BROWN-HEADED COWBIRD (*MOLOTHRUS ATER*) MORTALITY IN AN URBAN WINTER ROOST

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ABSTRACT.—We studied mortality experienced by Brown-headed Cowbirds (*Molothrus ater*) at a communal winter roost in live oak groves on the Rice University campus, Houston, Texas. Objective "circle count" estimates of the roosting population suggest that about 500,000 birds occupied the roost from late January through mid-March of each year (1974–1976), and that an additional 400,000 birds joined them in February 1975. About 40% of the roosting birds were Brown-headed Cowbirds. The cowbird population was predominately (80–95%) male at this location. In January their weights were directly correlated with ambient temperature, which suggests difficulty in maintaining fat reserves. Most mortality occurred following exposure to freezing temperatures in February. Autopsies showed that bacterial infections were prevalent among sick birds; intestinal coccidiosis was also important, especially among males in 1975. Neither metazoan parasites nor pesticide residues were implicated as causes of death. Males were overrepresented among the dead in 1975 but not in 1976.

A comparison of the characteristics of live (decoy-trapped) and dead cowbirds during 1976 indicated that adult males were overrepresented among the dead and that within each age class the dead males had significantly longer wings. There was a significant positive correlation between daily temperature minima and the mean wing length of male cowbirds dying each day. Mortality tends to reinforce sexual dimorphism with respect to tarsus length. These results suggest that mortality is related to depletion of winter food supplies. Aggressiveness, a trait unrelated to size, was found to have important survival value under these circumstances. *Received 17 January 1978, accepted 5 January 1980.*

RECENT attempts to induce mass mortality among inhabitants of winter blackbird roosts (U.S. Department of the Army 1975) have created an urgent need for improved understanding of factors regulating population size in these species (Dolbeer 1976). Winter mortality is thought to be an important factor regulating many bird populations (Lack 1966, Fretwell 1972, Wiens 1974), yet available literature on migratory blackbirds provides little information relevant to this point.

Each winter since 1972–73, there has been a major blackbird roost in live oak (*Quercus virginiana*) groves on the campus of Rice University, Houston, Texas. Brown-headed Cowbirds (*Molothrus ater*) and Red-winged Blackbirds (*Agelaius phoeniceus*) have been the predominant species, with American Robins (*Turdus migratorius*), Common Grackles (*Quiscalus quiscula*), Great-tailed Grackles (*Quiscalus mexicanus*), and Starlings (*Sturnus vulgaris*) also represented. Late-winter mortality has been characteristic of this roost since its establishment (Anonymous 1973). Our efforts to understand the cause of this mortality were focused on Brown-headed Cowbirds, the most abundant dead birds at the roost site; we also collected a modest amount of information on Red-winged Blackbirds.

This research has exploited a unique opportunity provided by having a major blackbird roost located on a university campus. Daily access to the roost site, the assistance of numerous student "volunteers," and cooperation of other university

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employees made it possible to accomplish nearly continuous monitoring of certain phenomena, which would have been prohibitively expensive had the roost been located elsewhere. On the other hand, the reader should be aware of the limitations associated with this sort of opportunistic research: (1) we restricted our study to the immediate vicinity of the roost; (2) we were able to study this problem intensively for only 2 yr (1975 and 1976), each of which proved to be quite different from the other in several respects; (3) we were inexperienced when we started and had to modify our methods and refine our questions as we proceeded. A more experienced team might have made more of this opportunity, and we might have learned more given several years to compare; but the opportunity was ours, it proved to be brief, and we have learned what we could from it. Additional information concerning the Rice University roost is reported by Johnson et al. (1976 and MS). Alteration of the roost for management purposes is reported by Good and Johnson (1976, 1978). Good (1979) continued these studies through 1977 and has refined our understanding of both the internal structure of the roost and mortality patterns.

METHODS

Roosting population size.—Estimates of the number of birds inhabiting large communal roosts are often quite subjective, and their accuracy depends upon the observer's experience. Objective methods take advantage of the fact that birds leave the roost to forage far afield during the day and return during a discrete period before sunset (Krantz and Gauthreaux 1975). Objective "block counting" methods are applicable when the birds approach a roost along a few discrete flight lines (Meanley 1965, Coon 1974). During this study, we were favored with neither experience nor discrete flight lines, so we devised a "circle count" method that has proved quite useful for our purposes.

Observers were stationed at 30 locations spaced at 12° intervals around a circle of diameter $(D) = 4.64$ km centered on the Rice University campus. At each station the observer selected two landmarks (buildings, trees, telephone poles, etc.) defining a line segment (L) approximately tangent to the circle. The angle of arc subtended by this line segment is

$$\theta = 2 \arctan (L/D).$$

The arcs of adjacent stations did not overlap. As birds returned to roost in the evening, during about 2 h before sunset, they were counted if they passed between the landmarks; those flying away from the roost were subtracted to obtain net flight into the circle at each station. These counts were standardized by conversion to number of birds per degree of arc.

In principle, all observations should be made simultaneously, but in practice we found it necessary to extend the sampling period for 3–8 days. This procedure was used to estimate the size of the Rice roost on 6 occasions: 6–9 March 1974; 30 January–3 February and 7–12 March 1975; 9–12 January, 13–20 February, and 7–14 March 1976.

Characteristics of live birds.—Characteristics of live birds were obtained from data collected during a bird-banding program conducted by students in a population ecology lab supervised by some of the authors (D. J., B. M., P. S.) in cooperation with Dr. K. A. Arnold (Texas A & M University). Decoy traps (Coon 1974) caught both Brown-headed Cowbirds and Red-winged Blackbirds as they returned to roost at Rice University in the evening. Birds were removed from the traps within a few hours and transported to the laboratory in small holding cages. Sex and age determinations based on examination of plumage (Selander and Giller 1960) made it possible to assign birds to the following categories: cowbird females (F), males hatched the previous summer (2ND), older males (A2Y); red-wing females (F), immature males (IMM), adult males (ADU). The weight of each bird was recorded before banding. In 1976, wing length (chord of the extended wing) and tarsus (tarsometatarsus) length were measured to the nearest millimeter, and an index (0–5) of visible fat deposits was estimated (Helms and Drury 1960).

Many of the cowbirds banded in 1976 were scored for aggressiveness using procedures described by Burtt and Giltz (1969). Each bird was held in a gloved hand for 60 s, provided a standard sequence of stimuli and opportunities to express aggression toward the tester, and then assigned a score from 1 (submissive) to 5 (aggressive). All aggression tests were administered by the same person (W. N.) to insure uniformity. On 1 February 1976, 30 birds were tested once, returned to holding cages, and then retested

to estimate the reliability of this subjective scoring method. The correlation between the two sets of scores was $r = 0.94$ ($P < 0.01$).

Our estimates of the characteristics of live birds at the Rice roost may be biased if the traps attracted a nonrandom sample of the cowbird population. Good (1979) reports that trapped birds had attributes of the less fit part of the roosting population; those that were less successful at foraging for native seeds and frequently used domestic bird feeders roosted in marginal low-density areas within the roost and experienced greater mortality than the more fit birds. Thus, there may be a part of the cowbird population, the more fit birds, that rarely entered our traps. K. A. Arnold (Texas A & M University) shared with us his unpublished data from banding operations using floodlight traps (Mitchell 1963) at roost sites and decoy traps along flight lines during 1970–71 near College Station, Texas. His data suggest that decoy traps tend to capture more female cowbirds and fewer young males (hatched the previous summer) than would be expected from their proportions in the roost. We have not attempted to adjust our data to correct for these sources of bias but will consider their potential influences on our data where appropriate.

