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MIGRATION PATTERNS FOR AGE AND SEX CLASSES OF BLACKBIRDS AND STARLINGS

By Richard A. Dolbeer

Red-winged Blackbirds (*Agelaius phoeniceus*), Brown-headed Cowbirds (*Molothrus ater*), and Starlings (*Sturnus vulgaris*) are ubiquitous breeding birds in much of North America. The Common Grackle (*Quiscalus quiscula*) is an abundant breeding bird east of the Rocky Mountains (Dolbeer and Stehn 1979). Although these species are widely dispersed and generally unassociated during the nesting season, they often associate closely in winter roosts containing up to 10 million birds in the southern United States (Meanley and Webb 1965, Meanley 1971). Little is known about the comparative migration patterns of the four species and the resulting mixture of local breeding populations in winter. Comparative analyses within and among these species provide the opportunity for testing hypotheses about migration. Furthermore, a better understanding of blackbird (Icteridae) and Starling migration is of practical importance because of increased conflicts between these species and humans, especially at winter roost sites (Graham 1978).

My first objective in this study was to compare dispersal distances from one breeding season to subsequent breeding seasons among species and age classes. Dispersal of animals from site of birth to place of breeding is recognized as an important mechanism of population regulation, gene pool mixing, and species range expansion (e.g. Howard 1960, Murray 1967). Thus, I hypothesized that birds banded as nestlings or fledglings and recovered in subsequent breeding seasons would be found at greater mean distances from banding sites than would birds banded as adults. A second objective was to compare the timing and distances of migration from the nesting area to the wintering area among species and age and sex classes. Specific hypotheses to be tested were that the smaller species or sex class from a given nesting locality would migrate farther south because of bioenergetic constraints (Ketterson and Nolan 1976) and that hatching-year (HY) birds would migrate farther south than would after-hatching year (AHY) birds because of social subordinance (Gauthreaux 1979). A third objective was to compare among species the dispersion in winter of local breeding populations to gain insight into the degree of intermingling of populations at winter roost sites.

METHODS

Band recovery records for the four species from 1924 through 1979 were obtained from the U.S. Fish and Wildlife Service, Laurel, Maryland. Only records containing the date (to the nearest 10 days) and the latitude and longitude (to the nearest 10 minutes) of banding and recovery were used. Analyses were based primarily upon distances be-

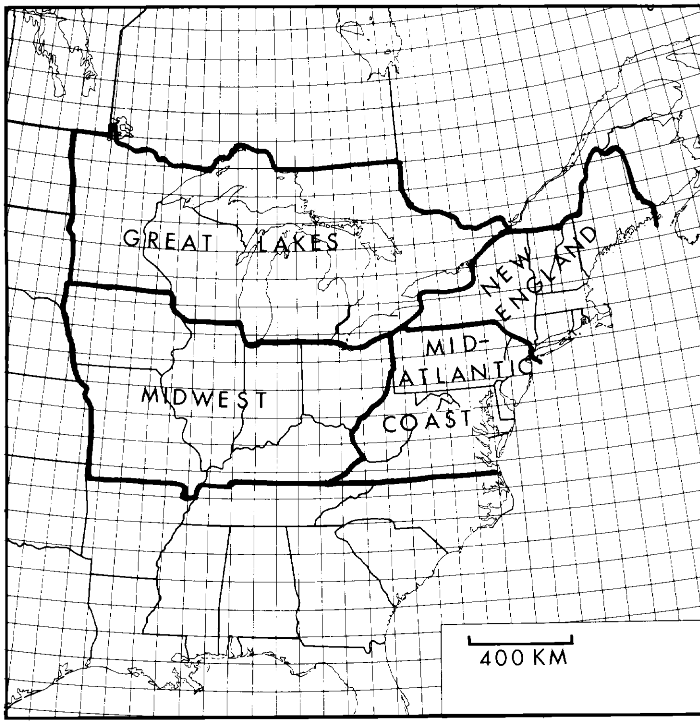

FIGURE 1. Location of four regions containing 70–85% of bandings for Red-winged Blackbirds, Common Grackles, Brown-headed Cowbirds, and Starlings.

tween banding and recovery sites; thus, all recoveries at banding stations were excluded because these stations are located non-randomly.

For some analyses, recovery records for the entire continent were used. To examine migration patterns on a regional basis, the continent was initially divided into 16 geographical regions. However, only four regions (New England, Great Lakes, Midwest, and Mid-Atlantic Coast) had sufficient data to make meaningful comparisons among the species (Fig. 1). These regions contained about 70% (Red-wings) to 85% (cowbirds) of the usable recoveries. In addition, to examine migration in relation to latitude of breeding populations, I used as geographical units 2° intervals of latitude from 32° to 47° between 75° and 100° longitude. This area included most of the four regions (Fig. 1) except the coastal area of New England.

In these analyses I was primarily concerned with measuring movements from one seasonal location to another. The reproductive period, when movements should be at a minimum, was established for each species by a review of the literature. The reproductive period used for Red-wings and grackles was 20 April–20 July (Erskine 1971, Dolbeer

1978); for cowbirds, 20 April–20 June (Scott and Middleton 1968); and for Starlings, 1 April–20 July (Kessel 1957, Collins and de Vos 1966). The winter roosting period, established as 1 January–28 February, was the period when the birds were at a maximum distance from their locations during the reproductive period (see results). These periods, although not precise for populations from all geographic areas of North America, are accurate for the regions from which the majority of bandings used in the analysis were derived.

RESULTS

Sample Sizes

Usable band recoveries totaled 3528 (31% of all recoveries) for Red-wings, 20,352 (59%) for grackles, 4952 (37%) for cowbirds, and 13,828 (58%) for Starlings (Table 1). The greater proportion of non-banding station recoveries for grackles and Starlings is perhaps because these species associate with people more than do Red-wings and cowbirds. Of the resulting usable recoveries, 2116 Red-wings (60%), 7734 grackles (38%), 2971 cowbirds (60%), and 3457 Starlings (25%) were identified by sex and age (HY or AHY). Sample sizes were further restricted in the various analyses in that only birds banded or recovered in specific periods of the year could be used.

