GONADAL AND BEHAVIORAL CYCLES IN THE GREAT-TAILED GRACKLE

By Robert K. Selander and Ronald J. Hauser

The annual cycle in the Great-tailed Grackle (*Quiscalus mexicanus*) is of special interest because the species has a promiscuous mating system in which first-year males do not effectively participate in the breeding effort of the population. It has seemed desirable to determine the gonadal condition of first-year males during the breeding season and to compare the testis cycles in the two age groups, first-year and adult. The results of this investigation are compared with those of Wright and Wright (1944) for the polygynous Redwinged Blackbird (*Agelaius phoeniceus*), which hitherto was the only species of the family Icteridae studied from the standpoint of annual gonadal cycles.

This investigation of annual gonadal and behavioral cycles in the Great-tailed Grackle in the Austin region, south-central Texas, was undertaken as part of a research program on the biology of grackles and other icterids. Previously published aspects of this work relating to grackles of the genus *Quiscalus* include studies of molt and age determination in *Q. mexicanus* (Selander, 1958), sex ratios and clutch size (Selander, 1960, 1961), autumnal breeding in the Boat-tailed Grackle (*Q. major*) in Florida (Selander and Nicholson, 1962), the comparative biology of *Q. mexicanus* and *Q. major* in a zone of sympatry (Selander and Giller, 1961), and a discussion of mating systems and sexual selection (Selander, 1965).

For reasons that will be discussed elsewhere, we regard all species of grackles formerly assigned to "*Cassidix*," "*Holoquiscalus*," and *Quiscalus* as congeneric, following a precedent set by Bond (1963).

This research was supported by the National Science Foundation (grants 20873 and GB 1624).

MATERIALS AND METHODS

A regular program of collection of specimens for study of gonadal cycles was initiated in August, 1956, and terminated in July, 1957; but a second collection period extended from September 14 to October 31, 1957, and additional material was taken in February, 1958, July, 1960, and June, 1961 (table 1). A total of 509 specimens, including 328 males and 181 females, was collected in Travis County within a 10-mile radius of the campus of The University of Texas, Austin. In fall and winter, grackles were taken with shotguns in agricultural fields east of Austin; but in the breeding season, when most birds were at nesting colonies in the city, specimens were also collected with traps and mist-nets. Observations of behavior at nesting colonies were made on the campus of The University of Texas and at Zilker Park and Montopolis.

Specimens were processed as follows: The left testis or the ovary was removed and placed in Bouin's fixative. Body weight was recorded within two hours of death, and notes were made on the extent of molt, types and numbers of juvenal feathers retained through the postjuvenal molt, and other characters of use in age determination (Selander, 1958). Approximately 10 per cent of the specimens were prepared as study skins or skeletons.

In the laboratory, the long and short diameters of the testes were measured, and selected testes were imbedded in paraffin wax, sectioned at either 7 or 10 micra, stained with iron haematoxylin, and counter-stained with eosin. Testis volume in

TABLE 1

SPECIMENS COLLECTED IN AUSTIN REGION FOR STUDY OF GONADS

Period	Sex and age group					
	Males			Females		
	Juv.	First-year	Adult	Juv.	First-year	Adult
Aug., 1956, through July, 1957	10	94	133	4	46	46
Sept.–Oct., 1957		39	19		58	6
Feb., 1958		6	2			
July, 1960	13	1	5	9		9
June, 1961	2	1	3	1		2
Totals:	25	141	162	14	104	63

cubic millimeters was calculated using the formula for the volume of an ellipsoid: $V = \frac{4}{3} \pi a^2 b$, where $a = \frac{1}{2}$ the shorter diameter and $b = \frac{1}{2}$ the longer diameter.

THE TESTIS CYCLE

Histologic stages.—Our system of dividing the spermatogenic cycle into histologic stages is similar to that employed by Wolfson (1942) for the Oregon Junco (*Junco oreganus*) and by Bartholomew (1949) and Davis and Davis (1954) for the House Sparrow (*Passer domesticus*), despite some differences in numbering of the stages. Histologic stages 1 to 4 (see beyond) of our system correspond to those of similar designation used by these workers; but, in order to indicate in greater detail the degrees of activity achieved by testes in autumnal recrudescence, we have found it convenient to subdivide stage 2. Our stage 4 corresponds to stage 4 of Wolfson, which is represented by Bartholomew's stages 4 and 5 (Davis and Davis, 1954:339). Finally, we have subdivided stage 5, which corresponds to stage 5 of Wolfson and stage 6 of Bartholomew, on the basis of presence or absence of free mature spermatozoa in the tubular lumina.

In establishing histologic stages and interpreting our material, papers on the gonadal cycle of the male Jackdaw (*Corvus monedulus*) by Threadgold (1956*a*, 1956*b*) have been of special value.

Stage 1: Single row of spermatogonia and a few primary spermatocytes.—Testes in stage 1 are of minimum size, and the seminiferous tubules have smaller diameters than in any other stage (table 3). Neither in this stage nor in more advanced stages are tubule diameters larger in adult than in first-year individuals.

The tubules of testes in stage 1 are separated by large areas of interstitial tissue; and within each tubule there is a single row of spermatogonia lying against the basement membrane (tunica propria), with a few large primary spermatocytes and spermatogonia forming a partial second row in some tubules (see fig. 1 for illustration of this and other histologic stages). A tubular lumen is present, which in adults at the end of regression contains debris, probably lipoidal (see Threadgold, 1956*a*:21; and Marshall, 1961:310); debris was not seen in the tubules of juvenal and first-year males.

Stage 2: Two or three rows of spermatogonia and spermatocytes.—Two substages, 2a and 2b, are distinguished. In substage 2a, testis volume and tubule diameter (table 3) have increased slightly over stage 1, but the tubules remain separated by tracts of interstitial tissue. The majority of tubules contains two complete rows of spermatogonia interspersed with primary spermatocytes. Little or no debris is present in the tubular lumina. With respect to tubular histology, this substage is apparently identical to the "October . . . 2nd week" condition in the Jackdaw, as described by Threadgold (1956*a*:22).

In substage 2b, testis volume and tubule diameter show further increase (table 3). Viewed

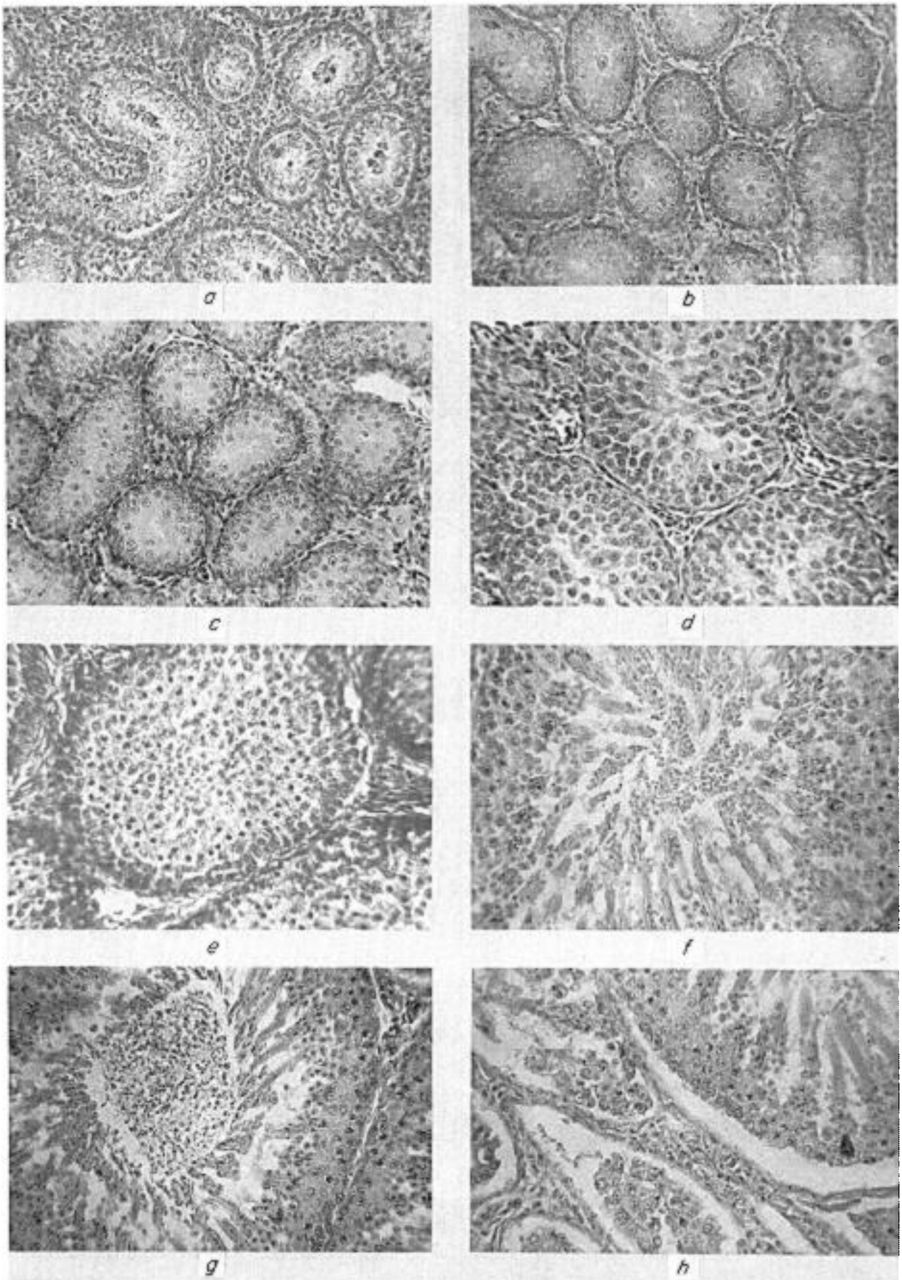

Fig. 1. Sections of testes of the Great-tailed Grackle showing histologic stages described in the text. *a*, stage 1; *b*, stage 2a; *c*, stage 2b; *d*, stage 3; *e*, stage 4; *f*, stage 5a; *g*, stage 5b; *h*, regression.