Daily mortality.—Throughout the roosting period, we conducted almost daily searches for dead birds on the Rice University campus. We did not recover dead birds from adjacent residential areas nor from the extensive area where birds foraged during the day. Dead birds were collected in plastic bags and returned to the laboratory, where they were refrigerated for less than 24 h until they could be sorted by species and sex, counted, and then destroyed by incineration. In 1975, separate records were kept for two areas of the campus (east and west); in 1976, all birds roosted on the east side of campus. When an area could not be searched daily, the accumulated dead were divided among the intervening dates. In 1976, one of us (A. K.) measured the weight, wing length, and tarsus length of all dead birds collected at the roost.

Parasitology.—We attempted to identify factors that might have been contributing to the observed mortality by collecting both healthy and sick birds, sacrificing them, and performing autopsies on the freshly killed bodies. This part of the research was supervised by one of us (G. S.) and conducted by several undergraduate students, including some of the authors (M. C., R. G., E. O.). Healthy birds were captured in decoy traps; they were all active, resisted handling, and could walk or fly without difficulty. Sick birds were captured by hand; they did not fly, had difficulty walking, and were often found sitting with their eyes closed for extended periods. The unhealthy birds invariably died within 48 h.

During the 1975 season (12 December 1974–18 March 1975), we autopsied a total of 31 Brown-headed Cowbirds (7 healthy females, 11 healthy males, and 13 sick males). One thick and two thin blood smears, obtained by toe-clipping each bird, were inspected for parasites. Each bird was examined for external gross pathology and ectoparasites. Internal organs were removed and inspected for gross pathological changes and parasites. A similar inspection was made of body cavities, esophagus, trachea, gizzard, and intestines. A sample of fecal material, suspended in 5% formalin, was inspected at 100× for evidence of parasitism, especially coccidial oocysts.

During the 1976 season (4 February–26 March 1976), we autopsied 47 sick cowbirds (4 females and 43 males). In addition to procedures described above, several drops of blood obtained by toe-clipping were diluted with 1 ml of sterile saline, streaked out on sterile nutrient agar, and incubated at 40°C for 24 h. Samples were also removed from any lesions observed on internal organs and treated in the same way. All bacterial cultures were inspected within 24 h and again after 48 h. Identification of bacteria was based upon colony morphology on nutrient, MacConkey's and Endo agar, and upon the result of Gram's stain of samples from colonies.

Additional information on the incidence of coccidial infections among healthy cowbirds was obtained during the 1976 season. Twice each week approximately 15 cowbirds being banded were held overnight in individual cages lined with clean aluminum foil. Feces collected from each bird were weighed and suspended in 2 ml of formalin, and a 0.05-ml sample was examined microscopically (400×) for coccidial oocysts. If oocysts were found, two additional samples were counted to obtain a mean, which was then converted to an estimate of number of oocysts per gram of feces. A total of 286 Brown-headed Cowbirds were screened using this program.

Pesticide analysis.—In 1975, one of us (J. H.) analyzed pesticide residues in the bodies of healthy, sick, and dead male cowbirds. Procedures used were those described by Wilson (1967) as modified by Ginn and Fisher (1974). The following standards were used for comparison: C2-Aldrin, Dieldrin, C7-Lindane, Heptachlor, Heptachlor epoxide, Aldrin, DDE, DDD, DDT, Mirex, Arochlor 1254, Arochlor 1260, Arochlor 1248.

Weather.—Records of daily minimum temperatures were obtained for a station maintained by the Federal Aviation Administration at Hobby Airport, approximately 5.5 km southeast of Rice University (U.S. Department of Commerce 1975–1976).

TABLE 1. Analysis of variance for circle-count data after a three-parameter logarithmic transformation, $Y' = \ln(Y + 1{,}486)$.

Source	df	SS	MS	F	P
Dates	5	4.9777	0.9955	10.37	<0.001
Stations	29	11.5029	0.3967	4.13	<0.001
Error	142[a]	13.6389	0.0960		
Total	176[a]	30.1195			

[a] Three df lost by replacement of missing data.

RESULTS

Roosting population size.—Inspection of the "circle count" data revealed that they did not fit a normal distribution; the distributions were skewed toward lower values, and cumulative probit diagrams (Bliss 1967: 101) were nonlinear. This may be attributed to a strong relationship between means and standard deviations that is best represented by the linear regression,

$$SD = 0.432\bar{Y} + 642.272.$$

Following the procedure described by Bliss (1967: 178), we used a three-parameter logarithmic transformation,

$$Y' = \ln(Y + Y_o),$$

where Y_o = intercept/slope from the regression above: $Y_o = 1{,}486$. Frequency distributions of transformed data formed satisfactorily linear cumulative probit diagrams and were assumed to fit the normal distribution sufficiently well to be subjected to statistical analyses.

One datum was identified as an outlier on the basis of Dixon's Gap test [$n = 28$, P $(R_3 = 0.388) < 0.05$] and was omitted from statistical analyses. Three missing observations (including the one rejected as an outlier) were estimated using the procedure described by Steele and Torrie (1960: 139). The degrees of freedom associated with the error sum of squares in an analysis of variance were, therefore, reduced by three. Transformed "circle count" data were subjected to an analysis of variance (Table 1), which detects significant effects attributable to differences among dates. An a posteriori comparison using the Student-Newman-Keuls test (Sokal and Rohlf 1969: 239) found that the mean transformed number of birds per degree for 30 January–3 February 1975 was significantly larger ($P < 0.01$) than for any other date. There were no significant differences among the means resulting from counts made in February 1976 and in March of all 3 yr. The mean for January 1976 was the lowest and proved to be significantly different from that for February 1976 ($P < 0.01$) and March 1975 ($P < 0.05$).

Using the error mean square from Table 1 as an estimate of the variance, we calculated 95% confidence intervals for the means of transformed data for each date (Bliss 1967: 194). We then converted these values back to numbers per degree ($Y = e^{Y'} - 1{,}486$) and multiplied by 360 to estimate the total number of birds roosting in the vicinity of Rice University on each date (Table 2). We concluded that about 500,000 birds (mean = 483,882) were roosting at Rice from late January through mid-March each year and that about 400,000 joined them in February 1975. These are estimates of total roost size, including all species. In an attempt to separate "circle count" observations into 3 taxa during the February and March 1976 periods,

TABLE 2. Means and confidence intervals from transformed circle-count data converted to estimates of total birds (in thousands), $360(e^{Y'} - 1,486) \times 10^{-3}$.

Dates	Birds	95% CI
1. 6–9 March 1974	409	309–521
2. 30 January–3 February 1975	880	730–1,048
3. 7–12 March 1975	514	403–639
4. 9–12 January 1976	289	202–387
5. 13–20 February 1976	571	453–703
6. 7–14 March 1976	442	338–557

we estimated that about 70% of these birds were "blackbirds," 12% "grackles," and 18% robins. During 1975, many birds roosted in residential neighborhoods adjacent to the Rice University campus (Good and Johnson 1976). These areas were within the circle used for "circle counts" but were not covered by our daily search for dead birds. Therefore, we have attempted to obtain alternative estimates of the on-campus roosting population. Good (1979) provides objective estimates based upon a modification of Stewart's (1973) fecal deposition method. These are included in Figs. 1 and 2 as kilograms of droppings deposited on-campus per night, where each gram represents approximately one bird. We have also included two subjective estimates by K. A. Arnold (Texas A & M University), an experienced observer of blackbird roosts. In 1976, when the entire roost was located on the campus, these alternative estimates were remarkably consistent with "circle count" data (Fig. 2); in 1975, they were the only estimates available for the on-campus part of the roost (Fig. 1).

Cowbird population size.—A total of 1,985 Brown-headed Cowbirds was banded between 28 December 1974 and 22 February 1975; 3,000 cowbirds were banded between 30 December 1975 and 23 March 1976. Cowbirds banded at Rice University in January were recaptured and recovered among the dead throughout the roosting season, and none was reported far from the vicinity of Houston until spring migration in March. Therefore, we believe that there was little turnover at the roost and that it is possible to treat the banded cowbirds as a marked sample of the population roosting at Rice. To estimate population size during any particular interval, we assumed that the number marked (n_1) were those banded but not yet found dead. Birds captured in decoy traps or recovered dead were combined to determine both the number sampled during each interval (n_2) and the number of recaptures of marked individuals (m_2). Because Good (1979) found that a subset of the roosting cowbirds neither visited the traps nor experienced much mortality, we assume that our estimates of population size are somewhat low.