Distances Moved: Reproductive Period to Subsequent Reproductive Period

Mean distance between banding and recovery sites for AHY birds banded and recovered in the reproductive period of different years was 31 km or less for Red-wings, grackles, and Starlings (Table 2). This indicates that adults of these species usually return to near their previous

TABLE 1. Number of banded blackbirds and Starlings recovered at banding stations and at random in North America, 1924–1979.

How obtained[a]	Number of recoveries (% of total)			
	Red-wing	Grackle	Cowbird	Starling
Total	11,478 (100)	34,205 (100)	13,429 (100)	23,760 (100)
Band station recovery				
Local (99)[a]	5292 (46)	7534 (22)	5528 (41)	4896 (21)
Foreign (89)	1010 (9)	893 (3)	1414 (10)	536 (2)
Misc. (10, 51)	192 (2)	186 (1)		
Random,[b] but unusable,[c] recovery	1456 (12)	5240 (15)	1535 (12)	4500 (19)
Random,[b] usable recovery	3528 (31)	20,352 (59)	4952 (37)	13,828 (58)

[a] See "how obtained" codes in North American Bird Banding Manual (U.S. Fish and Wildlife Service and Canadian Wildlife Service, 1976).
[b] Found dead, shot, or accidentally captured, but not at a banding station.
[c] Inexact date or location or experimentally treated bird (status = 6).

TABLE 2. Mean distance (km) ± standard deviation between banding and recovery site for hatching year (HY) and after-hatching-year (AHY) birds banded during the reproductive period of 1 year and recovered during the reproductive period of a subsequent year.

Species	Banded as AHY: Male	Banded as AHY: Female	Banded as AHY: All[1]	Banded as HY[1]	Mean difference (AHY-HY)
Red-wing	31 ± 98 (194)[2]	34 ± 116 (31)	31 ± 100 (228)a	35 ± 95 (110)a	−4
Grackle	26 ± 125 (1106)	14 ± 59 (844)	24 ± 110 (2625)a	35 ± 128 (869)a	−11*
Cowbird	44 ± 158 (169)	95 ± 264 (68)	59 ± 193 (243)b	17 (3)	
Starling	15 ± 51 (99)	10 ± 37 (109)	16 ± 61 (390)a	80 ± 197 (400)b	−64*

[1] Within a column, mean values with different letters are significantly ($P < .05$) different. Duncan's Multiple Range Test.
[2] Sample size.
* Significant at $P < .05$, t-test.

nesting site. The mean recovery distance of 59 km for AHY cowbirds was significantly greater than that for the other 3 species. AHY male grackles were recovered at a greater mean distance (26 km) than were AHY females (14 km); this was the only significant difference recorded between sexes.

I hypothesized that birds banded as nestlings or fledglings and recovered in subsequent reproductive seasons would be found at greater mean distances from banding sites than would be birds banded as adults. There was no significant difference between these age classes for Red-wings; grackle HY birds showed a significant 11 km (46%) increase over AHY birds; and HY Starlings showed a significant 64 km (400%) increase over AHY Starlings. The sample size of HY cowbirds was too small (3) to make comparisons with AHY birds (Table 2).

About 30% of the HY Starlings were recovered in subsequent breeding seasons over 50 km from their nest location compared with 10–12% of HY Red-wings and grackles. About 12% of HY Starlings had dispersed distances greater than 200 km (Fig. 2).

Distances Moved: Reproductive Period to Subsequent Monthly Periods

Mean distances between banding and recovery sites for AHY birds banded during the reproductive period and recovered during subsequent monthly periods of any year were calculated for four regions (Table 3). This analysis was undertaken to determine the times of year AHY birds undertake major movements away from or toward their breeding locations. Insufficient sample sizes of known sex and age birds were available on a monthly basis to break down the analysis by age and sex.

In all four regions, grackles and Starlings remained in the vicinity

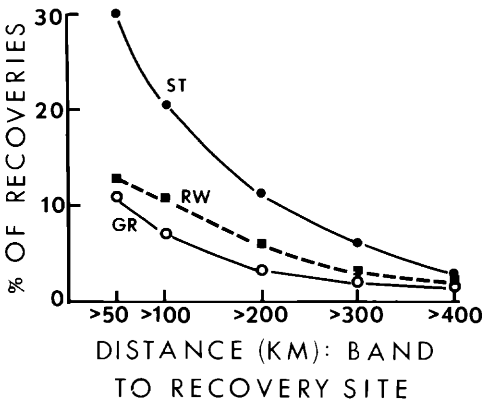

FIGURE 2. Percent of recoveries that exceeded various distance intervals from banding sites for 113 Red-wings (RW), 876 grackles (GR), and 468 Starlings (ST) banded as nestlings or fledglings and recovered during the breeding season of a subsequent year.

(<130 km) of their nesting sites until November when fall migration occurred. Red-wings were sedentary in late summer in the Great Lakes and Midwest regions; however, in New England, Red-wings often moved 200–350 km from their nesting sites by August. Cowbirds showed the greatest degree of late summer and early fall movements; by October, they were found a mean of 500 km from their location during the reproductive period in all but the Mid-Atlantic regions.

In the four regions, all species were at the maximum migration distance from their nesting locality in January or February (Table 3). Spring migration occurred mainly in March; and by April, individuals of all four species were generally recovered within 100 km of their breeding locality of previous years. One notable difference among species was that during March cowbirds had not progressed as far in their northward migration as had the other species. Thus, of the 4 species, cowbirds were the first to leave and last to return to their breeding season locality.

Cowbirds and Red-wings consistently migrated farther than did grackles in all four regions. Starlings migrated the least distance. The comparison of migration distances among species is statistically treated below.