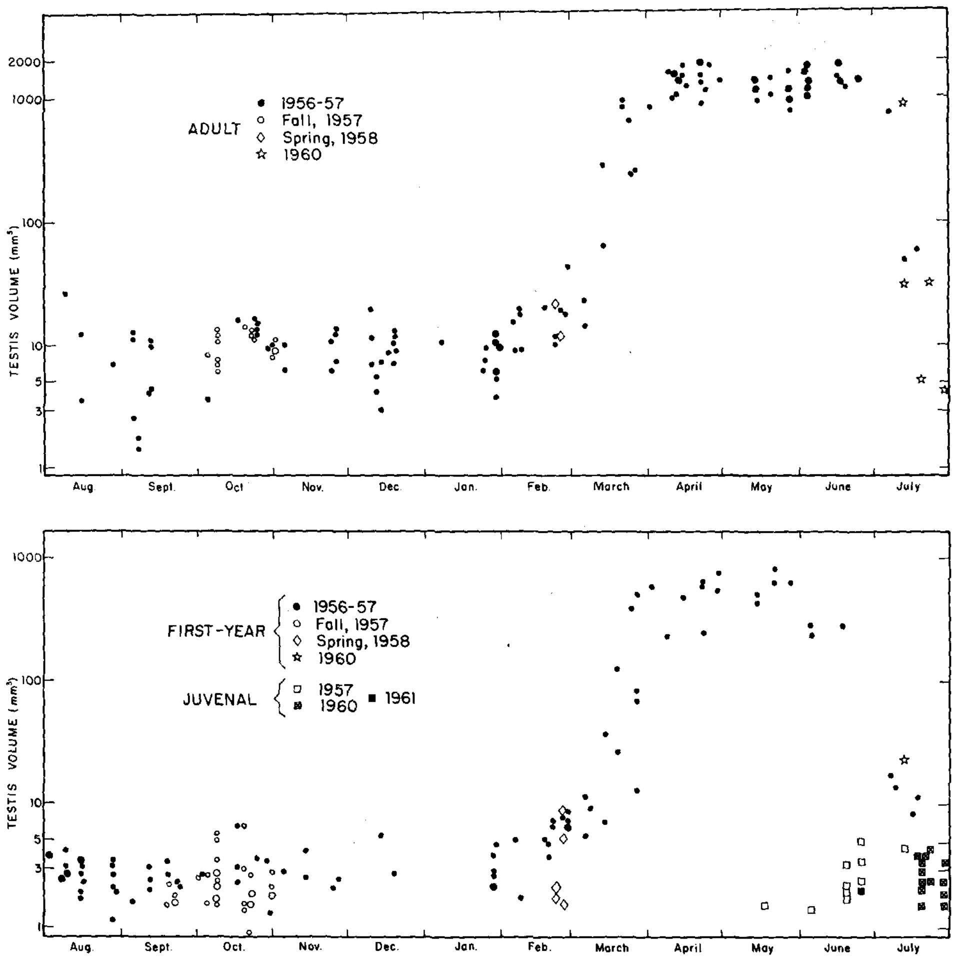

Fig. 2. Annual cycle of testis volume in the Great-tailed Grackle at Austin, Texas. Large symbols represent two or more testes of same volume.

in cross section, adjacent tubules are in contact along their margins, and large areas of interstitium are no longer connected by inter-tubular bands or tracts. Most tubules contain three more or less complete cellular rows composed of spermatogonia, primary spermatocytes, and, occasionally, secondary spermatocytes. Many of the primary spermatocytes are in synapsis. This substage is similar to the "Early March" condition of the testis of the Jackdaw (Threadgold, 1956*a*: 26–27).

Stage 3: Secondary spermatocytes common.—In this stage, most of the tubule is filled with spermatocytes, which may form five or more rows above the basal row of spermatogonia. Cell division is much in evidence. The tubules are further expanded in size over substage 2b, and they are more nearly circular in cross section than in previous stages. This stage is equivalent to Threadgold's (1956*a*:27–28) "Late March" condition, except that spermatids are not present.

Stage 4: Spermatids.—This stage is characterized chiefly by the appearance of spermatids bordering the lumina of the tubules; spermatozoa are not present.

Stage 5: Full spermatogenic activity with many spermatozoa.—Testes in this stage are assignable to either of two different substages that are defined primarily on the basis of differences in distribution of spermatozoa within the tubules.

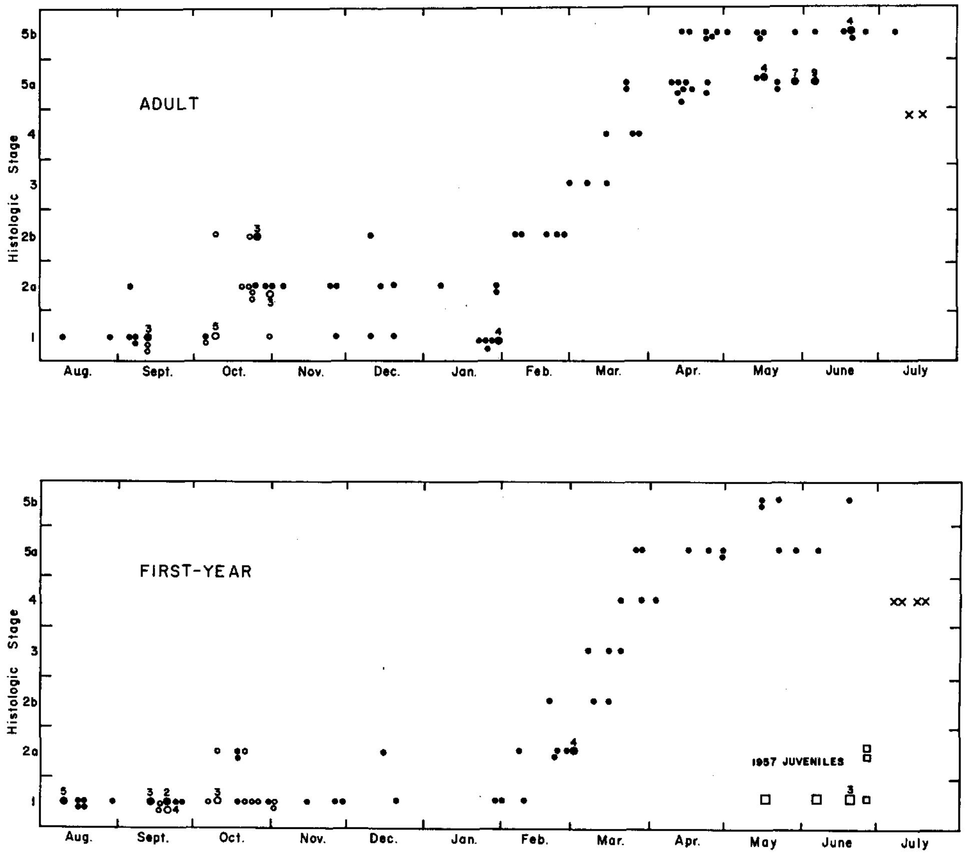

Fig. 3. Annual cycle of histologic stage of testes in the Great-tailed Grackle at Austin, Texas. Numbers adjacent to large symbols indicate numbers of gonads represented by symbols. "X" indicates testis in regression from breeding condition. Circles represent testes collected in fall, 1957.

In substage 5a, there are no free mature spermatozoa present in the lumen, and bundles of spermatozoa are not in the process of passing into the lumen. Otherwise, substage 5a is similar to substage 5b, which is characterized by the presence of free spermatozoa in the lumina of at least some tubules. Tubule diameter does not differ significantly in the two substages (table 3). In some testes assigned to substage 5b, the lumina of nearly all tubules are packed with free spermatozoa, but in others only a few scattered spermatozoa are present in an occasional lumen.

At the beginning of regression, which should not be confused with substage 5b, whole bundles of spermatozoa, along with other cell types and cellular debris apparently pass as units into the lumen. This process may occur before there is any decrease in testis volume or tubule diameter. In breeding testes in substage 5b, the bundles appear to break up near the periphery of the lumen and the spermatozoa disperse individually or in small groups into the lumen. And in breeding testes, spermatozoa from only a relatively few bundles move to the lumen at any one time, whereas in early regression many or all bundles may have passed simultaneously into the lumen. For these reasons, it seems probable that Johnston's (1956:158) stage 7, defined for the California Gull (*Larus californicus*), in which "the majority of the sperm bundles have been shed into the lumen of the tubule," represents the beginning of regression, as Johnston suspected, and is not equivalent to our substage 5b.