Chapman's modification of the Lincoln Index (Seber 1973: 59–61) was used to estimate cowbird population size for nine successive 10-day intervals beginning on 1 January of both years (Table 3). For 1975, 5 estimates meet the criteria recommended for reliable estimates (Seber 1973) that $\mu > 4$ and $m_2 \geq 7$: 2 of these cover the interval 21 January–9 February 1975 and average about 100,000; the other 3, 10 February–11 March 1975, average about 300,000. For 1976, 3 estimates meet these criteria, 20 February–20 March 1976, and average about 200,000. These may be very crude estimates, but they are consistent with estimates of total roost size (above) and suggest that cowbirds composed about 30–40% of the Rice roost.

Daily mortality, weather, and weight.—Nearly daily searches of the Rice campus resulted in the collection of 7,387 dead cowbirds in 1975 and 2,167 in 1976. Only 6 of 85 days after 10 January were skipped in 1975 and 16 of 85 in 1976. On those

TABLE 3. Mark-recapture estimates of the number of Brown-headed Cowbirds roosting at Rice University during successive 10-day intervals in 1975 and 1976; based on the number of banded birds at the start of each interval (n_1), the number of birds trapped or recovered dead during each interval (n_2), and the number of those that had been banded prior to start of the interval (m_2).

Date	n_1	n_2	m_2	N^{*a}	v^{*b}	μ^c	$(\bar{N}^*, m_2 \geqslant 7, \mu \geqslant 4)$
1975							
1–10 January	94	524	0	—	—	—	
11–20	256	870	2	74,615	37,026	3	
21–30	796	1,097	8	97,233	30,448	9	106,180
31–9 February	1,191	1,158	11	115,126	31,605	12	
10–19	1,363	3,139	10	390,599	112,105	11	
20–1 March	1,832	1,545	9	283,381	84,906	10	309,230
2–11	1,939	1,176	8	253,708	79,737	9	
12–21	1,931	150	2	97,243	48,099	3	
22–31	1,929	0	0	—	—	—	
1976							
1–10 January	0	234	0	—	—	—	
11–20	202	622	0	—	—	—	
21–30	798	713	1	285,242	164,248	2	
31–9 February	1,473	533	3	196,788	87,553	4	
10–19	1,754	534	6	134,131	47,018	7	
20–29	2,041	1,041	8	236,417	74,274	9	
1–10 March	2,475	597	7	185,080	61,181	8	198,080
11–20	2,719	644	9	175,439	52,389	10	
21–30	2,942	236	5	116,248	43,146	6	

[a] $N^* = [(n_1 + 1)(n_2 + 1)/(m_2 + 1)] - 1$.
[b] $v^* = [(n_1 + 1)(n_2 + 1)(n_1 - m_2)(n_2 - m_2)/(m_2 + 1)^2 (m_2 + 2)]$.
[c] $\mu = (n_1 n_2/N^*)$.

occasions, the dead birds that accumulated were divided equally among the 2 or 3 days in the interval. (We never missed more than 2 days in succession.) Thus, the number of dead birds collected each day (Figs. 1 and 2) reflect very closely the actual numbers dying. Estimates of on-campus roosting population size (of all species combined) from K. A. Arnold (pers. comm.), Good (1979), and 1976 "circle counts" (see above) are also included in Figs. 1 and 2. Note that in both years the onset of significant mortality lags several weeks behind roost establishment. Minimum temperatures below freezing often presage dramatic increases in daily mortality. An exception to these generalizations is the large number of birds found dead at the roost on 2 January 1975 (Fig. 1); this mortality was caused by a violent rainstorm associated with passage of a cold front the preceding evening.

The mean weight of male cowbirds captured in decoy traps during the banding program is also presented in Figs. 1 and 2. Comparison of the weight and temperature graphs suggests a relationship between the two, which can be inspected more closely in Fig. 3. Though the overall pattern of weight vs. temperature suggests no correlation, there are positive correlations if one limits the analysis to means with values of at least 47 grams, which occur early in the roosting season (before 5 February).

For 1975 only 10 of 24 means exceed 47 g, but their correlation with temperature is $r = 0.71$ ($P < 0.05$) (Steele and Torrie 1960: 453); in 1976 19 of 20 means exceed 47 g, and the correlation is $r = 0.57$ ($P < 0.05$). During the same period there is an inverse relationship between the mean and standard deviation of fat class ($r = -0.59$, $P < 0.05$).

After 5 February in both years the mean weights of male cowbirds are generally lower than before and are not significantly correlated with temperature; they do
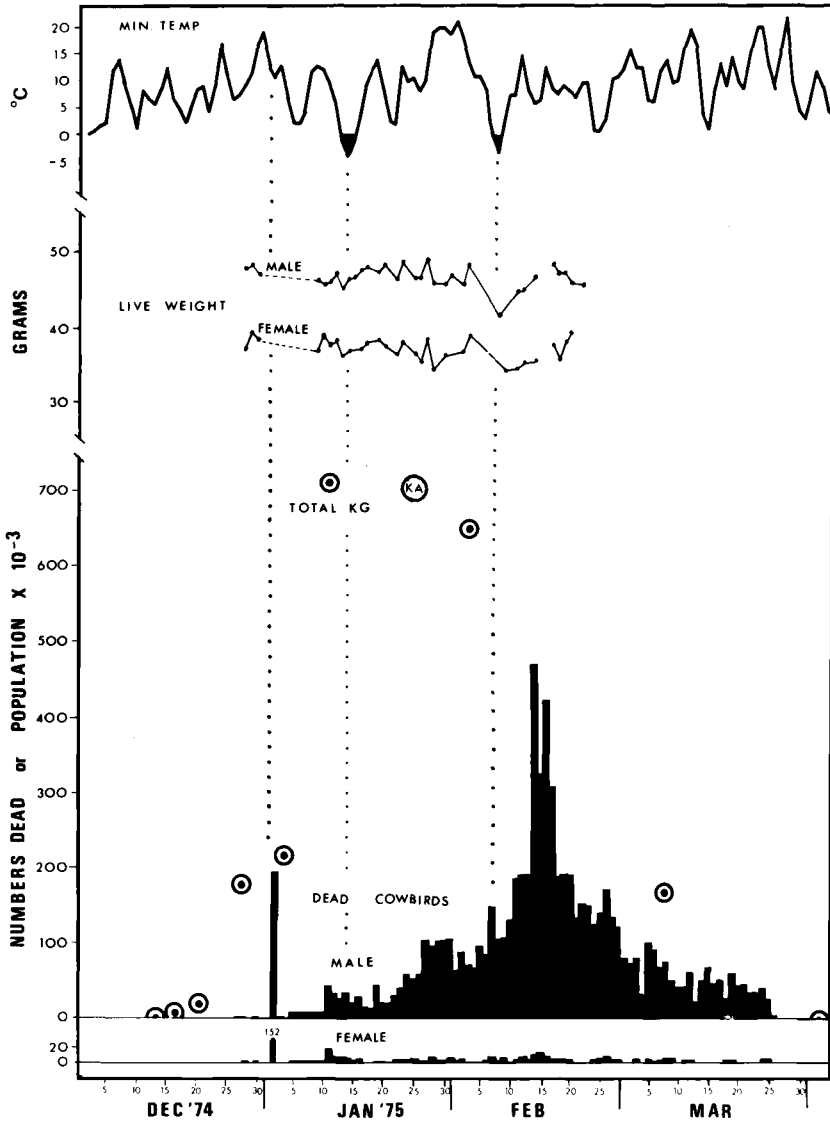
Fig. 1.   Daily Brown-headed Cowbird mortality observed at the Rice University roost in 1975 compared with daily temperature minima, mean weight (or fat class) of decoy-trapped cowbirds, and estimates of the number of birds roosting on campus—all species combined. Circled dots are estimates from Good (1979) based on fecal deposition rates (1 kg $\simeq$ 1,000 birds), and others (KA) are subjective estimates by Keith Arnold.