Distances Moved: Reproductive Period to Winter Period

AHY males vs AHY females.—The hypothesis tested was that for the 3 blackbird species, the smaller females (Table 4) would migrate greater distances than the larger males and that sexually monomorphic Starlings would show no differences in migration distances.

Red-wings, with the greatest sexual dimorphism (female weight about

TABLE 3. Mean distance from banding to recovery site for after-hatching-year birds banded in reproductive period and recovered in subsequent monthly periods of any year.

		Distance (km) ± standard deviation (N)			
Region	Period	Red-wing	Grackle	Cowbird	Starling
Great Lakes	Aug.	57 ± 153 (42)	33 ± 98 (440)	186 ± 362 (16)	62 ± 124 (42)
	Sept.	24 ± 34 (22)	29 ± 93 (302)	299 ± 334 (19)	89 ± 206 (32)
	Oct.	60 ± 103 (36)	43 ± 117 (188)	508 ± 523 (35)	129 ± 291 (40)
	Nov.	564 ± 530 (34)	489 ± 426 (108)	849 ± 630 (28)	200 ± 388 (60)
	Dec.	1087 ± 374 (22)	838 ± 435 (90)	982 ± 705 (35)	242 ± 353 (143)
	Jan.	1166 ± 293 (40)	933 ± 432 (125)	1225 ± 545 (38)	534 ± 544 (200)
	Feb.	1140 ± 309 (32)	1032 ± 328 (157)	1137 ± 581 (52)	375 ± 446 (186)
	Mar.	483 ± 528 (44)	509 ± 471 (289)	826 ± 670 (51)	279 ± 368 (318)
	Apr.	40 ± 121 (79)	94 ± 249 (743)	156 ± 323 (97)	34 ± 88 (72)
Midwest	Aug.	63 ± 50 (44)	21 ± 62 (467)	320 ± 593 (7)	62 ± 161 (74)
	Sept.	88 ± 123 (39)	32 ± 88 (325)	58 ± 74 (6)	57 ± 75 (89)
	Oct.	114 ± 226 (32)	46 ± 123 (275)	506 ± 555 (12)	70 ± 96 (72)
	Nov.	479 ± 454 (24)	326 ± 351 (159)	712 ± 592 (21)	188 ± 345 (96)
	Dec.	936 ± 223 (18)	643 ± 353 (130)	756 ± 438 (5)	184 ± 320 (150)
	Jan.	1000 ± 214 (22)	719 ± 319 (224)	1008 ± 476 (15)	233 ± 352 (275)
	Feb.	900 ± 220 (25)	687 ± 304 (237)	974 ± 478 (30)	133 ± 232 (253)
	Mar.	242 ± 355 (35)	302 ± 363 (549)	728 ± 580 (26)	108 ± 169 (293)
	Apr.	46 ± 61 (47)	79 ± 198 (805)	50 ± 124 (35)	74 ± 154 (89)
New England	Aug.	183 ± 187 (29)	17 ± 50 (179)	346 ± 414 (33)	6 ± 9 (35)
	Sept.	357 ± 151 (12)	28 ± 62 (92)	334 ± 370 (18)	16 ± 40 (52)
	Oct.	293 ± 271 (271)	26 ± 49 (69)	518 ± 531 (32)	56 ± 94 (32)
	Nov.	551 ± 386 (14)	220 ± 252 (45)	630 ± 465 (29)	125 ± 221 (85)
	Dec.	187 ± 374 (26)	366 ± 310 (46)	464 ± 344 (34)	233 ± 300 (152)
	Jan.	769 ± 431 (19)	458 ± 328 (49)	782 ± 617 (28)	376 ± 420 (254)
	Feb.	647 ± 319 (13)	458 ± 304 (53)	750 ± 421 (30)	268 ± 333 (213)
	Mar.	296 ± 436 (35)	210 ± 247 (171)	426 ± 330 (61)	222 ± 307 (251)
	Apr.	48 ± 124 (74)	62 ± 160 (328)	85 ± 172 (125)	25 ± 57 (50)
Mid-Alantic States	Aug.	116 ± 185 (30)	21 ± 59 (216)	37 ± 64 (11)	12 ± 26 (61)
	Sept.	109 ± 196 (13)	32 ± 62 (106)	99 ± 181 (7)	50 ± 111 (54)
	Oct.	110 ± 131 (13)	29 ± 55 (94)	234 ± 278 (13)	34 ± 76 (70)
	Nov.	328 ± 458 (6)	121 ± 168 (67)	276 ± 321 (13)	46 ± 139 (109)
	Dec.	436 ± 382 (14)	272 ± 211 (66)	404 ± 534 (18)	60 ± 182 (247)
	Jan.	596 ± 345 (17)	277 ± 243 (65)	520 ± 503 (16)	122 ± 273 (304)
	Feb.	342 ± 422 (34)	287 ± 228 (105)	768 ± 548 (25)	112 ± 240 (259)
	Mar.	38 ± 141 (40)	52 ± 92 (234)	256 ± 417 (30)	63 ± 137 (293)
	Apr.	72 ± 215 (36)	20 ± 97 (433)	30 ± 115 (83)	22 ± 72 (83)

65% that of male), showed the strongest support for the hypothesis. AHY females recovered in winter were significantly farther from their nesting locations by 187 to 300 km than were AHY males in the 4 regions. For all Red-wing recoveries, the mean difference in distance was 247 km (Table 5). Grackles, with female weights about 81% that of males, also showed the same trend but not as strongly as did Red-wings. In all four regions, mean distance for female grackles was greater, but in only one (Midwest) was it statistically significant ($P \leqslant .05$). For all recoveries, there was a significant difference of 112 km in mean migration distance. Sample size was sufficient to compare AHY male and female grackle recoveries by 2° intervals of latitude for eastern North America, and this comparison also suggested that, for a given nesting

TABLE 4. Mean body weights (g) of blackbirds and Starlings in Pennsylvania, November–March. Sample size is in parentheses (from Clench and Leberman 1978).