TABLE 2

TESTIS VOLUME FOR MONTHLY SAMPLES

Period	Number of testes	Mean volume (mm.³)	Range
ADULT MALES			
Aug., 1956	4	12.69	3.61– 27.92
Sept., 1956	9	6.53	1.40– 12.69
Oct. 5, 1956	1	3.61	– –
17–31, 1956	7	13.10	9.45– 16.12
5–9, 1957	7	9.03	5.88– 13.13
20–24, 1957	4	12.47	11.11– 13.58
31, 1957	4	8.97	7.87– 10.27
Nov., 1956	7	9.35	6.04– 13.08
Dec., 1956	12	8.85 ± 1.27	2.89– 19.04
Jan., 1957	14	8.32 ± 0.70	3.67– 11.92
Feb. 5–8, 1957	5	13.68	8.75– 19.04
18–27, 1957	6	19.92	9.80– 42.59
20, 23, 1958	2	15.95	11.16– 20.74
March 6–14, 1957	4	94.66	13.64– 281.2
22–27, 1957	5	585.90	238.0 – 951.9
April 2–15, 1957	9	1296.10	840.5 –1596.0
16–27, 1957	9	1480.09	871.4 –1943.0
May 1–15, 1957	10	1246.05 ± 15.89	926.7 –1427.5
21–28, 1957	11	1111.90 ± 22.54	770.9 –1601.5
June 5, 1957	10	1342.92 ± 28.25	993.0 –1767.3
17–25, 1957	7	1445.54	1207.6 –1797.4
27, 28, 1961	3	909.50	241.8 –1653.4
July 7–13, 1957, 1960	4	411.35	28.00– 733.0
18–28, 1957, 1960	4	23.59	4.36– 29.62
JUVENAL AND FIRST-YEAR MALES			
Juvenal			
May, 1957	1	1.65	– –
June, 1957, 1961	9	2.64 ± 0.40	1.40– 5.14
July, 1957, 1960	14	2.94 ± 0.27	1.47– 4.46
First-year			
Aug. 2–15, 1956	14	2.92 ± 0.30	1.69– 4.11
16–29, 1956	8	2.32	1.12– 3.42
Sept., 1956, 1957	14	2.10 ± 0.16	1.34– 3.37
Oct. 3–30, 1956	7	3.31	1.29– 6.80
2–9, 1957	17	2.62 ± 0.28	1.50– 5.68
20–24, 1957	10	2.27 ± 0.52	0.89– 6.63
31, 1957	4	2.12	1.77– 2.72
Nov., 1956	5	2.82	2.10– 4.19
Dec., 1956	2	4.19	2.79– 5.59
Jan., 1957	6	3.09	2.14– 4.71
Feb. 6–8, 1957	2	3.46	1.75– 5.18
18–27, 1957	10	6.56 ± 0.44	4.11– 8.40
20–23, 1958	6	3.64	1.59– 8.85
March 6–14, 1957	5	14.29	5.59– 37.79
19–27, 1957	7	176.17	13.09– 517.7
April, 1957	8	516.76	235.3 – 759.2
May, 1957	5	609.55	437.2 – 833.2
June, 1957	3	271.99	243.3 – 286.6
1961	1	5.45	– –
July, 1957, 1960	5	15.07	8.40– 24.00

TABLE 3

TUBULE DIAMETERS (IN MICRA) FOR SEVERAL HISTOLOGIC STAGES

Histologic stage	Age group	Number of individuals	Tubule diameter: Mean ± standard error	Tubule diameter: Range
1	Adult	29	51.1 ± 1.8	35–74
	First-year	27	47.2 ± 0.9	39–55
2a	Adult	19	55.7 ± 1.4	46–71
	First-year	4	57.0	51–64
2b	Adult	11	64.7 ± 4.4	51–97
	First-year	1	71	
5a	Adult	28	345.1 ± 3.7	317–394
5b	Adult	13	343.3 ± 6.4	317–394

TESTIS CYCLE IN JUVENAL AND FIRST-YEAR MALES

Data on the testes of 24 juvenal males in May, June, and July and on 22 testes of first-year males in August suggest that at least some juvenal testes increase slightly in volume and show the beginning of spermatogenesis in late June and July (figs. 2 and 3; and table 2). Juvenal testes collected on May 16 and June 6, 1957, had volumes of 1.65 and 1.40 mm.^{3}, respectively, and were in histologic stage 1. In the last two weeks of June, the mean volume of juvenal testes increased to 2.64 mm.^{3}, and one individual taken on June 25 had a testis volume of 5.14 mm.^{3}. This latter testis had progressed histologically to stage 2a, as had another with a volume of 3.52 mm.^{3} taken on the same day. Other testes collected in the last two weeks of June were assigned to stage 1, but one was approaching stage 2a, and another also showed slight activity.

Testis volume remained at an average level of about 2.9 mm.^{3} through July and the first two weeks of August but decreased slightly in the latter part of August and in September, reaching an average of 2.10 mm.^{3} in September. All sectioned testes of first-year birds collected in August, 1956, and in September, 1956 and 1957, were in stage 1.

Between October 9 and 20, 4 of 18 (22 per cent) first-year testes showed a significant increase in volume, and 4 of 9 (44 per cent) sectioned were in stage 2a. There is a positive relation between volume and histologic stage, with a few notable exceptions: one testis taken on October 9, 1957, had a volume of 5.09 mm.^{3} but had not progressed beyond stage 1; and another, collected on October 17, 1956, was in stage 2a but had a volume of only 2.30 mm.^{3}. By the last week in October, mean volume had returned nearly to the September level, and all testes were in stage 1. No testis of a volume greater than 4.19 mm.^{3} was collected in this period or in November.

There apparently was a slight increase in volume from November to the last week of January, when testes averaged 3.09 mm.^{3}. An individual taken on December 14, with a testis volume of 5.59 mm.^{3}, was in histologic stage 2a, but the testes of most birds remained in stage 1 in December and January.

Vernal spermatogenesis was initiated in first-year males in the last two weeks in February. Mean volume showed a significant increase in that period, and sectioned testes were in stages 2a and 2b. Development continued rapidly in March, and by late March some individuals had testes which were nearly maximum in size (for first-year birds) and represented stage 5a. In April and May, all testes examined contained spermatozoa. A plateau of maximum volume was maintained from late April to the end of May. It is noteworthy that all first-year testes reached volumes greater than 235 mm.^{3} and all underwent complete spermatogenesis. The largest first-year testis (833.2 mm.^{3}) was that of a bird collected on May 21, 1956.

Regression of first-year testes began in June, as indicated by three testes with a mean volume of 271.99 mm.^{3}. Regression was well advanced in early July.

Testis Cycle in the Adult Male

Our data indicate that, in August, testes of some adult males were still decreasing in size from breeding volume; mean volume was 12.69 mm.^{3}, and one testis taken on August 9, 1956, had a volume of 27.92 mm.^{3}. This testis and one other testis taken in August when sectioned were found to be in stage 1. Minimum average size was reached in September, a month characterized by great variability in volume. In September, all adult testes were in stage 1, with the exception of one taken on September 5, which was in stage 2a; this was also the largest testis (12.69 mm.^{3}) collected in September.

Fall recrudescence was first evident on October 9, 1957, at which time mean volume had increased to about 9.0 mm.^{3} and the largest testis (11.81 mm.^{3}) was in stage 2b. A slight further increase in size followed between October 17 and 24, in which period 33 per cent of the testes sectioned had advanced to stage 2b, and the others were in stage 2a. By the last week of October, a drop in average volume was noted and testes were in stage 2a or 1.

In November mean testis volume had decreased to 9.35 mm.^{3}. Our data suggest a progressive but slight decrease in volume through December and January, although the observed differences in monthly means are not statistically significant. Great individual variation in testis volume was evident in December and January, which condition contrasted with the relative uniformity of size recorded in late October and November. It will be noted that, following autumnal recrudescence, mean testis volume did not return to the low level of September. Although most testes returned to histologic stage 1, a few remained in stage 2a, and some remained in stage 2b, as shown by a testis collected on December 10, 1956. This exceptional testis had the largest volume (19.04 mm.^{3}) recorded in November, December, and January.

No evidence of advance in spermatogenesis or increase in size was seen in a large sample of testes taken on January 28 and 29, but vernal recrudescence was definitely under way in the sample period February 5 to 8. Five testes taken in that period had a mean volume of 13.68 mm.^{3}, and the two testes sectioned were in histologic stage 2b. In the last two weeks of February, only a relatively small increase in mean volume occurred, but by February 22 one testis had reached a volume of 42.59 mm.^{3} and was in stage 3. Development proceeded rapidly in the first half of March; and on March 22 spermatozoa were present (stage 5a) in two testes sectioned, although maximum testis volume was not reached until April.

All sectioned testes of adult males taken in the period from April 10 to June 25 contained spermatozoa. Thus, males were in breeding condition for a period of at least 75 days. Two minor peaks in volume occurred, one in April and another in June; and a slight but statistically significant decrease in mean volume was noted in May. The smallest breeding testis (770.9 mm.^{3}) was collected on May 28; all others were larger than 919 mm.^{3}. The largest testis (1943.0 mm.^{3}) was obtained on April 23.