seem to be particularly sensitive, however, to freezing temperatures such as occurred on 7 February 1975 (Fig. 1) and 23 February 1976 (Fig. 2). The mean weight of all male cowbirds banded in 1975 was 46.2 g ($n = 1,625$, SE = 0.3); for 1976 it was 48.6 g ($n = 2,824$, SE = 0.1). The 2.4-g difference is highly significant [P ($t \geqslant$ 9.1) < 0.001]. Female mean weights, 37.0 g ($n = 360$, SE = 0.7) for 1975 and 37.7 g ($n = 174$, SE = 0.25) for 1976, reveal no such difference [P ($t \geqslant 0.7$) > 0.40].
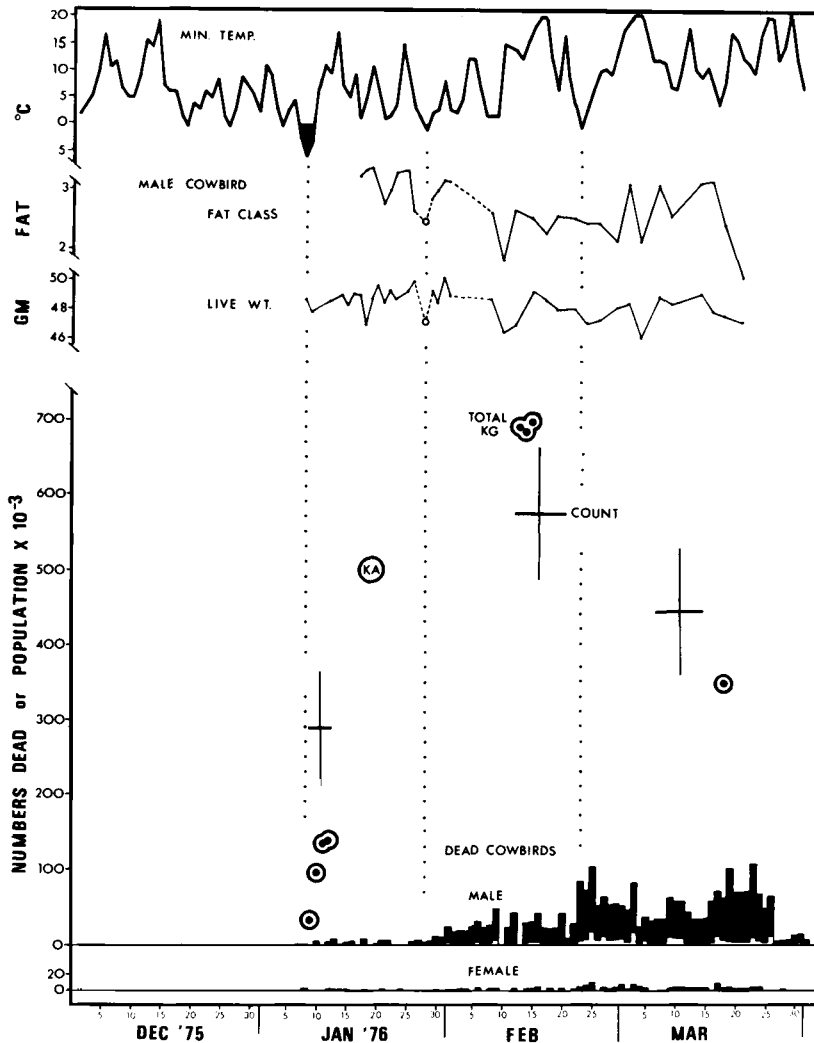
Fig. 2. As Fig. 1, for 1976; white areas at the base of male histograms indicate young (2ND) birds, and bars (±95% CI) are based on circle counts (Table 2).

Sex composition.—Inspection of Figs. 1 and 2 reveals that many more male than female cowbirds died at the Rice roost. Much of this apparent difference is attributable to the fact that males predominated among the living cowbirds roosting in this location, but a comparison of the sex composition of live (decoy-trapped) and dead cowbirds (Table 4) suggests that males may nevertheless be overrepresented among the dead in 1975. This would imply that they experienced somewhat higher mortality rates. It is important to note that this result could also have been caused by a tendency for the decoy trap to attract a disproportionate number of females. When the numbers of dead males and females in Table 4 were altered to correct for the magnitude of the bias suggested by Arnold's data, however, we found that the results were not changed [for 1975 (west) P ($\chi^2 \geq 33.8$) < 0.001; for 1975 (east), P ($\chi^2 \geq 11.1$) < 0.001]. Therefore, we conclude that males seem to have experienced
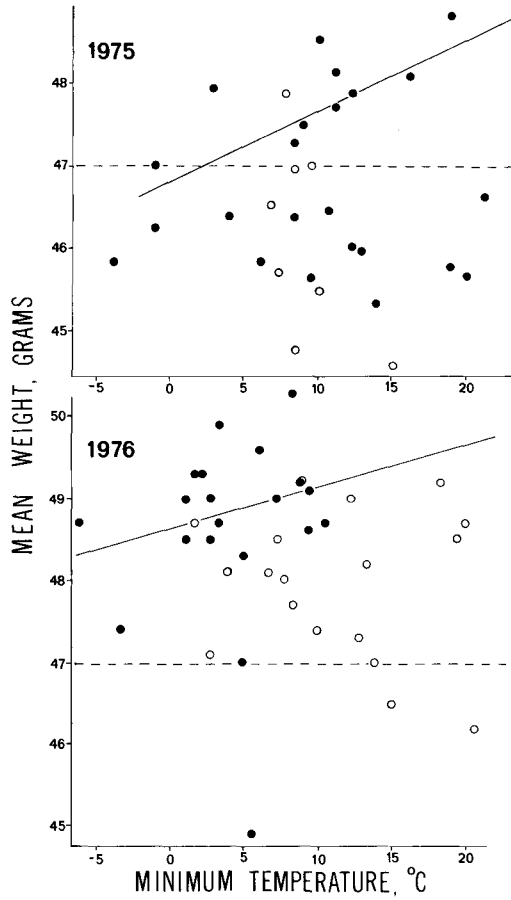
Fig. 3.   The relationship between daily temperature minima and mean weight of male Brown-headed Cowbirds. Solid circles indicate dates before 5 February; open circles, dates after 5 February. Least squares linear regression lines indicate that the best fit to means that exceed 47 g before 5 February has a positive slope in both 1975 and 1976.

greater mortality than females in 1975. There is no evidence of differential mortality among the sexes in 1976.

Parasitology.—Autopsies performed on healthy and sick cowbirds in both years suggest that internal metazoan parasites (tapeworms, trematodes, and nematodes)

TABLE 4.   Sex composition of Brown-headed Cowbirds wintering at Rice University and of those found dead.[a]

Year	Source	M	F	% M	χ^2	P
1975	Trap (west)	1,266	339	79	77.0	<0.001
	Dead (west)	1,872	224	89		
	Trap (east)	359	21	95	23.1	<0.001
	Dead (east)	5,191	100	98		
1976	Trap (east)	2,826	174	94	0.4	n.s.
	Dead	2,032	135	94		

[a] Those killed by a violent storm on the evening of 1 January 1975 have been omitted from this analysis.

TABLE 5. Incidence of coccidial infections among healthy and sick Brown-headed Cowbirds wintering at Rice University.