Age-sex class	Red-wing	Grackle	Cowbird	Starling
AHY male	71.6 (15)	118.2 (3)	53.0 (2)	80.6 (9)
AHY female	45.4 (11)	96.2 (2)	40.4 (7)	79.3 (9)
HY male	69.5 (21)	117.3 (13)		79.4 (2)
HY female	45.4 (28)	93.4 (14)	40.5 (3)	78.8 (2)

locality, females migrated slightly farther (about 100 km) than did males (Fig. 3).

Recovery distances of male and female cowbirds did not support the hypothesis. Although female weight is about 76% that of males, there were no significant differences in migration distances between sexes within regions or for total recoveries (Table 5). Male and female Starlings, as hypothesized, showed no significant differences in migration distances.

HY vs AHY.—In examining migration distances from natal to winter site of HY birds recovered in their first winter, I could not separate sex classes because of small sample sizes of birds of known sex. Thus, I tested the hypothesis that distances migrated by HY birds were greater than those of AHY birds by comparing all HY birds with AHY male birds and AHY female birds separately (Table 5).

In at least some regions, HY Starlings migrated longer mean distances than did either male or female AHY Starlings. Mean distances of HY birds were significantly greater than either male or female AHY birds by 249 to 508 km in the Great Lakes and Midwest regions, and by 114 to 121 km for all recoveries combined. The analysis of migration distances by 2° intervals of latitude for eastern North America also strongly supported the hypothesis that Starlings migrate farther in their first winter than they do as adults (Fig. 3).

For grackles and Red-wings, the analysis indicated that at least in some regions, HY birds migrated farther by 200 to 350 km than did AHY males (Table 5). The analysis of grackle migration distances by 2° intervals of latitude also suggested that HY birds migrated farther than AHY males and that these HY birds migrated about the same or slightly farther than did AHY females (Fig. 3). There was no consistent evidence that HY Red-wings were migrating lesser or greater distances than were AHY females, although small sample sizes may have precluded a meaningful analysis. Too few HY cowbirds were recovered in their first winter to make meaningful comparisons with AHY birds.

Comparison among species of AHY birds.—As mentioned earlier in reference to Table 3, consistent differences appeared among the 4 species in the distances migrated from the nesting season location to the winter location. A comparison among AHY males of the mean distance between banding and recovery sites revealed that in all 4 regions, Starlings

TABLE 5. Mean distance (km) ± standard deviation between banding and recovery site for after-hatching-year male (AHY M) and female (AHY F) Redwings (RW), grackles (GR), cowbirds (CB), and Starlings (ST) banded during the reproductive period and recovered during a subsequent winter roosting period (Jan.–Feb.), and for hatching-year birds of both sexes (HY MF) banded during the reproductive period and recovered during their first winter. Sample sizes are in parentheses.

		Age and sex class			Mean diff.	Mean diff.	Mean diff.
Region	Species	AHY M	AHY F	HY MF	(AHY M – AHY F)	(AHY M – HY MF)	(AHY F – HY MF)
N. Eng.	RW	693 ± 414 (23)	880 ± 252 (7)	1018 ± 144 (10)	–187*	–325*	–138
G. Lakes		992 ± 429 (29)	1222 ± 260 (14)	1177 ± 258 (13)	–230*	–185	45
Midwest		887 ± 241 (34)	1187 ± 152 (3)	929 ± 216 (13)	–300*	–42	258
Mid-Atl.		347 ± 363 (40)	595 ± 414 (10)	461 ± 351 (7)	–248*	–113	126
Total		506 ± 502 (197)	753 ± 562 (51)	858 ± 488 (60)	–247*	–352*	–105
N. Eng.	GR	437 ± 357 (37)	520 ± 312 (28)	574 ± 430 (12)	–83	–137	–54
G. Lakes		870 ± 504 (58)	885 ± 442 (45)	1022 ± 244 (32)	–15	–152	–137
Midwest		571 ± 300 (91)	744 ± 356 (75)	788 ± 299 (47)	–173*	–217*	–44
Mid-Atl.		252 ± 256 (54)	322 ± 200 (41)	202 ± 129 (13)	–70	50	120
Total		594 ± 500 (328)	706 ± 514 (251)	825 ± 456 (118)	–112*	–231*	–119*
N. Eng.	CB	738 ± 501 (23)	689 ± 583 (25)	889 ± 324 (7)	49	–151	–200
G. Lakes		1062 ± 603 (62)	1119 ± 692 (17)	1046 ± 606 (4)	–57	16	73
Midwest		984 ± 516 (28)	1127 ± 403 (7)	958 ± 227 (2)	–143	26	169
Mid-Atl.		665 ± 578 (22)	641 ± 446 (10)	443 ± 333 (4)	24	222	198
Total		861 ± 580 (162)	841 ± 591 (67)	789 ± 450 (18)	20	72	52
N. Eng.	ST	218 ± 380 (49)	235 ± 435 (46)	354 ± 532 (30)	–17	–136	–119
G. Lakes		437 ± 491 (70)	249 ± 345 (38)	757 ± 673 (22)	188	–320*	–508*
Midwest		206 ± 299 (65)	205 ± 282 (36)	455 ± 438 (40)	1	–249*	–250*
Mid-Atl.		88 ± 258 (103)	90 ± 247 (50)	99 ± 226 (44)	–2	–11	–9
Total		237 ± 410 (398)	230 ± 401 (218)	351 ± 482 (161)	7	–114*	–121*

* Significantly ($P < .05$) different from zero, *t*-test.