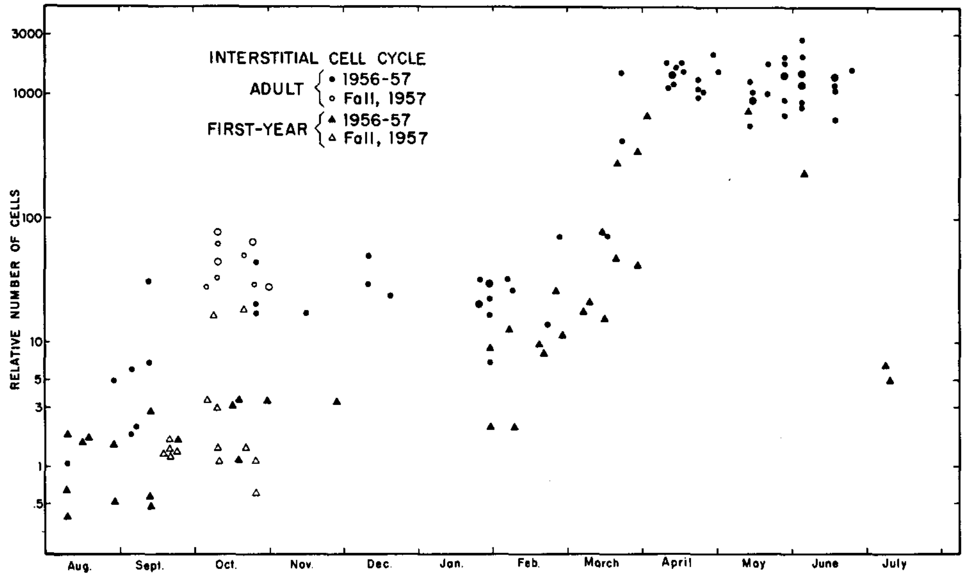

Fig. 4. Annual cycle in relative numbers of testicular interstitial cells in the Great-tailed Grackle at Austin, Texas. Large symbols represent two or more gonads.

Correlated with variation in mean testis volume in April, May, and June are average differences in percentages of birds in the two substages of stage 5. In the period from April 10 to May 1, 44 per cent of the sectioned testes were in stage 5b; between May 14 and June 5, 18 per cent were in that stage; and, in the period June 17–25, all 7 testes sectioned represented stage 5b.

Regression was under way on July 7, as indicated by a bird having a testis volume slightly below the range of size of breeding testes. Testes taken on July 13 and 18 were midway along in regression, which was completed, as noted earlier, by the latter part of August or, at the latest, by September.

Interstitial Cell Cycle

Relative numbers of interstitial cells were estimated by a method employed by Threadgold (1956*b*:46–47). For each sectioned testis a count was made of numbers of Leydig cells in each of five microscopic fields of view selected at random. The mean number obtained from the five counts was then multiplied by a factor (a^2b) which was proportional to the volume of the testis, thus providing an index to the total number of Leydig cells in the testis.

Individual, age, and seasonal variation in numbers of Leydig cells is shown in figure 4. The cycle is similar to that of testis volume (fig. 2), with a low point in August and September, an increase in numbers of cells in mid-October, and a slight decline in numbers through late October, November, December, and January. In April, May, and June there is a bimodal peak in numbers of cells in adult testes, corresponding to the bimodal peaks in testis volume (fig. 2) and histologic stage (fig. 3). Note that at all seasons the testes of first-year males have fewer Leydig cells than those of adult males.

Bimodal Feature of Breeding Period

Partial regression of the testes of adult males of *Quiscalus mexicanus* in May, midway in the breeding season, produces a bimodal form in the cycles of testis volume, histologic stage, and interstitial cell numbers. There is also a corresponding slight depression in body weight of adult males in May, as compared with April and June (Selander, 1958:fig. 5, p. 374). A comparable bimodal pattern has been reported in the cycles of testis volume, seminiferous tubule diameter, and interstitial cell numbers in four populations of the House Sparrow studied by Threadgold (1960) and in the cycles of testis volume (but not of tubule diameter) of this species studied by Selander and Johnston (MS). Whether there is in *Passer* a bimodal pattern in histologic stage in the breeding season, as observed in *Quiscalus*, has not been determined.

Contrasting the bimodal form of the testis cycle in the breeding season in *Passer domesticus* with the unimodal cycle of the Jackdaw, Threadgold (1960:195) has suggested that these differences illustrate "an essential distinction between single and multi-brooded species, the latter obviously requiring a longer period of testicular activity." As an explanation for the bimodal pattern, he has offered two possibilities: First, the transfer to the seminal vesicles of spermatozoa produced in the spring, or their use in copulation, may cause a reduction in the volume of the seminiferous tubules and, hence, of the testis as a whole. Second, sex hormones produced earlier in the season may inhibit secretion of follicle stimulating hormone by the pituitary, with a consequent reduction in the rate of spermatogenesis and decrease in testis volume.

From our study of the testes of *Quiscalus mexicanus*, we doubt that partial regression of the testes in May can be attributed merely to the transfer of mature spermatozoa from the seminiferous tubules, for it appears that there is a decrease, if not an actual suspension, in the rate of spermatogenesis. Moreover, there is no significant decrease in tubule diameter in May. Threadgold's claim of a decrease in size of the seminiferous tubules in *Passer* was based on a small series of measurements of testes taken at Belfast and London. However, the apparent decreases in volumes in the Belfast and London samples are probably not significant statistically; and, more importantly, we note that they do not correspond in time with the observed decreases in testis volume in these samples (compare figs. 2 and 4 of Threadgold, 1960). In 70 testes of *Passer domesticus* taken in Austin, Texas, from March through July, 1962, there is no variation in mean tubule diameter (Selander and Johnston, MS), although the testis volume shows the typical bimodal pattern, with a decrease in late May and early June. Therefore, the decrease in testis volume in *Passer*, as in *Quiscalus*, cannot be attributed to a decrease in diameter of the seminiferous tubules.

While Threadgold's postulated mechanism of an androgen feedback effect on the pituitary is attractive as an explanation, we believe it may be worthwhile to consider another possible factor. In the population of *Quiscalus mexicanus* at Austin, Texas, the major nesting effort of the females in 1956 occurred in April, and fewer females started their nesting activities in May (see beyond). Therefore, there were relatively fewer opportunities for males to mate in May than in April; and it seems possible that, as a result of a diminished amount of vocal and visual stimuli provided by the females in May, there was a slight diminution in the rate of production of gonadotropins by the pituitaries of adult males. There was not only an apparent slowing in the rate of spermatogenesis but possibly also a decrease in the rate of production of androgen by the testes, as suggested by the fact that the sexual response of males to female dummies diminished in May as compared with the level in April. The second peak of testis activity in June corresponded with, and was perhaps in part stimulated by, the second major nesting effort of the females.

Our suggestion that maintenance of maximum volume and activity of the testes depends upon stimulation from the females may help to explain the relatively early regression of the testes of first-year males, since birds of this age do not manage to establish territories at the nesting colonies and are unsuccessful in stimulating mating behavior in females (Selander, 1965). The suggestion is in line with observations on the effect of the presence of females on gonadal development in male birds. For example, Burger (1953), working with the Starling (*Sturnus vulgaris*), has shown that the presence of females in experimental photoperiod cages induces an increase of 45 per cent in the magnitude of testicular response of males obtained using a 14-hour photoperiod.

It is perhaps surprising that the diameters of the seminiferous tubules are not smaller in first-year than in adult testes, especially considering the marked difference in testis volume in birds of these two age groups. For the California Gull, in which second-year males undergo partial gonadal development but do not breed, Johnston (1956:155) claims that the tubules of second-year birds are not as large as those of adults, but his data (Johnston, *op. cit.*:table 11, p. 154) actually do not show this. At maximum size (in May) second-year tubules averaged 0.145 mm. in diameter, while adult tubules at maximum size (in April) averaged 0.144 mm.

Comparison of Testis Cycles in First-year and Adult Males

Comparing the testis cycles in the two age groups, the following points of difference are noteworthy: (1) Testes of first-year birds are at all times smaller than those of adults; and in any given period there is little if any overlap in volume in the two age groups. At maximum breeding size, the mean volume of testes of first-year males is only 41.2 per cent of that of adult males. (2) In late June and July, juvenal testes increased slightly in volume and showed the beginnings of spermatogenesis, while in the same period adult testes were regressing from breeding condition. (3) Autumnal recrudescence was more marked in adult that in first-year birds. A greater percentage of adults showed an increase in testis volume, and the testes of 33 per cent of adults reached histologic stage 2b, whereas no first-year testis advanced beyond stage 2a. (4) Vernal recrudescence of testes began two or three weeks earlier in adults than in first-year birds. The testes of adults achieved stage 5b in April, but those of first-year birds apparently did not reach this condition until May. (5) Testes of adults were in breeding condition from April through June (90 days), with a minor decrease in volume and activity in May, whereas the plateau of maximum development in testes of first-year birds extended only from April through May (60 days). Regression began in June in first-year birds but not until July in adults.

Testis Cycles in Other Years

The foregoing accounts relate to the testis cycles as studied in material collected in 1956 and 1957. A small amount of data obtained in 1958, 1960, and 1961 suggests that there is little year-to-year variation in timing of events in the testis cycle, notwithstanding marked yearly fluctuations in climate in the Austin region.