Year	Source		+	−	%+	Fisher's exact probability		
1975	Healthy	F	1	6	14	0.06		
		M	5	6	45			
	Sick	M < 4 February	2	4	33	n.s.		
		M > 4 February	6	1	86	0.09		
						χ^2		P
1976	Healthy	F < 23 February	0	16	0	5.7		<0.025
		F > 23 February	9	22	29		2.2	n.s.
								1.3 n.s.
		M < 23 February	14	99	12	2.3		n.s.
		M > 23 February	25	102	20			
	Sick	F	0	4	0			
		M < 23 February	0	23	0	5.1		<0.025
		M > 23 February	4	16	20			

do not play a significant role in the observed mortality. Pathogenic mites were associated with bald scaly spots on the wings, chest, and head of a few sick birds, but the infections did not appear to be sufficiently severe to cause death.

The most frequently encountered parasitic infection was intestinal coccidiosis, which was accompanied by severe pathology (intestinal hemorrhaging, thin-walled guts, excess mucous secretion), especially among sick birds. Certain trends in the incidence of infection suggest that coccidiosis may have been an important factor contributing to the observed pattern of mortality in 1975 (Table 5): (1) among healthy cowbirds, males had a higher incidence of infection than females; and (2) the incidence of infection among sick males increased dramatically in early February, as did male mortality (Fig. 1).

More comprehensive documentation of the incidence of coccidial infection is available for 1976 (Table 5). Coccidiosis seems to have been a much less important factor in that "lower mortality" year; yet the incidence of infection still fits the observed pattern. Very few cowbirds, healthy or sick, were infected until after the 23 February freeze; then less than 30% were infected, with no significant difference between the sexes. Among the cowbirds infected, the intensity of the infection, as judged by oocyst counts, was relatively low in January and then increased in February and March in 1975.

Bacteriological examination of blood samples from sick cowbirds in 1976 found 91% to be bacteremic. The following bacteria were identified: *Enterobacter* sp. (58% of cowbirds infected), *Pasturella* sp. (36%), *Staphylococcus aureus* (15%), *Bacillus* sp. (13%), *Escherichia coli* (8%), *Clostridium* sp. (2%), and *Streptococcus* sp. (25%).

Pesticide residues.—Male cowbirds wintering at the Rice roost in 1975 contained detectable concentrations of Dieldrin, DDE, DDT, Heptachlor epoxide, and Mirex. Analyses of 8 healthy, 10 unhealthy, and 6 dead male cowbirds revealed no apparent differences in the pesticide load among these groups. In nearly all cases, the mean concentration was less than 0.1 ppm and exceeded 1 ppm in only one case (unhealthy, 3 March, Mirex).

Measurement bias affecting living/dead comparisons.—Twenty-seven cowbirds banded during the 1976 roosting season were recovered among the dead birds at the roost. Comparisons of wing and tarsus measurements recorded during banding and

TABLE 6. Sex/age class composition of live (decoy-trapped) and dead birds at the Rice University roost, January–March 1976 (expected values in parentheses).

Category	Live	Dead	χ^2	P
Brown-headed Cowbird				
Females	174 (179.4)	135 (129.6)	0.39	n.s.
Males, 2ND	853 (639.2)	248 (461.8)	170.50	<0.005
Males, A2Y	1,973 (2,181.3)	1,784 (1,575.7)	47.43	<0.005
Red-winged Blackbird				
Females	15 (18.1)	101 (97.9)	0.63	n.s.
Males, IMM	60 (33.5)	154 (180.5)	24.85	<0.005
Males, ADU	24 (47.4)	279 (255.6)	13.69	<0.005

after death reveal important biases that must influence our interpretation of these data. The mean wing length for measurements after death is greater than for those made during banding [$\bar{d} = 0.214$ cm, SE $= 0.0488$, P ($t_{26} \geq 4.402$) < 0.001]. We suspect that this results from some students' failure to extend the wing completely when measuring the living bird. Inexperience is further implicated by the fact that the magnitude of the bias declines with time [WING BIAS $= 0.441 - 0.006$ DATE, P ($r_{25} = 0.516$) < 0.01]. Mean tarsus length is also greater for measurements after death [$\bar{d} = 0.0615$ cm, SE $= 0.0266$, P ($t_{26} \geq 2.312$) < 0.05], but this bias does not change with time. A comparison of age determinations reveals that three of the 26 for male cowbirds do not agree. The net effect of these errors is that one more bird (4%) was classified young (2ND) when alive than after death. Each of these sources of bias must be carefully considered as we interpret comparisons based upon these measurements. Where appropriate, we have assumed that Red-winged Blackbird data are affected by similar errors, proportional to their respective means.

Age-selective mortality.—More comprehensive measurements on live and dead birds during the 1976 season may be examined for additional evidence of selective mortality. Comparison of sex/age class frequency in samples of live and dead birds (Table 6) reveals similar trends for both Brown-headed Cowbirds and Red-winged Blackbirds. There is no evidence of sex-selective mortality, but adults compose a larger than expected proportion of the dead males. Young males (2ND) compose 30% of those banded but only 12% of the dead, a difference much greater than the estimated 4% bias toward misclassifying male cowbirds 2ND while banding them. Because our estimate is that decoy traps are biased against catching young males, we must interpret these results to mean that adult males experienced higher mortality at the roost.

TABLE 7. Mean wing lengths of live (decoy-trapped) and dead birds at the Rice University roost, January–March 1976.

Category	Live[a]	Dead	t	P[b]
Brown-headed Cowbird				
Female	10.10	10.12	−0.582	n.s.
Male, 2ND	11.10	11.10	−0.008	n.s.
Male, A2Y	11.32	11.38	−4.550	<0.00005
Red-winged Blackbird				
Female	10.78	10.45	+3.178	<0.002
Male, IMM	12.22	12.20	+0.347	n.s.
Male, ADU	12.79	11.67	+1.358	n.s.

[a] Measurement bias corrected by adding 0.2148 cm for cowbirds and 0.2358 cm for red-wings (see text).
[b] These probabilities assume no uncertainty concerning the value of the measurement bias (see text).
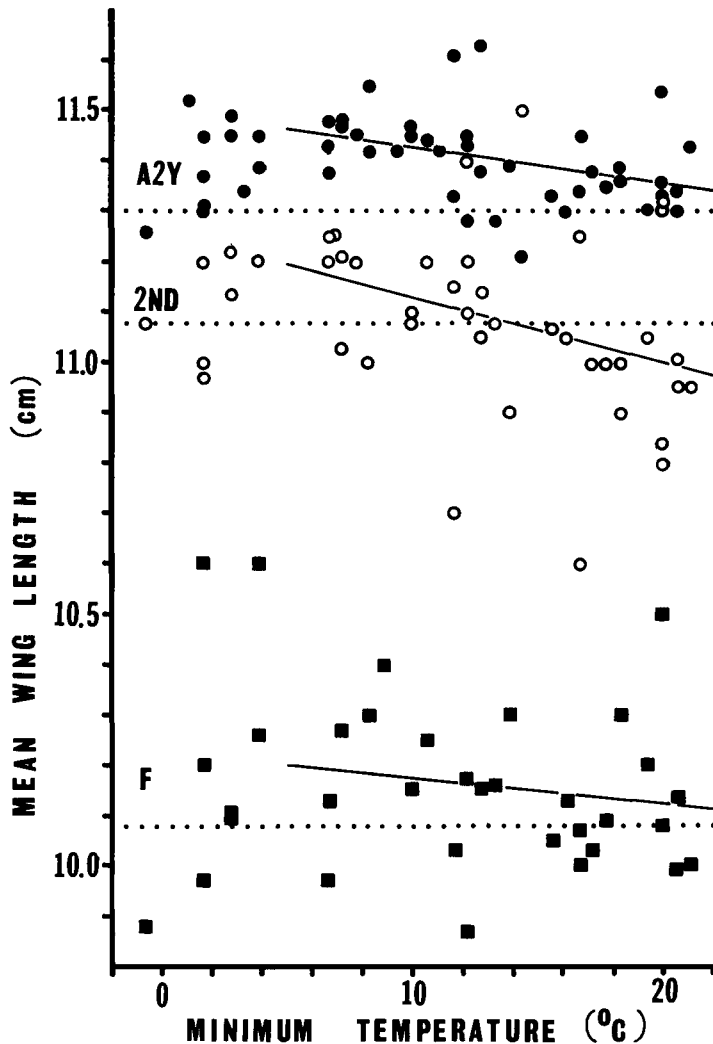
Fig. 4. The relationship between daily temperature minima and the size of dead Brown-headed Cowbirds recovered at the Rice roost during January–March 1976. Dots represent daily mean wing lengths of adult males (A2Y); open circles, 2nd-yr males (2ND) hatched the previous summer; and squares, females (F). Dotted lines indicate the overall average for live birds in each category. Solid lines are linear regressions for temperatures exceeding 4°C (see text).