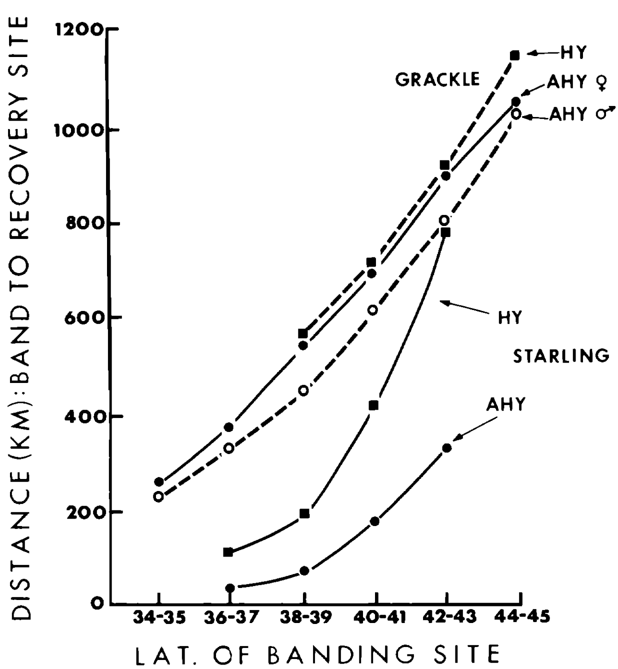

FIGURE 3. Mean distance from banding to recovery site for 87 hatching-year, 177 after-hatching-year female, and 233 after-hatching-year male Common Grackles, and for 84 hatching-year and 961 after-hatching-year Starlings banded during the reproductive period in eastern North America (75–100° longitude) and recovered in winter (Jan.–Feb.).

migrated the least distance with grackles, Red-wings, and cowbirds migrating progressively farther (Table 6). A 2-way analysis of variance (species and regions) indicated that for the 4 regions, grackles migrated significantly farther than did Starlings, and that Red-wings and cowbirds migrated significantly farther than did grackles. The pattern for the 3 blackbird species was consistent with the hypothesis that mean migration distance is inversely related to body size. Starlings did not fit into this pattern; they weighed less than grackles but also migrated significantly less distance.

A comparison of AHY Starling and grackle recoveries by 2° intervals of latitude for eastern North America also showed that grackles migrated farther than did Starlings at all latitudes from 32° to 47° (Fig. 4). One notable result of this analysis was that, although grackle populations appeared to be migratory at all latitudes, Starling populations below 40° latitude revealed little evidence of migration in winter away from the nesting location. Cowbird and Red-wing migration patterns in relation to latitude appeared similar to that of grackles; however, sample sizes

TABLE 6. Mean distance (km) ± standard deviation between banding and recovery site for AHY male birds banded during the reproductive period and recovered during the winter period (Jan.–Feb.). Sample sizes are in parentheses.

Region	Starling	Grackle	Red-wing	Cowbird
New England	218 ± 360 (49)	437 ± 357 (37)	693 ± 414 (23)	738 ± 501 (23)
Great Lakes	437 ± 491 (70)	870 ± 504 (58)	992 ± 429 (29)	1062 ± 603 (62)
Midwest	206 ± 299 (65)	571 ± 300 (91)	887 ± 241 (34)	984 ± 516 (28)
Mid-Atlantic	88 ± 258 (103)	252 ± 256 (54)	347 ± 363 (40)	665 ± 578 (22)
Mean of 4 regions[1]	237a	532b	729c	837c

[1] Means with different letters are significantly different ($P < .05$), 2-way analysis of variance and Duncan's Multiple Range Test.

were less than 5 for several latitudes so these data are not presented in Fig. 4.

Distribution of Recoveries in Winter

I examined the pattern of winter recoveries for birds banded during the reproductive period within single degree blocks of latitude and longitude (an area about 80 by 110 km at 42° latitude) to determine the degree of dispersal in winter of local breeding-season populations. I

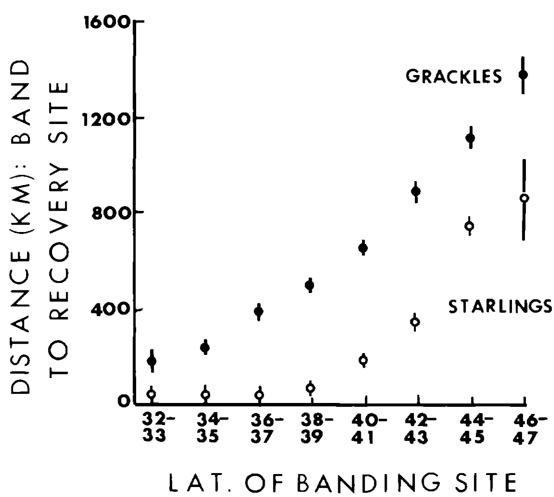

FIGURE 4. Mean distance (±SE) from banding to recovery site for after-hatching-year Common Grackles (N = 855) and Starlings (N = 1116) banded during reproductive period in eastern North America (75–100° longitude) and recovered in winter (Jan.–Feb.).

first determined for each species those degree blocks north of 40° latitude that contributed at least 10 recoveries in winter of summer-banded birds (the reproductive period was extended to 31 July for cowbirds and 31 August for the other species to increase sample sizes). I then calculated for each of these data sets, the geographic center of the winter recovery sites (i.e., mean latitude and longitude of recoveries), the mean distance of each recovery from the geographic center (mean dispersive distance), and the land area of an ellipsoid containing 50% of the recoveries (Table 7). The mean dispersive distance and the land area of the ellipsoid were my measures of the magnitude of dispersion in winter of a population from a single 80 × 110 km area during the breeding season.

The mean dispersive distance was 283 km (range 164–423) for 6 Red-wing populations, 285 km (240–338) for 8 grackle populations, 272 km (83–465) for 5 Starling populations, and 451 km (370–552) for 3 cowbird populations. The area of the ellipsoid containing 50% of the recoveries averaged 197,000 to 246,000 sq km for the grackle, Red-wing, and Starling populations, and 495,000 sq km for the cowbird populations (Table 7). This indicates that, on the average, the populations of grackles, Red-wings, and Starlings from an 80 × 110 km area in summer disperse in winter such that half the birds are recovered within an ellipsoid having an area about the size of Tennessee and Kentucky combined.