The period from January through March, 1958, was one of unusually cool tem-

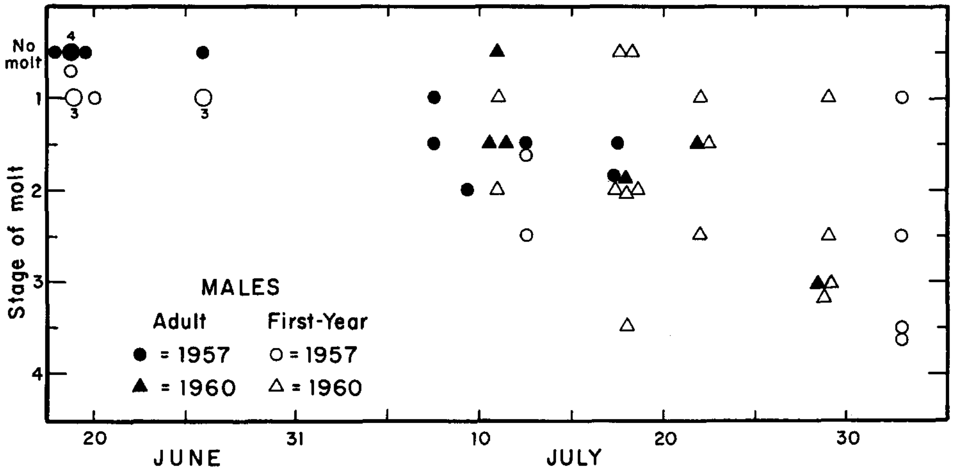

Fig. 5. Timing of inception of fall molt in the Great-tailed Grackle at Austin, Texas, in 1957 and 1960. Numbers 1 to 4 refer to progressive stages of molt.

peratures and heavy rainfall in the Austin region. Average temperature for February, 1958, was 48.8° F., which was 5.3° F. below normal for that month; and a low of 22° F. was recorded on February 22. (In February, 1957, mean monthly temperature was 60.9° F., and the lowest temperature, recorded on February 28, was 38° F.; see table 5.) Despite the cool, rainy weather which prevailed in January and February, 1958, the gonads of two adult males collected on February 20 and 23, 1958, show an increase in volume over the winter level and fall within the range of size variation of a sample collected in the latter part of February, 1957 (table 2). However, a sample of six testes of first-year birds collected from February 20 to 23, 1958, averages smaller than a sample of 10 taken in late February, 1957, and only two of the six gonads show an increase in volume over the winter condition. These data suggest that the vernal gonadal development of first-year males is more strongly influenced by adverse climatic conditions than is that of adult males.

A small sample of testes collected in July, 1960, demonstrates that the timing of regression in 1960 was the same as in 1957 (fig. 2). Similarly, there was no difference in timing of fall molt in the population in these two years (fig. 5). A sample of 22 males and 18 females in molt in July, 1960, showed no difference in average stage of molt from a large sample taken in July, 1957 (see Selander, 1958:fig. 4, p. 362).

In 1961 the beginning of regression of testes in adult males was recorded at the end of June (table 2). The testes of two of three adult males collected on June 28, 1961, were regressing (volumes: 241.8 and 833.3 mm.^{3}) but that of the third male collected on June 27 was still in breeding condition (volume: 1653.4 mm.^{3}). The testis of a first-year male collected on June 27, 1961, was fully regressed, with a volume of 5.45 mm.^{3} (table 2). On the basis of these meager data, it seems probable that the timing of regression in the population in 1961 was similar to that recorded in 1957 and 1960.

Comparison with the Redwinged Blackbird

Comparing our findings on *Quiscalus mexicanus* with the results of the study by

Wright and Wright (1944) on the Redwinged Blackbird in Montana and Wisconsin, the following points of similarity were noted. (1) In *Agelaius*, as in *Quiscalus*, testes of juvenal birds apparently increase slightly in size in the first few weeks following the nestling stage and then decrease in size to a minimal low level. Mean testis weight in *Agelaius* was 1.9 mg. in June, 3.0 mg. in July, and 1.4 mg. in August (sample sizes 2, 7, and 5, respectively). (2) Testes of adult birds average larger than those of first-year individuals at all times. However, the degree of difference in size between breeding testes of adult and first-year males is less in *Agelaius* than in *Quiscalus*. In *Agelaius*, data of Wright and Wright (1944) indicate that the first-year testis is 66.8 per cent of the weight of the adult testis, whereas in *Quiscalus* the comparable figure, derived from volumes, is 41.2 per cent. (3) The period of most rapid vernal growth in adult testes precedes that in first-year testes by three weeks; and regression occurs earlier in first-year males than in adults. (4) Testes of adults remain in breeding condition for a longer period (50–75 days) than do those of first-year birds (30–55 days).

THE OVARY CYCLE

The ovaries of 83 specimens provide information supplementing field observations on the female reproductive cycle. Each ovary was examined under a low-power dissecting microscope, and the diameter of the largest follicle visible on the surface was measured (table 4). In the ovaries of many first-year females, surface follicles were not visible macroscopically or under the dissecting microscope, but, by cutting into an ovary, it was sometimes possible to find follicles; internal follicles were not measured, however.

Ovary Cycle in Juvenal and First-year Females

In ovaries of three juvenal birds taken in June and August, macroscopic follicles were not present. The same held true for eight first-year specimens taken between September 17 and 20, but one female collected on September 17 had follicles up to 0.21 mm. in diameter. By the period of October 5 to 9, 30 per cent of the ovaries of first-year birds had visible follicles, and the mean diameter of the largest was 0.035 mm. From October 20 to 24, mean diameter increased to 0.138 mm., and 83 per cent of the ovaries had visible follicles. A slight reduction in follicle diameter in November and December is suggested by our data; in these months mean diameter was 0.104 mm., and follicles were evident in less than half the ovaries examined.

By late January and February, about 60 per cent of the ovaries showed follicles, and mean diameter had definitely increased. This increase continued through March and April; and, on April 18, a bird with an incubation patch and a very active ovary was collected.

The presence of incubation patches in the two first-year females shown in table 4, and in dozens of other first-year females that we have examined but whose ovaries were not collected, demonstrate that females of *Quiscalus mexicanus* breed in their first year. As previously noted by McIlhenny (1937:292), females of *Q. major* also breed in their first year.

Ovary Cycle in the Adult Female

Visible surface follicles were found in ovaries of all adult females examined (table 4). In all probability there was a slight increase in diameter of follicles in late October, as in first-year females, but more material would be needed to prove

TABLE 4

DIAMETER OF LARGEST OVARIAN FOLLICLE IN MILLIMETERS

Age and period	Number of ovaries	Diameter of follicle Mean	Range	Per cent with visible follices
Juvenal				
June 25	1	0.00		0
First-year				
Aug. 2	2	0.00		0
Sept. 17–20	9	0.023	0.00–0.21	11
Oct. 5–9	10	0.035	0.00–0.14	30
20–24	6	0.138	0.00–0.35	83
Nov. 23–Dec. 19	9	0.104	0.00–0.35	44
Jan. 24	2	0.385	0.35–0.42	100
Feb. 6–20	8	0.275	0.00–1.68	62
March 8	3	0.513	0.00–0.84	67
April 18	1	2.80[1]		100
June 20	1	3.40[1]		100
Total	52			
Adult				
Aug. 9–23	6	0.723	0.42–1.05	100
Sept. 20	1	0.56		100
Oct. 4–9	2	0.660	0.62–0.70	100
Oct. 25–31	2	0.770	0.56–0.98	100
Nov. 5–Dec. 19	9	0.705	0.56–0.91	100
Jan. 25–28	3	0.583	0.49–0.70	100
Feb. 8	2	0.630	0.56–0.70	100
20	3	0.957	0.70–1.12	100
March 8–27	2	1.855	1.47–2.24	100
June 25	1	0.70[1]		
Total	31			

[1] Ovaries from individuals with incubation patches.

this supposition. Definite enlargement of follicles was noted on February 20, followed by an increase in size in March. As regards follicle diameter in the period of vernal development of the ovary, adult females were at all times well ahead of first-year females, a fact which suggests that adult females come into breeding condition before first-year females.

THE BEHAVIORAL CYCLE IN RELATION TO THE GONADAL CYCLES

In this section, a brief, qualitative account of seasonal variation in behavior is presented in an attempt to correlate the major events in the behavioral cycle with those of the gonadal cycles, as previously described. Except as noted, the account refers to the period extending from August, 1956, through November, 1957. Climatic data for this period are presented in table 5. The displays and vocalizations of the Great-tailed Grackle mentioned in this account have been described by Selander and Giller (1961).

For convenience of discussion, the annual cycle has been divided into five periods, as follows: I, winter; II, preparation for breeding; III, breeding; IV, postbreeding; and V, autumnal sexual behavior.