Size-selective mortality.—Comparison of mean wing lengths for live and dead birds in each sex/age category (Table 7) reveals little difference for female or young male cowbirds but suggests that the adult male cowbirds that died had significantly longer wings than their peers. Considering the importance of this result, it is necessary that the potential influence of measurement bias be thoroughly explored. The wing lengths for live birds in Table 7 have been adjusted by adding the mean of 27 bias estimates to the mean wing length for each category. But we have seen that the bias estimates declined significantly during the banding season. If one adjusts the mean wing length of each age/sex category on each date by an amount determined by the linear regression equation reported above and then uses these adjusted data

TABLE 8. Mean tarsus (tarsometatarsus) lengths of live (decoy-trapped) and dead birds at the Rice University roost, January–March 1976.

Category	Live[a]	Dead	t	P[b]
Brown-headed Cowbird				
Female	2.33	2.38	−2.99	<0.005
Male, 2ND	2.56	2.52	+3.81	<0.0002
Male, A2Y	2.58	2.56	+4.67	<0.00005
Red-winged Blackbird				
Female	2.80	2.55	+6.88	<0.00005
Male, IMM	2.96	2.93	+1.68	<0.10
Male, ADU	3.10	2.92	+3.06	<0.005

[a] Measurement bias corrected by adding 0.0615 cm for cowbirds and 0.0709 cm for red-wings (see text).
[b] These probabilities assume no uncertainty concerning the value of the measurement bias (see text).

to calculate the overall mean, there are slight changes in the values of mean wing length and of t, but the patterns, with respect to significance levels, remain unchanged. It is possible, however, to eliminate the statistical significance reported in Table 7 if one's estimate of the value of the bias is increased by a sufficient amount. Using our estimate of the standard error of the mean bias, we calculated successively larger confidence intervals (50%, 67%, 80%, 90%, and 95%) around the mean, then added values for bias representing the extremes for each interval, and recalculated the t-tests reported in Table 7. The results reported for A2Y cowbirds are, of course, enhanced if the bias (underestimates for live birds) is actually less than the mean, but statistical significance ($\alpha = 0.05$) is lost for the A2Y comparison as the value of the bias approaches the upper limit of the 67% confidence interval. Because the confidence intervals are calculated from two-tailed probabilities, the probability associated with this value of the bias is 17%. This is sufficiently unlikely that we conclude, with some caution, that we have detected selection against large body size among adult male cowbirds.

We have not scrutinized the results of Red-winged Blackbird wing lengths as thoroughly. The comparisons in Table 7 suggest that dead females were smaller than average: note that measurement bias would only strengthen this trend. Size differences within age classes of males are not significant.

Because accumulated dead birds were typically removed from the roost site daily, we may assume that nearly all of those collected on a given day died during the preceding night. Considering the importance of thermoregulation as an energy drain while birds are roosting (e.g. Helms 1968) and the theoretical interest in relationships among temperature, body size, and mortality (Fretwell 1972), we sought evidence of relationships between the size (wing length) of birds dying and the temperatures experienced during a given night. The data available for Brown-headed Cowbirds (Fig. 4) suggest an inverse relationship, with the correlations highest when temperatures less than 4°C are omitted [A2Y, P ($n = 39$, $r = -0.37$) < 0.01; 2ND, P ($n = 36$, $r = -0.33$) < 0.05; F, P ($n = 26$, $r = -0.18$) > 0.05]. A similar analysis of data available for Red-winged Blackbirds revealed no such trend.

Comparison of mean tarsus lengths for live and dead birds in each age/sex category (Table 8) suggests that the observed mortality selects for small tarsi among female cowbirds but for large tarsi among the males of both age classes. The bias in tarsus measurement is sufficiently large compared to the differences detected that one may eliminate the statistical significance ($\alpha = 0.05$) of these results by substituting the upper and lower extremes of its 50% confidence interval for the mean bias for live

TABLE 9. Aggression scores for Brown-headed Cowbirds banded at Rice University, and for those subsequently recovered dead, January–March 1976.

Aggression score	Released		Recovered dead		Log likelihood[a] $[f \log_{10}(f/\phi)]$
	Number	Proportion	Expected (ϕ)	Observed (f)	
1	191	0.13623	2.7246	4	0.66703
2	230	0.16405	3.2810	7	2.30364
3	306	0.21826	4.3652	5	0.29483
4	328	0.23395	4.6790	3	−0.57910
5	347	0.24750	4.9500	1	−0.69461
Totals	1,402	0.99999	19.9999	20	1.99179

[a] Log likelihood ratio test (Bliss 1967: 38): $\chi_4^2 = 4.60517 \Sigma[f \log_{10}(f/\phi)] = 9.17253$, $0.05 < P < 0.06$.

females and males, respectively. Because the observed differences are in the opposite directions, however, it is impossible to select one estimate of the bias that will eliminate the significance of both results simultaneously. Comparable analysis of red-wing tarsus lengths (Table 8) suggests that selection has the effect of removing individuals with small tarsi in both sexes. The t-test for females is significant even if one assumes no measurement bias, but substituting the lower limit of the 80% CI of bias eliminates the significance of the effect for adult males.

Selective mortality among banded cowbirds.—A total of 20 cowbirds tested for aggressiveness when banded were subsequently recovered dead during the roosting season. Most of these were found during collection of dead birds at the roost, and a few were reported to the Bird Banding Laboratory (U.S. Fish and Wildlife Service) by other persons. Analysis of the frequency distribution of aggression classes (Table 9) suggests that less aggressive birds (classes 1 and 2) are overrepresented and more aggressive birds (classes 4 and 5) are underrepresented compared to the set that were banded and released ($P < 0.06$).

A multivariate statistical program was used to compare characteristics of a set of 1,152 banded cowbirds for which all data had been recorded (weight, wing length, tarsus length, fat class, and aggression) to those of 17 such birds that were subsequently recovered dead. Simple correlations among the five variables (Table 10) show that aggression score is not correlated with any other variable (i.e. it is independent of size). A multivariate analysis of variance detected a significant difference between the mean vectors for live and dead birds $[P\ (F_{5,\ 1,163} \geq 3.16) < 0.008]$, with three of the variables (tarsus length, weight, and aggression) contributing significant univariate effects (Table 11). The discriminate function that best separates live and dead sets with a canonical correlation of 0.49 has the following standardized coefficients (in order of decreasing absolute value): weight (0.64), aggression (0.63),

TABLE 10. Simple correlation coefficients among characteristics of Brown-headed Cowbirds banded at Rice University, January–March 1976. Asterisks indicate those that are statistically significant ($\alpha = 0.05$).