The data for cowbirds, although limited to only 3 populations, suggest that this species disperses in winter to a greater extent than do the other species. The average ellipsoid containing 50% of the winter recoveries covers an area about the size of Tennessee, Kentucky, Mississippi, and Alabama combined. Based on the standard deviations of mean latitudes and longitudes of winter recoveries (Table 7), longitude of recovery was considerably more variable for cowbirds than for the other species, especially Red-wings and grackles. This suggests that cowbirds disperse to a greater extent in an east-west orientation than do the other species.

Unfortunately only one banding degree block (lat. 42°, long. 82°, southwestern Ontario) had at least 10 winter recoveries of each species to make direct comparisons among species of dispersal from a given breeding locality (Table 7). A Duncan's Multiple Range Test indicated that cowbirds from southwestern Ontario had a significantly greater mean dispersive distance (532 km) than did Starlings (289 km) or grackles (338 km). The mean dispersive distance of Red-wings (423 km) was not significantly different from that of the other species. To demonstrate visually the extent of dispersal, the locations of winter recoveries for each species of bird banded during the reproductive period at latitude 42°, longitude 82° are shown in Fig. 5.

The above analysis provides, for a given breeding locality of about 80 × 110 km, a view of the distribution of recoveries in winter over all years, 1924 to 1979. To determine if in a given year the dispersal pattern is much more restricted, I examined, where sample size permitted, the

TABLE 7. Mean latitude and longitude (geographic center) of winter recovery sites and two measures of the magnitude of dispersion of recovered birds from the geographic center for birds banded during the reproductive period in various degree blocks of latitude and longitude in eastern North America. Only degree blocks that had at least 10 bandings resulting in recoveries were used.

	Band site in summer			Geographic center of winter recoveries		Magnitude of dispersion of winter recoveries	
Species	Lat.	Long.	N	Mean lat. ± SD	Mean long. ± SD	Mean distance ± SD of recov. from geo. center	Area (1000 sq km) of ellipsoid containing 50% of recoveries[1]
Red-wing	41	69	11	36.7 ± 2.6	76.0 ± 3.1	291 ± 252	112
	41	82	31	33.4 ± 2.4	82.6 ± 2.3	308 ± 135	291
	42	77	28	35.3 ± 2.0	78.3 ± 1.9	219 ± 163	169
	42	82	10	34.0 ± 4.2	82.5 ± 2.4	423 ± 259	477
	42	83	11	32.6 ± 1.5	84.0 ± 3.1	290 ± 145	222
	43	79	10	33.2 ± 1.5	80.7 ± 1.4	164 ± 126	65
Mean						283 ± 173	223
Grackle	41	82	19	35.1 ± 2.7	86.6 ± 2.3	288 ± 214	200
	41	87	35	35.0 ± 2.4	88.9 ± 1.4	243 ± 179	184
	42	71	16	39.6 ± 2.2	74.4 ± 2.2	240 ± 172	123
	42	82	11	36.2 ± 3.1	85.2 ± 2.2	338 ± 176	275
	42	83	14	38.2 ± 3.2	85.0 ± 1.5	334 ± 154	124
	42	84	29	35.6 ± 2.7	87.6 ± 1.9	270 ± 213	198
	42	87	65	34.6 ± 3.1	89.4 ± 1.4	301 ± 213	218
	44	93	35	34.1 ± 2.2	91.7 ± 1.9	242 ± 171	257
Mean						285 ± 194	197
Starling	41	82	30	38.4 ± 3.0	85.3 ± 3.8	392 ± 240	470
	42	71	16	42.2 ± 0.8	71.5 ± 1.1	83 ± 90	102
	42	76	18	39.7 ± 4.0	79.6 ± 4.7	465 ± 343	388
	42	82	17	41.0 ± 2.3	84.1 ± 2.9	289 ± 195	102
	42	83	12	40.0 ± 2.6	85.8 ± 3.4	361 ± 154	250
Mean						272 ± 223	246
Cowbird	41	69	11	33.7 ± 2.2	80.4 ± 5.0	370 ± 348	348
	42	82	13	35.4 ± 3.6	87.0 ± 5.4	552 ± 259	387
	46	85	11	31.8 ± 1.5	90.7 ± 4.9	431 ± 195	751
Mean						541 ± 274	495

[1] Calculated from equation (12) in Jennrich and Turner (1969).

mean dispersive distances for single years and compared this with the mean dispersive distance for all years. In only one of the 7 cases where 5 or more birds of the same species from a single degree block were recovered in the same winter was mean dispersive distance significantly

