedures indicated that ($\varphi_{[a^*s^*t]}p_{[a^*s^*t]}$) was the best fit model for our data set, which provided separate estimates of survival probabilities for each age and sex group (Table 5) and recapture–resighting probabilities for each year (Table 5). Those probabilities and their corresponding standard errors (SE) are summarized in Table 6. LR tests were used to test effects of each parameter (age, sex, and year) on survival and recapture–resighting probabilities. Survival probabilities for both sexes were lower for new birds (initial capture interval) than for returning birds (subsequent capture intervals), but LR tests indicated that those differences were not significant ($\chi^2 = 4.426$; $df = 2$; $P = 0.109$). Male survival probability was significantly higher than female survival probability for both new and returning birds (Table 6, LR test: $\chi^2 = 10.355$; $df = 2$; $P = 0.006$) and there were significant differences in the annual recapture–resighting probabilities (Table 6; LR test: $\chi^2 = 42.598$; $df = 4$; $P < 0.001$).

Using individual capture histories, we estimated minimum longevity of cowbirds in the

TABLE 6. Parameter estimates and standard errors (SE) from the most parsimonious model $\varphi_{(a^*)}p_{(t)}$ in which survival (φ) varied with relative age (a). Under this model, survivorship was constant across years but differed between the sexes and relative age classes. Recapture-resighting probabilities (p) differed among years but not between sexes or between capture intervals.

Parameter	Estimate	SE
φ (male—initial capture interval)	0.753	0.051
φ (male—subsequent capture intervals)	0.901	0.043
φ (female—initial capture interval)	0.647	0.079
φ (female—subsequent capture intervals)	0.696	0.075
p (1993)	0.606	0.064
p (1994)	0.789	0.053
p (1995)	0.425	0.056
p (1996)	0.493	0.060
p (1997)	0.308	0.044
p (over all years)	0.550 ^a	0.036 ^a

^a Estimated using model $\varphi_{(a^*)}p_{(t)}$ which is identical to our selected model $\varphi_{(a^*)}p_{(t)}$ except that p is held constant over years. This approach is equivalent to using a weighted mean estimate where weights are based on the variance-covariance matrix.

Delta Marsh population. Eleven of the males first trapped in 1993 were known to be alive in 1998. Six were at least 7 years old (assessed as ASY in 1993). Three females first banded in 1993 were last seen in 1997. They were at least one year old when banded and, therefore, had lived at least five years.

DISCUSSION

Demographic parameters.—Cowbirds in the Delta Marsh population showed higher annual survival and higher breeding-site fidelity than in other populations. Previous survival estimates range from 40 to 50% for females and 49 to 63% for males (Darley 1971, Fankhauser 1971, Yokel 1989a). Male survival in our population was 75 to 90% and female survival was 65 to 70% (Table 6). Our survival values are noteworthy because they are higher than those previously reported and confirm that there were significant differences in male and female survival. Additionally, our estimates are more reliable because they result from the robust statistical analyses of both survival and recapture probabilities. One possible limitation of our results is the low recapture probability of cowbirds that are known to be alive. The mark-recapture analysis indicates that, on average, only 55% of birds that were alive are recaptured or resighted in a given year (Table 6). Those estimates are the same for males and females and therefore will not influence estimates of sex ratio, but do suggest that both sexes might be quite mobile during the breeding seasons. That is supported by an investigation

of the genetic mating system of cowbirds (Woolfenden 2000) that indicated that most resident males and females did not breed on the study area.

Return percentages (males 66%; females 47%) indicate that Delta Marsh cowbirds were more faithful to the breeding site than cowbirds in other areas (Fankhauser 1971, Darley 1982, Dolbeer 1982, Ortega 1998). There were, however, differences between the annual survival estimates calculated by the mark-recapture analysis (Table 6) and return percentages (Table 2), which suggested that some resident birds were not seen in every year. That was confirmed by our estimates of annual recapture probability, which indicated that, on average, only 55% of birds that were alive and on site were captured in a given year (Table 6). The high return percentages combined with high annual survival suggest that there was likely low recruitment of new birds into the population. Taken together, those findings may mean that breeding opportunities were scarce and competition for the limited breeding opportunities was intense.

Male-biased sex ratios are characteristic of most cowbird populations (Darley 1971, Dufty 1982b, Teather and Robertson 1986, Yokel 1989a; but see Elliott 1980) and ours was no exception. However, the degree of the male bias varies geographically. Sex ratios in eastern populations tend to be closer to unity than those in western populations. The male bias in the Delta Marsh population (1.9 M:1 F) was similar to estimates for other western populations (Yokel 1989a), supporting the trend of

more male-biased populations in the West. Those differences are likely due to differences in the ecological conditions in different geographical locations. For example, density of host nests may determine availability and defensibility of females and thus indirectly determine numbers and distributions of males and their access to potential mates (Teather and Robertson 1986, Yokel 1989a). Alternatively the skewed sex ratio in western populations (Rothstein et al. 1980, Yokel 1989a) may be due to higher female mortality rates resulting from increased costs of breeding in harsher environments (but see Ankney and Scott 1980).

Variation among populations.—Clearly, there are differences in estimates of survival, breeding site fidelity, and sex ratios between cowbirds at Delta Marsh and in other areas. There are several possible explanations for the observed variation in those estimates, including differences in methodology and data analyses. However, some differences among populations are likely real and result from individual cowbirds adapting their behavior and distribution in response to local environmental variation. Below, we discuss each of those alternatives.