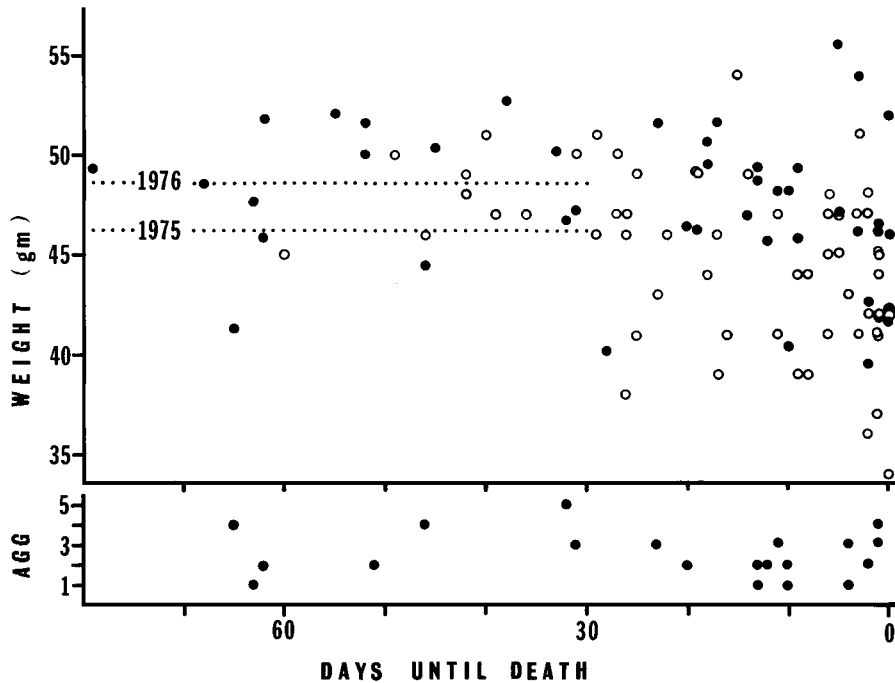|	WL	TL	WT	FAT	AGG
Wing length (WL)	1.00				
Tarsus length (TL)	0.47*	1.00			
Weight (WT)	0.45*	0.38*	1.00		
Fat class (FAT)	−0.01	0.06	0.48*	1.00	
Aggression (AGG)	0.01	0.04	−0.02	−0.04	1.00

Fig. 5. The weight and aggression score for male Brown-headed Cowbirds that were banded and then recovered dead vs. the time until they died. Dots represent data from 1976; open circles, 1975. Dotted lines indicate the overall weight of male cowbirds banded in each year.

tarsus length (0.48), wing length (−0.28), and fat class (−0.16). Because this function gives dead cowbirds lower scores, we may conclude that those destined to die at the roost tended to be less heavy and less aggressive and to have shorter tarsi, longer wings, and more fat than their peers when they were banded.

It is likely that lower weights for birds destined to die result from the fact that many were already sick when banded. A plot of weight vs. days until death (Fig. 5) confirms this suspicion. For the 1976 season, male cowbirds banded more than 30 days before their death averaged 48.7 g ($n = 15$, SE $= 0.8$), which is essentially identical to the mean of all males banded that season, 48.6 g ($n = 2,824$, SE $= 0.1$). Comparable data for the previous year, when competition may have been more intense because the total number of birds roosting at or near Rice was significantly larger (Table 2), show that males banded more than 30 days before their deaths

TABLE 11. Multivariate analysis of variance comparing the characteristics of 1,152 banded Brown-headed Cowbirds to those of 17 that subsequently died; F-tests for the significance of univariate effects.

Character-istics	Effect	Variance	MS	$F_{1, 1,167}$	P
Wing length	0.05323	0.202786	0.1899	0.9363	0.3335
Tarsus length	0.04495	0.022969	0.1354	5.8941	0.0154
Weight	1.25362	17.843746	105.3123	5.9019	0.0153
Fat class	0.08088	1.195045	0.4384	0.3668	0.5449
Aggression	0.41358	1.745595	11.4620	6.5663	0.0106

weighed more (48.1 g, $n = 8$, SE $= 0.8$) than their peers (46.2 g, $n = 1,625$, SE $=$ 0.3).

We suspected that illness might account for lower aggression scores among cowbirds destined to die at the roost. The relevant data are presented in the lower panel of Fig. 5. Though there is a slight suggestion that aggression scores were lower for birds near death, the trends are not statistically significant. The number of individuals involved is very low, however, and the power of our statistical tests considerably diminished. We may conclude only that there is no evidence that illness is responsible for the result and that, if it did have an influence, it was not very dramatic.

DISCUSSION

Though the numbers of dead cowbirds that accumulated at the roost site each night seemed quite large to those of us who were collecting them, it is important to emphasize that they represent a very small percentage of the cowbird population roosting on the Rice campus. The accumulated deaths over the entire roosting season represent only 2% and 1% of the average mark-recapture estimates (Table 3) for 1975 and 1976, respectively. This is a very small proportion of the annual mortality of 50–60% estimated by Fankhauser (1971) from banding returns, and it may even be a small proportion of winter mortality. It is not at all like the 10% mortality during a few days observed by Kessler et al. (1967). Mortality at the roost site has been a component amenable to study, and we hope that an understanding of this component may provide insight applicable to more comprehensive studies in the future.

Contributing factors.—Recent emphasis on the importance of winter mortality for bird population regulation (Lack 1966, Fretwell 1972, Wiens 1974) has focused attention on accompanying selective pressures, especially those related to body size. The physiological advantage of large size in cold climates, long recognized as Bergmann's Rule, must be weighed against the ecological disadvantage of greater food requirements (Kendeigh 1969). Fretwell (1972) has shown that selection against large individuals is expected when the winter food supply is limiting but that this effect may be offset somewhat if size is directly related to social dominance (Fretwell 1969b). Selander (1965, 1966) and Orians (1969) suggest that the larger males of sexually dimorphic polygynous blackbird species may be subject to particularly intensive selection during winter food limitation because sexual selection has forced them to be larger than optimum and large size conveys less social advantage within winter feeding flocks than among contestants for breeding territories.

Brown-headed Cowbirds are sexually dimorphic with respect to size. They have been reported to be both monogamous (Friedmann 1929, Selander 1958) and polygynous (Darley 1971, Payne 1973). During the winter they join other blackbird species in sharing large communal roosts from which they forage in mixed flocks (Meanley 1971, Arnold and Coon 1976). If sexual dimorphism with respect to size results in some resource partitioning (Selander 1966), then males, composing 80–95% of the cowbirds at Rice (Table 4), would encounter more intensive competition. This may explain why male weights were lower in 1975 when the total roosting population in Houston was larger (Tables 1 and 2), while females were not affected. Another indication of this sex differential with respect to competition is the observation reported elsewhere (Johnson et al. 1976), that color-marked males composed a larger-

than-expected proportion of the visitors to residential feeders in 1975 but not in 1976.

Even if the males were not subjected to more intensive competition, Selander (1965) and Orians (1969) have suggested that, being larger than optimum due to sexual selection, males should suffer most during food limitation simply because they require more food per individual for survival. This hypothesis is corroborated by results of our study of selective mortality among male cowbirds in 1976. We found that, even in that less crowded year, the males that died were both larger and less aggressive than average, though these two traits were not correlated (Tables 6–11). The significant inverse correlation between mean fat class and its standard deviation during late January 1976 suggests that some males may have been affected more by food limitation than others, such that individual differences were accentuated during the most stressful days.

The direct relationship between male cowbird body weight (or fat class) and minimum daily temperatures may be used as indirect evidence concerning the adequacy of winter food supplies. Nearly every previous study of this weight–temperature relationship has found an inverse correlation: birds gain weight through fat deposition in response to cold temperatures (Baldwin and Kendeigh 1938, Odum 1949, Helms and Drury 1960, King and Farner 1966, Helms et al. 1967, Helms 1968). Clearly, this response is only possible if food supplies are adequate (Odum 1949). The positive correlation found in this study indicates that cowbirds were able to replenish fat reserves only when warmer temperatures reduced energy demands. Their inability to increase or even to maintain fat reserves on cold days is strong evidence that sufficient food was not available. After early February, they seemed unable to replenish these reserves even during warm days, presumably because food resources were seriously depleted. It is important to note that these inferences apply to both 1975 and 1976. Good (1979) found evidence of food limitation in her studies of body fat, crop content, and liver glycogen levels of cowbirds roosting at Rice University in 1977.