TABLE 5

SEASONAL CLIMATIC CHANGES AT AUSTIN, AUGUST, 1956, TO NOVEMBER, 1957

Month	Temperature (°F.) Mean	Min.	Max.	Rainfall in inches	Hours of sunshine	Daylength on first day of month	Comments
1956							
Aug.	85.9	65	104	1.21	313	13 hrs. 36 min.	Warmer than usual; dry
Sept.	81.7	58	103	0.09	308	12 hrs. 46 min.	Warm and sunny; very dry
Oct.	73.7	48	96	0.84	250	11 hrs. 53 min.	Warm and dry; scant rainfall
Nov.	57.3	31	85	2.13	210	10 hrs. 59 min.	Cooler than usual; rainfall normal
Dec.	56.6	33	80	2.76	206	10 hrs. 20 min.	Sunny and mild; rainfall normal
1957							
Jan.	50.5	22	81	0.55	93	10 hrs. 13 min.	Exceptionally long overcast period
Feb.	60.9	38	88	3.14	122	10 hrs. 46 min.	Vegetation growing rapidly; no freeze
March	59.5	31	82	4.58	161	11 hrs. 33 min.	Above normal rain; violent spring storms
April	66.0	37	86	9.93	160	12 hrs. 24 min.	Cooler than normal; 25 days with rain
May	73.5	51	90	7.38	276	13 hrs. 22 min.	Cool and wet; excess rain
June	80.9	63	97	5.25	236	13 hrs. 58 min.	Slightly cooler than normal; excess rain
July	86.3	73	104	1.10	368	14 hrs. 5 min.	Hot and dry
Aug.	86.0	71	101	Trace	347	13 hrs. 36 min.	Hot and dry; no measurable rain
Sept.	77.0	56	101	6.43	293	12 hrs. 46 min.	Cool, and rain 50 per cent above normal
Oct.	65.3	32	88	8.79	197	11 hrs. 53 min.	Cool and rainy; record low of 32°F. on October 28
Nov.	55.9	33	84	2.95	119	10 hrs. 59 min.	Cool and rainy; rain on 15 days

I. WINTER PERIOD, NOVEMBER TO JANUARY

During the day grackles foraged in flocks in fields surrounding Austin or in parks, golf courses, and other open areas in the city; at night they roosted communally in the city. The grackles left their roosts in groups of three to 50 birds approximately one hour before sunrise and began a slow movement through the city toward the surrounding farm areas. They made stops in the city in search of food and water, and then in groups of ten to 100 left the area, searching for freshly plowed fields and other areas in which to forage.

In the late afternoon, the foraging flocks began their return flight to the city. Before flying to the communal roost, the birds stopped briefly at one of several pre-roosting assembly points, which were localities where water was available for bathing and drinking. In the winter all birds within a ten-mile radius of Austin roosted in trees in an area of about 36 city blocks in the eastern part of the city. The final flights from the pre-roosting assembly points to the roosts occurred just at sunset (fig. 6), and the timing of these flights was obviously related to light intensity.

Males showed a stronger tendency to frequent foraging areas in the city than did females (Selander, 1965); and occasionally on warm days lone adult males visited the sites of former breeding colonies, most of which were located in the city, where they sometimes displayed and sang weakly. With this exception, the grackles did not exhibit sexual behavior.

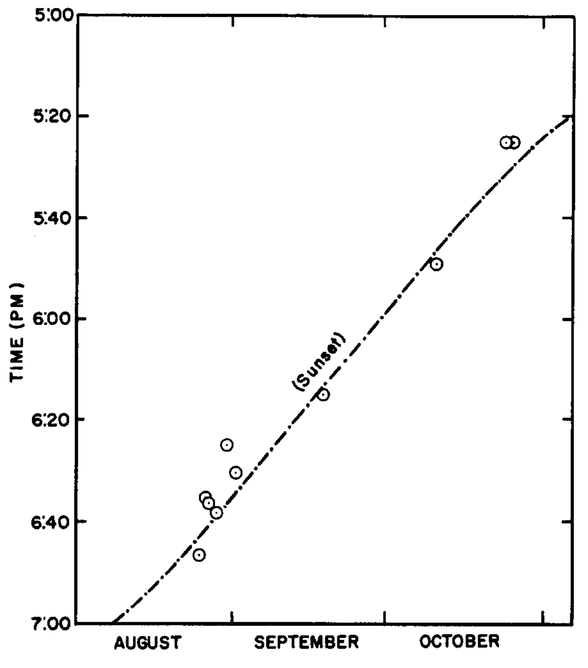

Fig. 6. Timing of flights of grackles from pre-roosting assembly point near Montopolis to roost in eastern part of Austin in fall, 1956.

In the winter period, as well as at other times of the year, the reactions of the male grackles to female dummies (mounted specimens) in copulatory posture were tested. In this posture the tail and head are elevated at an angle of about 45° from the horizontal. Dummies of this type evoke sexual and social responses on the part of grackles, varying from attraction to attempts to copulate (Selander and Giller, 1961). Using this technique, it was possible to assess the intensity of sexual motivation at different times of the year.

In the winter period, response to dummies was highly variable. Frequently no response at all was forthcoming, the dummies being ignored by birds which foraged only a few feet from them. Perhaps the typical response was a gathering of birds of both sexes about the dummies, in which the responding birds stared at the dummies but failed to display or mount. However, some elements of solicitation display, mounting, and copulation were observed in both sexes.

The following series of observations, made on January 5, 1957, illustrates the variety of responses to a female dummy in copulatory posture that was obtained in the winter period.

1. A mixed group of 10 grackles gathered about the dummy; no displays were given.

2. A female walked to the dummy, mounted, briefly attempted to copulate in the masculine pattern, then flew off. (As noted by Selander, *in* Nero, 1964:391, females of *Q. mexicanus* and *Q. major* frequently respond to female dummies by mounting and performing the masculine motor pattern of copulation.)

3. An adult male flew to the dummy, displayed weakly before it, giving the solicitation call, and attempted copulation with medium intensity. It then flew from the dummy giving the solicitation call.

4. A female flew down to the dummy, walked toward it giving soft *chut* warning notes and flicking the tail.

5. Several males gathered in a tree above the dummy; they seemed apprehensive.

6. A first-year male flew to the dummy, mounted without preliminary display, and attempted copulation weakly far forward on the dummy's back; it then dismounted and walked around the dummy, pecking lightly at the tail and the eye. The male mounted two additional times; each time the wings were flapped but copulation was not attempted; finally the male stood with one foot on the back of the dummy but failed to mount. Another first-year male joined the first at the dummy; there was no antagonism between the two, and after a few minutes both flew away.

7. A first-year female stood quietly two feet from the dummy for several minutes, then walked away foraging.

8. A first-year male flew toward the dummy, performed an abortive precopulatory display, and mounted far forward on the dummy's back but failed to copulate. At once eight other males and two females flew to the dummy. A short bout of fighting and threatening by three adult males in the group followed; first-year males did not participate in this bout. Suddenly a new adult male flew in, displaying weakly, and attempted to copulate with the dummy as the other birds stood nearby.

9. A first-year male flew down from a tree to the dummy, pecked at the tail, and left.

10. An adult male postured near the dummy, approached it closely, then flew.

11. A female mounted but did not copulate.

12. An adult male ran half-way around the dummy, displaying and calling, and then attempted copulation with medium intensity. As a second adult male approached, the first male hopped off the dummy, and a threatening bout followed. Then the first male again mounted and stood on the back of the dummy while it threatened the other male with head-up display.

The generally low intensity of sexual behavior noted in the winter period is correlated with the fact that testes are at or near minimum size and are spermatogenically inactive.

II. Preparation for Breeding, February and March

On warm days in the first two weeks of February, when temperatures were as high as 88°F. (table 5), a decided change occurred in the behavior of adult males correlated with an increase in testicular activity over the winter condition. For a few hours each day, many adult males left the foraging flocks and perched in trees, displaying and calling almost continuously. The complete song was heard regularly for the first time since October. Ruff-out displays were common and, occasionally, solicitation displays were seen. At this time of the year, the latter were imperfect and were not necessarily directed to females. The first solicitation display directed to a live female was recorded on February 17.

Weather conditions had a dramatic effect on sexual and territorial behavior in February. During cold periods, vocalizations of males concerned with courtship and territoriality were less frequent, weaker in volume, and shorter than normal; and in many cases the calls and songs were broken or otherwise irregular in pattern. On extremely cold or rainy days, the males became silent and returned to the foraging flocks. Cold weather also stimulated foraging activity. Especially evident during cold periods was an increased frequency of supplanting attacks and threat displays in contexts involving food items. A similar effect has been noted in several species of *Corvus* (Lockie, 1956) and in a variety of other birds.

First-year males did not display or call in the first half of February, in which period birds of this age group showed no increase in testis volume over the winter condition. Females continued to forage in fairly compact winter flocks, paying no attention to, if not actually avoiding, the displaying adult males.

In the last two weeks of February, temperatures were from 2° to 7° F. below normal and rain fell on seven different days. Fairly typical winter behavior was seen in males as late as February 23, occasioned by a week of rainy weather with temperatures below 54° F.; and, actually, less reproductive behavior was manifest than in the warmer first half of the month.

Sexual response to dummies by males was more frequent in February than in the previous two months. Responding males generally gave solicitation displays before mounting, but these were rarely as intense as they were later in the season. For the first time since October, adult males attempted to hold territories around the dummies for prolonged periods, driving other males away. The responses of first-year males were not significantly different from those in January, except that in the latter part of the month the first-year birds displayed more frequently before mounting. Females continued to behave as in January.

By March 9, large numbers of adult males and some first-year males were spending most of the day at the nesting colony sites. There was much agonistic activity as males attempted to establish and hold territories in trees in which nesting had occurred the previous year. Only a few first-year males were present at the nesting colonies; these were without exception dominated by adults and none managed to hold a territory. The number of first-year males visiting the colonies increased gradually in March.

Until March 9, females continued to forage in flocks and exhibited typical winter behavior. Some females visited the nesting colony sites for brief periods and sporadically manipulated material in old nests, but nest-site territories were not established and nest building was not undertaken in earnest.

There was a marked increase in activity at the breeding colonies on March 14. Adult males remained at the colonies the whole day, and females began carrying nesting material and building. By March 21, some nests were ready to receive eggs, and the first invitation to copulate was given by a female.