Typically, demographic estimates of cowbird populations have been derived from data collected over several years using radiotelemetry, field observations, or mark-recapture analyses. However, there is variability in the specific methods employed and the data analysis techniques utilized among studies. We suggest that those methodological differences may explain some of the population-level variability. For example, differences in the residency criteria used (Darley 1982, Dufty 1982b, Yokel 1989a) may influence estimates of some demographic parameters. Specifically, if transient birds (non-residents) are included in analyses, inflated estimates of population size and underestimations of the survival and site fidelity of residents may result. Based on our residency criterion, resident males and females were present on the study site for an average of 24 days and they exhibited high annual survival and reasonably high return percentages. Thus, differences between our population and others, in part, may be due to the inclusion of nonresidents, which would explain the lower survival and site fidelity estimates from other populations.

Another possible source of variation is that available survival estimates are based on either analysis of band returns (Fankhauser 1971, Searcy and Yasukawa 1981, Dolbeer 1982) or analysis of return rates (Darley 1971, Yokel 1986) rather than mark-recapture analyses. Analyses based on returns and recoveries of banded birds may be influenced by many different biases that affect the accuracy of parameter estimates (Anderson et al. 1985, Francis 1995). Use of return rates to estimate survival assumes that recapture probabilities are close to 100% and return rates are equated with survival probability. However, as is shown by our mark-recapture analysis, recapture-resighting probabilities in our study were closer to 55%. It is unlikely that high survival is unique to our population. Rather, we suggest that high adult survival has gone undetected because of a lack of multiyear studies that employ robust statistical analyses of the data.

However, some variation in demographic parameters across populations likely reflects real geographical differences. For example, sex ratios should not be affected by inclusion of non-resident birds. Our results indicated that there were no differences between the sex ratios of resident and total populations at Delta Marsh. Additionally, highly male-biased populations are consistently documented regardless of length of the study or the methods used to collect the data (Darley 1971, Dufty 1982b, Teather and Robertson 1986, Yokel 1989a). Studies using a variety of data-collection techniques across the geographic range of cowbirds have also consistently documented geographical differences in, (1) the spatial distribution of individuals (Darley 1982, Dufty 1982b, Teather and Robertson 1986); (2) the nature of the territoriality (Elliot 1980, Dufty 1982a, Darley 1982, Rothstein et al. 1986, Yokel 1989a); and (3) the degree of mobility of individual cowbirds during the breeding season (Teather and Robertson 1985, 1986; Rothstein et al. 1984, Thompson 1994). Some geographic variability in sex ratio, distribution patterns of individuals, and patterns of resource utilization as described in the above studies is also likely real and the results of the behavioral plasticity of cowbirds (but see Rothstein et al. 1986). Brood parasites avoid parental care and its associated costs, allowing them to adapt their behavior in re-

sponse to differences in local environments and resource distribution patterns (Barnard 1998).

Implications of demography for individual behavior.—High annual survival combined with breeding-site fidelity may influence the mating system and sexual selection through mate choice. Longevity and the relatively high rates of return for individuals across years create opportunities for long-term mating associations between male and female cowbirds. Analyses of annual genetic mating associations in the Delta Marsh population (Woolfenden 2000) provide evidence that some individuals maintain mating associations in multiple years, suggesting that cowbirds may use past experience with conspecifics as the basis for future mate choice.

Low annual recruitment of new adult birds into the resident population likely resulted from high annual survival and breeding-site fidelity of adult cowbirds. Low recruitment combined with a highly biased male sex ratio suggests intense competition for breeding opportunities may exist, especially among males, leading to strong sexual selection (Emlen and Oring 1977). That prediction is supported by several studies. Alderson et al. (1999) and Woolfenden (2000) determined that not all resident males in the Delta population successfully reproduced. Teather and Robertson (1986) showed that 50% of all males remained unmated during the breeding season. Similarly, D. A. Yokel (unpubl. data) and Dufty (1982b) both suggested that not all resident males in their populations were mated. If sexual selection is operating it may be acting on the age, experience, or dominance-ranking of male cowbirds. Several workers have found that older male cowbirds are dominant and more likely to be paired than SY males (Payne 1973, Teather and Robertson 1985, Yokel 1989b, Rothstein et al. 1986), which suggests that age may affect male reproductive success. At Delta Marsh, ASY males made up a larger proportion of the resident males than of the nonresident males and therefore may have had greater per capita access to breeding opportunities. Alderson et al. (1999) determined that of 14 males known to have bred in our population, only one was a SY bird. Similarly, Rothstein et al. (1986) reported that ASY males had higher mating success than SY males in a California population, although Darley (1968) suggested that there

was no difference in mating success in Ontario. Other research has shown that female preferences for male song play a role in cowbird mate choice and that California females prefer song types characteristic of ASY males (O'Loughlen and Rothstein 1995, Yokel and Rothstein 1991).

In summary, there appears to be geographic variation in cowbird demographic parameters across populations. Those differences combined with local ecological conditions can affect the social behavior and mating patterns of cowbirds. Our results indicate that Delta Marsh cowbirds have high annual survival, breeding-site fidelity, and a highly male-biased sex ratio. Those conditions may result in intense sexual selection on males, which in turn may influence mate choice and the mating system. Experimental studies and comparisons across populations are needed to test relationships among population demographic characteristics, ecological conditions, spatial distribution of individuals, and individual mating strategies.

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