The inability to maintain sufficient fat reserves may be the principal cause of cowbird mortality observed at the Rice roost. Individuals lacking sufficient reserves must be particularly susceptible to stress caused by occasional cold temperatures. Pesticide residues may contribute additional stress when fats are mobilized (van Velzen et al. 1972), though they do not approach levels considered lethal (Stickle et al. 1966). Good (1979) found evidence of stress in her study of adrenal weights at the Rice roost in 1977. Stress may lower an individual's resistance to disease (Selye 1955). Our autopsies suggest that bacterial diseases were prevalent in 1976, and we assume this was true of other years as well. Faddoul et al. (1966) report a high incidence of infection by *Salmonella* sp. among wintering cowbirds. Intestinal coccidiosis is also an important contributor to mortality among the cowbirds we have studied. Both the incidence of coccidiosis (Table 5) and the associated pathology seem to increase following periods of severe cold, an effect similar to that found in cattle (Marsh 1938, Fitzgerald 1962). The fact that coccidial infections were especially frequent among male cowbirds in 1975 but not the following year (Table 5) may indicate that they result from differential exposure to infection at residential feeders (Johnson et al. 1976) rather than from sex-specific susceptibility to infection or pathogenicity (i.e. Mankau and Hamilton 1972). Good (1979) also found that coccidiosis was implicated in cowbird mortality at Rice in 1977: the less fit birds

roosting in low-density marginal parts of the roost had a higher incidence of infection than the more fit, high-density birds.

Selective mortality.—Much of our research effort during the 1976 season was designed to determine whether or not the winter mortality being studied might be exerting the sort of selective pressures expected from theoretical considerations (Fretwell 1972). Considering the important implications of some of these results, it is necessary to emphasize two limitations associated with these data: (1) 1976 proved to be a relatively mild winter, with fewer birds exploiting the resources of the Houston area (Table 2), less mortality among the cowbirds that were there (Fig. 2), and no evidence that their mortality was sex-selective (Table 4); and (2) much of our information is based on a decoy-trapped and banded sample of the birds, which Good (1979) has found to be most representative of the less fit subset of cowbirds at the roost. Both of these factors might be expected to reduce the probability of our detecting selective mortality. The selective pressures suggested by our data might well have seemed even stronger had we done this part of our research in 1975 or with an unbiased sample that included the more fit, live birds.

Age-dependent mortality.—Botkin and Miller (1974) suggest that adult mortality in birds must increase somewhat with age if longevity records are to be consistent with survivorship curves. Results of the comparison of live and dead birds in 1976 tend to confirm this suggestion in a crude way for both cowbirds and red-wings (Table 6); males experiencing at least their second winter are clearly overrepresented among the dead. Because the comparison is with a decoy-trapped sample, these results could be attributable to a trap bias for young males, but our estimate of trap bias is in the opposite direction, and other evidence that large body size (wing length) is disadvantageous (Table 7, Fig. 4) leads us to conclude that older (and larger) adult males experience higher mortality in the winter.

Size-selective mortality.—Wing length is considered a useful indicator of body size for intraspecific comparison (James 1970). Large body size confers certain physiological advantages for tolerating cold stress, but, as Kendeigh (1969) has said, "the physiological advantages must outweigh the ecological disadvantages," especially the need for more food. Fretwell (1972) considers food limitation and cold stress to be the most likely causes of mortality for overwintering populations and shows that these alternatives lead to opposite expectations with respect to size selectivity of mortality. Johnston et al. (1972) present evidence that large male sparrows had the expected advantage under severe winter storm stress, but Baker and Fox (1978) found just the opposite for temperature-stressed male grackles sprayed with Turgitol in a winter roost. Our data (Table 7) show large adult male cowbirds to have been at a disadvantage, a result that is consistent with other evidence for food limitation at the the Rice roost. An inverse relationship between daily temperature minima and the mean wing length of dead cowbirds (Fig. 4) suggests that temperature stress is a factor contributing to cowbird mortality, but the fact that cooler temperatures affect the larger birds suggests that this influence is indirect, probably through depletion of fat reserves that were already low because of food limitation.

Tarsus length is considered to be more closely related to food-getting than wing length (Fretwell 1969b) and is sensitive to selective pressure at least partly independent of body size (Grant 1971). Among the characteristics recorded during our banding program at the Rice roost, tarsus length proved to be an especially significant component in discriminating cowbirds that subsequently died from their peers (Table 11). In light of evidence presented above, that cowbirds were faced with limited

food supplies while occupying the Rice roost, it is especially interesting to note that the mortality observed tended to select for sexual dimorphism with respect to tarsus length (Table 8). Selander (1966) reviews evidence that such sexual dimorphism is often related to differential niche utilization, but we know of no evidence suggesting such an effect among winter-feeding flocks of cowbirds. Because the sexes are known to forage together in mixed flocks (Arnold and Coon 1976), such differences may involve relatively subtle behavioral phenomena. One indication of a difference in feeding behavior is the observation, reported by Johnson et al. (1976), that, among the cowbirds marked with colored leg streamers during the winter of 1975, males were sighted disproportionately visiting residential feeders. We have hypothesized that this tendency for males to visit feeders more often was both a response to competition for food and a factor contributing to higher mortality through exposure to intestinal coccidiosis.

Aggression.—Perhaps the most interesting result of this study is the fact that a relatively simple index of aggressiveness proved to be such an important factor in discriminating the set of dead banded cowbirds from their peers (Tables 9 and 11). Only weight had a greater standardized coefficient in the discriminate function. Weight clearly declined with decreasing time until death (Fig. 5), leading us to conclude that low weight was a symptom of ill health, but aggressiveness did not exhibit a clear pattern. Furthermore, aggression scores show virtually no correlation with measures of size or fat class (Table 10). Burtt and Giltz (1969) found significant interspecific differences in aggressiveness (Brown-headed Cowbirds > Common Grackles > Red-winged Blackbirds > Starlings), as well as consistent individual differences within species. It now seems possible that these individual differences have an important influence on survival during the winter roosting season.

We do not know how aggressiveness as measured by the test we used is related to social behavior among cowbirds in a roost or flock. We hope that its apparent significance in this study will stimulate research into this relationship. There is sufficient evidence to tempt us to speculate on the value of aggressiveness to a roosting bird in winter. Good (1979) found a surprising amount of internal structure within blackbird roosts, with more fit, better-fed, less stressed birds concentrated at very high densities in certain, presumably favorable, locations. She suggests that social interaction in staging areas and during spectacular aerial maneuvers before entering the roost may determine which individuals can benefit from occupying such preferred locations. It is possible that individual differences with respect to aggressiveness could influence such social behavior. Some authors have observed aggressive encounters within feeding flocks of other roosting species (Lockie 1956, Murton et al. 1966) and have suggested that they play an important role in population regulation. Fretwell (1969a) demonstrated the existence of a dominance hierarchy among individually marked members of a winter flock of juncos and found that the more dominant individuals experienced better survival during the winter. In that case, dominance was directly related to body size. Rohwer (1975) found that dominance within flocks of Harris' Sparrows is determined by plumage characteristics ("studliness") rather than size and suggested that less stable flocks should have more variable plumage so that individual differences could be easily recognized and dominance hierarchies established with a minimum of fighting. Though this hypothesis was corroborated for a large number of species, Rohwer specifically excluded winter blackbird flocks from his analysis. Arnold and Coon (1976) have demonstrated that feeding flocks are not very stable, yet there is very little plumage variability. Fighting

among blackbird flock members would be consistent with Rohwer's reasoning. This might explain why cowbirds are so aggressive (Burtt and Giltz 1969) and why aggressiveness makes such an important contribution to survival during the winter.

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