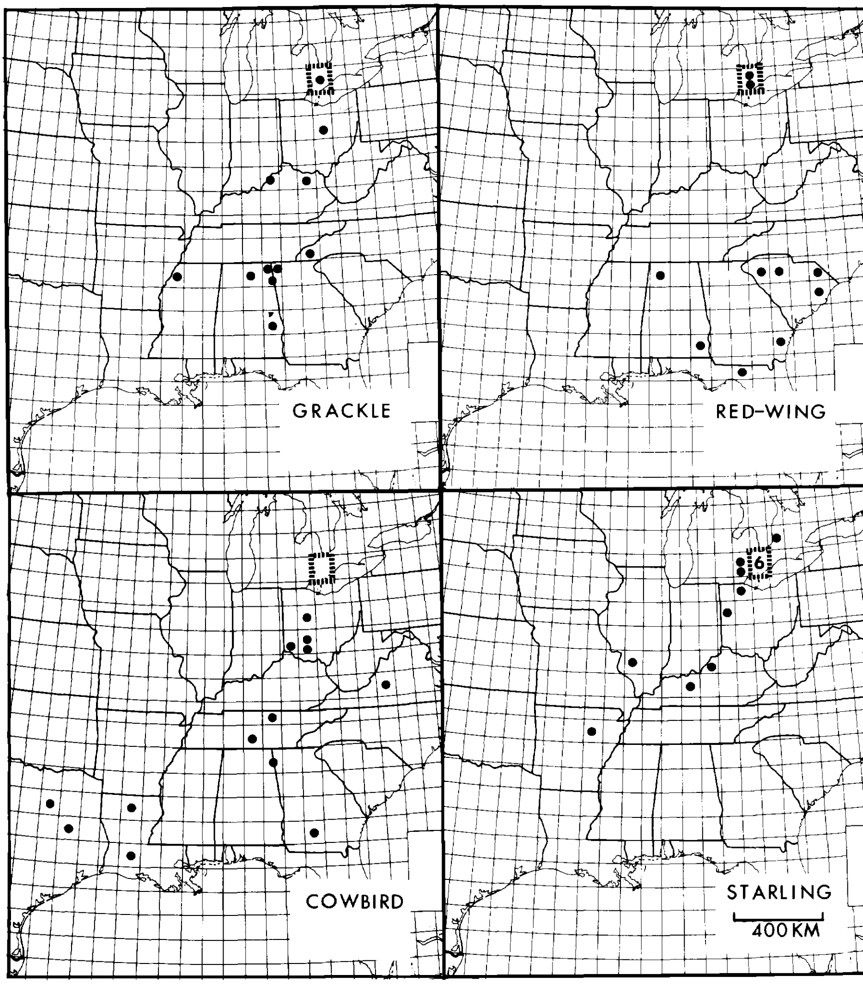

FIGURE 5. Location of recoveries during winter (Jan.–Feb.) for Red-wings, grackles, cowbirds, and Starlings banded in the single degree block, latitude 42°, longitude 82°, during the reproductive period.

less than that for all years combined (Table 8). In 3 of the 7 cases, the mean dispersive distance for a single winter was actually greater (although not significantly so) than that for all years combined. Thus, the limited data suggest that the dispersion in a single winter is similar to the pattern obtained for all years combined.

Distances Moved: Winter Period to Subsequent Winter Period

The mean distances between banding and recovery site for birds banded in one winter and recovered in a subsequent winter are pre-

TABLE 8. Mean distances ± standard deviation of recovered birds from the geographic center of winter recovery sites for all years and for specific years having at least 5 recoveries.

	Banding site in summer		Distance of individual recoveries from geographic center of winter range				
			All years[1]		Individual years		
Species	Lat.	Long.	N	Mean distance	N	Mean distance	Year
Grackle	42	87	65	301 ± 213	5	377 ± 293	1930
					5	265 ± 99	1933
					8	148 ± 87*	1940
						263 ± 170	Mean
Red-wing	42	77	28	219 ± 163	6	236 ± 166	1930
					6	158 ± 35	1933
						197 ± 120	Mean
Red-wing	41	82	31	308 ± 135	5	312 ± 118	1965
					8	285 ± 147	1967
						299 ± 137	Mean

[1] Data are from Table 7.
* Significantly ($P < .05$) different from mean for all years (t-test).

sented in Table 9. Red-wings showed significantly less distance between different winters' locations (88 km) than did the other 3 species (212–282 km). There was no significant difference in recovery distance between sexes for any of the 4 species. Overall, the 4 species showed considerably more faithfulness in returning to a previous year's breeding location (Table 2) than in returning to a previous year's winter location (Table 9).

DISCUSSION

Fidelity to breeding season location.—AHY cowbirds showed the least tendency of the 4 species to return in subsequent years to their approximate

TABLE 9. Mean distance (km) ± standard deviation between banding and recovery site for birds banded in winter roosting period (Jan.–Feb.) of 1 year and recovered in winter roosting period of a subsequent year. Sample sizes are in parentheses. Under "all birds" category, values with same letter are not significantly ($P < .05$) different (Duncan's Multiple Range Test).

Sex	Red-wing	Grackle	Cowbird	Starling
Male	57 ± 145 (46)	357 ± 589 (19)	288 ± 344 (85)	151 ± 318 (108)
Female	52 ± 114 (10)	263 ± 231 (22)	224 ± 313 (39)	155 ± 283 (84)
All birds	88 ± 157 (70)a	282 ± 314 (119)b	277 ± 315 (160)b	212 ± 325 (326)b

location during a previous nesting season. They also departed from their nesting season location considerably sooner than did the other species, and returned later in the spring. This behavior is not surprising, as the cowbird has a different reproductive strategy than the other species. Bray et al. (1974) and Burleigh (1972) have noted in South Dakota and Idaho that cowbirds depart early from and return late to the breeding grounds.

I hypothesized that HY birds would disperse farther than AHY birds in returning in subsequent years to their respective place of hatching or breeding. Contrary to expectations, HY and AHY Red-wings showed no differences and although HY grackles dispersed significantly farther than did AHY birds, the mean difference was only 11 km. Starlings were the only species to show a major difference (64 km) between HY and AHY birds in mean dispersal distance from one nesting season to a subsequent nesting season (Table 2, Fig. 2). This propensity for dispersal in HY Starlings is undoubtedly an important factor in the highly successful and rapid expansion of the population across North America in the past 90 years (Kessel 1953). It is also an important factor to consider in any program designed to control local breeding populations of Starlings or blackbirds. Starlings would more likely reinvade low density areas at a much faster rate than would Red-wings and grackles.

Although HY cowbird dispersal distances could not be compared with the other species due to small sample size, the greater dispersal distance of AHY cowbirds suggests this species would also reinvade more rapidly than grackles and Red-wings. The ability of cowbirds to reinvade a low density area has been amply demonstrated in a 5-county area in Michigan during the past 10 years. The removal of 3000 to 4000 cowbirds during each year's nesting season, a number sufficient to reduce parasitism in Kirtland Warbler (*Dendroica kirtlandii*) nests from over 60% to less than 5%, has had no apparent influence on the number of cowbirds trapped in subsequent years (Kelly and DeCapita 1982).

All 4 species damage certain grain and fruit crops in late summer and early fall. Although cowbird depredations at this time may be caused by far-ranging migrants, most grackle depredations in eastern North America apparently are by birds within 50 km of their nesting sites (Table 3). Red-wing and Starling crop depredations in eastern North America in summer and early fall are also mainly by local birds. However, some Red-wings from New England apparently migrate south in late summer (Table 3), probably along the Atlantic coast (Packard 1936). Previous studies (Bird and Smith 1964, Dolbeer 1978) suggest that Red-wings from central Canada also migrate in late summer.