In March males responded to female dummies with strong solicitation displays and calls and vigorous attempts to copulate. Usually the first male to arrive at the dummy held a territory around it, driving off other males with aggressive displays and chases. First-year males were never seen to dominate adults at the models, but, in the absence of adult males, they readily displayed before and copulated with the dummies.

Communal roosting continued through February and March.

The progressive increase in intensity of sexual and agonistic behavior in males seen in February and March is correlated with an increase in testis volume and an advance of spermatogenesis. In first-year males, the delay in appearance of reproductive behavior is associated with a delay in beginning of testis development, as previously discussed. At the end of the period, the testes of males were nearing maximum development and breeding was ready to begin.

III. Breeding Period, April to June

A maximum amount of activity at the breeding colonies was noted in April. The first eggs were laid in the first week of April, and some females were feeding young by April 19. At the same time other females were building nests. A few adult males held territories in the nest trees, while other adult males and first-year males, which could not establish territories at the colonies, remained in trees or fields surrounding the colonies. Males accompanied the females on their trips in search of nesting material and food, almost continually displaying and soliciting copulation.

In the breeding season, nesting females spent the night at their nests, but the males continued to roost together in the eastern part of the city.

Sexual response to dummies was consistent and intense throughout the month of April.

In early May large numbers of young had fledged and were moving about in the vicinity of the nesting colonies in flocks with the females. The sexual activity of the males had diminished, but occasional solicitations and copulations were noted.

The response of adult males to dummies diminished in early May, and by May 10 males no longer responded sexually to the dummies, despite repeated testing. Several factors may have influenced this change in male behavior. Undoubtedly, the sexual motivation of males was less intense than in April, as reflected not only in their failure to respond sexually to the dummies, but also in their general behavior at the nesting colonies. Also, at this time of the year, females gathered about the dummies, giving excited warning notes, which may have influenced the behavior of the males toward the dummies.

There was a definite increase in the sexual response to dummies in the last 10 days of May, together with a general increase in level of activity at the breeding colonies. Some females again were seen carrying nesting material in preparation for a second major breeding effort, which occurred in June. Solicitation displays by males were again commonly seen and the general atmosphere at the breeding colonies was similar to that in April.

The period of relative sexual inactivity of adult males in May was associated with a slight decrease in testis volume and a change in average stage of spermatogenesis from 5b to 5a.

IV. Postbreeding Period, July to September

In July the breeding colonies were deserted except for a few late-nesting females which were feeding nestlings. The great majority of birds, including adults, first-year birds, and juveniles, gathered in large flocks to forage in the agricultural fields surrounding Austin. The winter pattern of communal roosting was re-established. Molt was in progress. The postbreeding period was characterized by a general absence of sexual behavior; and attempts to elicit sexual responses to dummies were unsuccessful. Occasionally a gathering response similar to that seen in the winter period was obtained, but no solicitation displays or attempts to copulate were recorded. In this period, males infrequently called and they exhibited no territoriality.

In the postbreeding season, testes were at minimum size; those of adult and first-year birds were undergoing histologic regression and reorganization.

V. Period of Autumnal Sexual Behavior, October

In the second week of October, 1956, a slight increase in numbers of grackles visiting the city was noted. Adult males occasionally visited the sites of former breeding colonies for brief periods in the morning, where they called and displayed weakly. By mid-October some males were stationed in trees in the city, giving aggressive calls and displays and not infrequently presenting solicitation displays to females as they foraged nearby. Females, however, did not display or otherwise respond to the songs and solicitation displays of males. At this time, large numbers of males foraged in typical winter flocks in the fields east of Austin; thus, only part of the total male population, mainly adults, showed autumnal sexual behavior. This is correlated with the fact that the degree of gonadal activity in October was highly variable individually and was greater in adult than in first-year males. In the period of autumnal recrudescence, 33 per cent of adult males had testes in histologic stage 2b, whereas no first-year male reached this stage, and only 44 per cent of first-year males reached stage 2a.

An attempt to elicit sexual responses to a female dummy on October 10 proved unsuccessful, as had a series of attempts in August and September. However, on October 27, we obtained an extremely strong response on the part of one adult male and moderate responses from several other males. At noon on October 27, a female dummy in copulatory posture was placed on a lawn within view of a large flock of male grackles. Almost immediately an adult male (A) flew to the dummy, gave solicitation display of moderate intensity and attempted to copulate. This male continued to display and to mount the dummy at intervals of about 20 seconds until a total of 50 mountings had been performed. This sequence was interrupted as another adult male (B) approached the dummy and was driven off by the first male (A), which employed strong head-up and ruff-out displays, together with song and threat calls. Male A then flew to a nearby tree to display vigorously to another adult male (C), which flew from the area. Male A returned to the dummy and mounted 65 more times, displaying between mounts. Later, male A drove two first-year males from a tree near the dummy and chased away an adult male (D) that was giving solicitation display to the dummy.

Male A continued to hold a territory around the dummy for two hours, in which period it frequently courted the dummy and attempted copulation. Finally, male A was displaced by another adult male (E) after a vigorous fight. Male E then displayed to the dummy and mounted several times. Later in the day, in the absence of adult male E, two first-year males approached the dummy, displayed weakly, and mounted. Five females also approached the dummy but none displayed or mounted. Many adult and first-year males in the area failed to respond to the dummy.

As shown in table 5, October, 1956, was a month of warm, dry weather, with a mean temperature of 73.7° F. By the first week in November, temperatures dropped sharply, and the period of autumnal sexual behavior came to an end. Males which formerly had spent most of the day at the sites of the breeding colonies had joined the large foraging flocks in the fields surrounding Austin. Those few males which continued to exhibit sexual behavior did so sporadically and generally gave only weak displays and calls. By mid-November the behavior of the grackles was similar to that of birds in the winter period.

Autumnal activity in 1957.—As noted previously by Selander and Nicholson (1962:83–84), the degree of manifestation of autumnal territorial and sexual behavior by male grackles varies markedly from year to year, depending on the prevailing weather conditions. The fall of 1956 was unusually warm and dry, and the autumnal activity was relatively intense. However, in years in which cold, rainy weather occurs in September and October, as in 1957, there are only brief and relatively weak expressions of incipient reproductive behavior. Similarly, Pielowski and Pinowski (1962) found that the intensity of autumnal sexual activity in the European Tree Sparrow (*Passer montanus*) is strongly dependent upon the weather, particularly on the amount of insolation.

In September, 1957, mean temperature in the Austin region was several degrees below normal, and rainfall (6.43 inches) was 50 per cent above normal (table 5). Birds were in large foraging flocks during the day, and males were generally silent except for warning and aggressive calls. However, mild head-up display was seen and some adult males occasionally sang the third part of the song (see Selander and Giller, 1961). The few full songs that were given were comparatively weak in volume. Rarely, an adult male gave brief, weak solicitation calls.

Until the last few days of the month, the response to female dummies was poor. On September 14 and 28, weak gathering responses were forthcoming, but mountings were not attempted and males did not attempt to hold territories around the dummies. Females responding to dummies were wary and often hovered over the dummies, giving alarm notes; this behavior is typical of females which have fledged young. On September 15, an adult male directed a weak solicitation display (with call) to a dummy, but he failed to mount the dummy. A few adult males briefly visited the sites of nesting colonies, where they sang the third part of the song and gave weak solicitation calls.

On September 29, birds showed typical winter responses to female dummies. About 80 birds gathered around a dummy and returned to it several times after being frightened away. At least four adult and six first-year males mounted and/or attempted copulation with the dummy, but none gave solicitation displays or calls. The wariness of females had abated and they boldly approached the dummies.

Cool, rainy weather continued through October, 1957, with a mean temperature 4.6° F. below normal and rainfall 7 inches above normal for the month (table 5). On October 8, there was an increase in numbers of grackles visiting the city in the day, and two adult males sang parts of the song in trees at a nesting colony on the campus. However, typical winter response to dummies continued.

On October 19, which was a clear, moderately warm day following several days of heavy rain, there was a marked change in behavior. Several males stationed themselves at nesting colony sites on the campus in the morning and strongly sang the complete song; other aggressive calls were also given with vigor. For the first time since June, an adult male gave the full solicitation display as it flew down to a group of females on the ground. Females did not display, although they visited trees in which males were stationed. Elsewhere in the city and in the fields east of Austin, large numbers of birds continued to forage in typical winter flocks. Despite the obvious change in behavior of some males, many males failed to respond to dummies. Generally, only the typical winter response was obtained, but some males now displayed before mounting the dummies.

The next day, October 20, was overcast and chilly. Most of the males that were stationed at colony sites on the campus the day before failed to appear, having apparently returned to the foraging flocks. The response to dummies was poor, and those few males which responded failed to display before mounting. Heavy rains fell on October 21 and 22, all but completely suppressing sexual and territorial activity; but a few males were present on the campus, giving the complete song. October 23 was mild and dry, and there was a conspicuous increase in activity at colony sites on the campus, where several males displayed and sang strongly. Several days of unusually cold and rainy weather followed, with a record low of 32° F. being recorded on October 28. When mild weather returned in the first week of November, the autumnal period of incipient reproductive activity was apparently coming to an end. A few adult males sang weakly at the colony sites on the campus, mainly giving partial song, but a few days later there was little evidence of territorial or sexual behavior.