Migration distances to wintering areas.—The relation between the degree of sexual dimorphism and sex-specific migration distance from a given breeding area for Red-wings, grackles, and Starlings generally supports the hypothesis that differential winter locations between dimorphic sexes in temperate North America are related to bioenergetic constraints (Ketterson and Nolan 1976). Within a species, the larger sex should be able to endure fasting to a greater extent than the smaller sex, an important consideration in the mid-latitudes (33°–38°) of eastern North America where snow or ice cover can sometimes preclude feeding in winter. MacReynolds (1917), Odum and Pitelka (1939), and Stewart (1978) have reported instances of blackbird and Starling mortality related to winter storms. These accounts suggest that there could be selective pressure for the smaller female grackles and Red-wings to winter farther south than the larger males from the same breeding population.

The above hypothesis was not supported by data for cowbirds. Cowbirds, although a species with strong sexual dimorphism, showed no indication of differential migration distances between sexes. Perhaps cowbirds are less influenced by winter weather conditions than are Red-wings and grackles because of their association with livestock feeding operations in winter (Dolbeer et al. 1978). Cowbirds may have a more dependable source of food, even during periods of inclement weather and there may be little selective pressure for females to winter farther south than males. However, Kessler et al. (1967) noted a high incidence of cowbird mortality in Ohio after a winter storm.

This argument could also explain why AHY Starlings winter farther north than do the larger AHY grackles. Starlings also associate closely with feedlots in winter (Dolbeer et al. 1978) and often roost in man-made structures (e.g., barns, bridges) offering good protection from inclement weather. Thus, these behavioral adaptations may compensate for the bionergetic disadvantages of wintering farther north.

Kessel (1953) noted that HY Starlings had a greater tendency than AHY Starlings to migrate during their first winter. This analysis (Table 5, Fig. 2) strongly supported her findings and also suggested that the differential migration distance was more pronounced at higher latitudes. HY Red-wings and HY grackles also migrated greater distances than did the AHY males; however, small sample sizes precluded examining sexual differences in migration among HY birds of these species.

The greater migration distances of HY birds in their first winter compared with AHY birds does not fit the bioenergetics hypothesis since body weights of the 2 age classes are comparable in winter. The differential migration between age classes may be socially induced instead (Gauthreaux 1978). Older birds may dominate the more northern winter roosts, forcing the socially-subordinate HY birds to go farther south.

Dispersion in winter.—At least 125 major (i.e., 1 million or more birds) blackbird and Starling roosts and an unknown number of smaller roosts form each winter in the southern United States, mainly south and east of 38° latitude, 100° longitude (Meanley and Webb 1965, Meanley and Royall 1976). The analyses of migration distance from nesting season locality to winter locality suggest that there is considerable intermingling of local breeding populations within and among species at these winter roost sites. Previous analyses of Red-wing, grackle, cowbird, and Starling recoveries have indicated that birds wintering in a particular state in the southern United States come from a broad area of the species breeding range (Hicks 1938, Irwin 1956, Royall 1973, Stewart 1975, 1977, Coon and Arnold 1977, Meanley and Dolbeer 1978). This study indicates that at least part of the intermingling results from predictable age, sex, and species differences in migration based perhaps on bioenergetic and behavioral responses of the birds.

A wildlife management implication arises from the extensive intermingling of breeding populations in winter. By concentrating into dense roosting aggregations of up to several million birds, blackbird and Starling populations are vulnerable to large-scale die offs caused by disease (Clark and Locke 1962), severe local weather conditions (e.g., Odum and Pitelka 1939), or man-induced stress [e.g., roost spraying with surfactants (Lefebvre and Seubert 1970)]. Because local breeding populations are dispersed in winter, the effects of a high mortality rate at a given roost or cluster of roosts would be spread among blackbird and Starling populations indigenous to a wide area. Local breeding populations (and, thus, their gene pools) would not likely be seriously affected by localized high mortality rates at winter roost sites.

Another management implication that arises from this analysis concerns the rather extensive displacement of many grackles, Starlings, and cowbirds from one year's wintering site to another year's site (Table 9). Birds of these species were recovered a mean of 212 to 282 km from their banding site in a previous winter. The lack of faithfulness to winter roost sites had already been suggested for grackles (Royall 1973) and cowbirds (Coon and Arnold 1977) in Texas and for Starlings in various parts of the United States (Kessel 1953). It has been well documented for Starlings in Europe (Spaans 1977). This shifting between winters suggests that if a roosting population is removed from a local area in one winter, birds will readily repopulate the area in subsequent winters if suitable habitat and a source of food exist. Red-wings showed considerably less shifting between winters than the other species; thus, they would perhaps repopulate winter roosting sites less rapidly than grackles, cowbirds, and Starlings.

SUMMARY

Distances between banding and recovery sites were compared for age and sex classes of Red-winged Blackbirds, Common Grackles, Brown-headed Cowbirds, and Starlings. These species are widely dispersed during the reproductive period but associate closely in winter roosts in the southern United States. AHY cowbirds, compared to AHY birds of the other three species, spent the least time in the vicinity of breeding locations and showed the least faithfulness in returning to previous year's breeding locations. Starlings dispersed the greatest mean distance (80 km) from their site of fledging to their locality during a subsequent breeding season. Differences were noted between sex classes and species in distances migrated from breeding locations to winter locations. These differences generally, but not always, supported the hypothesis that

smaller-sized birds migrate farther south in eastern North America because of bioenergetic constraints. Greater migration distances were also noted for HY birds compared with AHY birds, especially for Starlings. This differential migration of species and age and sex classes helps explain the high degree of intermingling of breeding populations within and between species that apparently occurs at winter roost sites. Implications of these findings with regard to the management of blackbird and Starling populations are discussed.

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