DISCUSSION

It should be apparent from the foregoing account that there is a close, consistent relationship between events in the gonadal and behavioral cycles. Testicular activity in the breeding season and in October is accompanied by the appearance of sexual and territorial behavior, while, during periods of sexual inactivity following the breeding season and in the winter, the testes are relatively inactive. In May a slight decrease in testis volume and in number of adult males having mature spermatozoa in the tubular lumen is correlated with a diminution in intensity of sexual behavior.

The present work demonstrates that the failure of first-year males to breed cannot be attributed to incomplete spermatogenesis, since mature spermatozoa were present in the testes of all birds of this age taken in the breeding season. Moreover, the fact that first-year males regularly solicit matings with live females and attempt copulation with female dummies indicates that they are behaviorally capable of mating. The complex of factors which causes a delay in the age of first breeding in males of *Q. mexicanus* and other species having polygamous or promiscuous mating systems, and the adaptiveness of this delay, have been discussed by Selander (1965). Among these are the following: (1) First-year males have smaller testes than adult males and are presumably inferior as regards androgen titers. As a result, they display less intensely and are dominated by adult males in agonistic interactions. (2) By the time the testes of first-year males begin developing and reproductive behavior appears, adult males, which are ahead of first-year males in gonadal development, have already established territories at the nesting colonies. (3) Being inferior in the expression of morphological and behavioral "releasers" important in agonistic and sexual interactions, first-year males fail to establish breeding territories in competition with adult males and are rarely if ever successful in stimulating mating responses in females.

Autumnal sexual behavior and gonadal recrudescence in birds have been discussed by Marshall (1952), Morley (1943), Snow (1955), Kalela (1958), and Orians (1960). In the Rook (*Corvus frugilegus*), in which 13.6 per cent of adult males achieve full spermatogenesis in the fall, "autumn sexual behaviour strengthens the pair-bond and is demonstrably valuable in forming new pairs and in establishing territory long before the beginning of the secondary (productive [spring and summer]) sexual season" (Marshall and Coombs, 1957:585).

In the House Sparrow in England, which has been studied intensively by Summers-Smith (1963), there is a minor peak in frequency of male sexual display in late October. Although "only rarely do these displays stimulate the females to ovulation," this is a period of pair formation. "Immediately after the moult in autumn there is a recrudescence of sexual behavior and males that have disappeared since the end of the breeding season are quickly replaced." After this, sexual activity wanes, "and if one partner dies the remaining bird usually stays unmated until January or February when pair formation begins again."

Since pair bonds are not formed at any time of the year in the promiscuous Great-tailed Grackle, it is difficult to ascribe any adaptive significance to the autumnal expression of sexual and territorial behavior. Perhaps some first-year males gain experience which later in life is of value in encounters with territorial males and with females in the breeding season. Territories which are established by adult males in October invariably are abandoned a few days or weeks later, but the territorial behavior in the fall may help to fix in adult males the pattern of returning to territories, as suggested by Nice (1937) and Morley (1943) for other birds.

We have no evidence that males ever achieve full spermatogenesis in the Austin region in the fall, and we have no records of females nest building or performing other reproductive behavior. However, in city parks in Orlando, Florida, where conditions are favorable for reproduction in the fall, grackles of the closely related species *Q. major* breed in November (Selander and Nicholson, 1962), and it is likely that *Q. mexicanus* could respond similarly to favorable conditions. Observations of *Q. mexicanus* in Central America and México in late winter of 1962 indicate that populations in towns breed as early as December, and it would not be surprising to find breeding in October or November.

In the Austin region, gonad development as well as degree of expression of sexual and territorial behavior in October, 1956, was essentially similar to that in February. Spermatogenesis was initiated in a majority of adult males and in about 33 per cent of first-year males. But, instead of continuing development, by November the testes of at least some adult males and most first-year males had reverted to the September condition, and the intensity of the incipient reproductive behavior had diminished considerably. The question arises as to what factor or set of factors is responsible for the failure of the testes to progress further in the fall. Considering this general problem, Marshall and Coombs (1957) have suggested that "a gradual increase of daylight is needed to initiate normal full-scale gametogenesis." In the period of fall activity of grackles, light is, of course, decreasing; and the daily decrease in November is about equal to the daily increase in March (1.6 min./day in March; 1.3 min./day in Nov.).

Marshall and Coombs (1957), in their study of the Rook, were unable to find any factor potent enough to inhibit autumnal progression, and it is similarly difficult to do so in the case of the Great-tailed Grackle. Thus, it seems unlikely that the continuing annual molt could inhibit progression, since the molt is essentially complete when, in late October, testes are in maximum fall development. Temperature and precipitation can probably be ruled out as inhibiting factors. Mean daily temperatures in November (59.1° F.) are as high as in March (60.3° F.), the month in which the most rapid development of testes takes place in the spring; also, there are no important differences between November and March as regards temperature ranges. Precipitation in November (2.72 inches) is about equal to that in March (1.97 inches). We have no quantitative data on relative food abundance in these months, but it is our impression that food is at least as readily available in November as in March.

Notwithstanding these similarities, environmental conditions are not identical in the two periods. In November, leaves of elms and other deciduous trees, including those species most favored as nest sites by the grackles, are falling, whereas in March they are growing. The possibility that this and other, as yet unknown, environmental factors inhibit fall progression of the gonads cannot be overlooked, difficult as they are to evaluate.

SUMMARY

The annual testis and ovary cycles in the Great-tailed Grackle (*Quiscalus mexicanus*) were studied in the Austin region, Texas, from August, 1956, through October, 1957; and seasonal variation in behavior is discussed in relation to the gonadal cycles.

Vernal recrudescence of the testes of adult males was initiated early in February, and maximum testis volume was attained in the first part of April. Testes of adults were in breeding condition from April through June, with a minor decrease in volume and spermatogenic activity in May, followed by a second peak in June. In first-year males, vernal recrudescence of the testes began two or three weeks later than in adult males, and full breeding condition was not achieved until the latter part of April or May. Regression began in June in first-year males but not until July in adult males.

It is suggested that the bimodal form of the cycles of volume, spermatogenic activity, and interstitial cell numbers in the testes of adult males in the breeding season (April–June) was related to variation in the amount of visual and vocal stimuli provided by the breeding females. Peaks of testis volume and activity in April and June, 1957, corresponded with peaks in nesting activity of the females.

Throughout the year, testes of first-year males are smaller than those of adults; and, at maximum size in the breeding season, mean testis volume of first-year males is only 41.2 per cent of that of adult males.

Slight recrudescence of the testes occurred in October in many adult but in relatively few first-year males. This followed a period of minimal volume and spermatogenic activity in August and September. The testes of 33 per cent of adult males advanced from histologic stage 1 to stage 2b, but no first-year male advanced beyond stage 2a. No male of either age group achieved full spermatogenesis in October; and, in November, testes returned to a near-minimum level of volume and activity, which was maintained until February.

The timing of testis regression and of the inception of fall molt did not differ in the years 1957 and 1960.

In the ovary cycle of adult females, enlargement of follicles was noted on February 20, followed by an increase in size in March. The first eggs were laid in the first week of April. Adult females were at all times ahead of first-year females in follicle size, and, presumably, adult females came into breeding condition before the first-year females. There was a slight increase in mean diameter of ovarian follicles in October, at the time of recrudescence of the male gonads.

There is throughout the year a close correlation between the intensity of sexual and territorial behavior in males and events in the testis cycle. The level of sexual motivation of males was assessed by observing their responses to female dummies mounted in copulatory posture.

Some elements of territoriality, solicitation display, and copulation are shown by males even in the winter period, when the testes are small and inactive. In the first two weeks of February, 1957, when vernal recrudescence of the testes was first evident, many adult males left the winter foraging flocks and began displaying and calling at the sites of nesting colonies of the previous year; but first-year males did not exhibit marked sexual behavior until the latter part of February or March. Maximum activity at the nesting colonies occurred in April; and the level of intensity of sexual behavior of adult males diminished in May but increased again in June.

The postbreeding period, July through September, was characterized by a general absence of sexual behavior; attempts to elicit sexual responses to female dummies were generally unsuccessful.

In mid-October, 1956, some adult males held territories at the nesting colony sites and displayed agonistic and sexual behavior; however, the females, together with many adult males and most first-year males, remained in foraging flocks. Strong sexual responses to female dummies were shown by some adult males. Autumnal sexual behavior ceased with a drop in temperature early in November. In October, 1957, the expression of incipient reproductive behavior was largely suppressed by unseasonally cold and rainy weather.

Autumnal gonadal recrudescence of the gonads is terminated at a time when environmental conditions seem favorable for reproduction, and the proximate factors which inhibit gonadal progression in the fall are not readily apparent.

LITERATURE CITED

Bartholomew, G. A., Jr.
1949. The effect of light intensity and day length on reproduction in the English sparrow. Bull. Mus. Comp. Zool., 101:433–476.

Bond, J.
1963. Derivation of the Antillean avifauna. Proc. Acad. Nat. Sci. Phila., 115:79–98.

Burger, J. W.
1953. The effect of photic and psychic stimuli on the reproductive cycle of the male starling, *Sturnus vulgaris*. Jour. Exper. Zool., 124:227–239.

Davis, J., and Davis, B. S.
1954. The annual gonad and thyroid cycles of the English sparrow in southern California. Condor, 56:328–345.

Johnston, D. W.
1956. The annual reproductive cycle of the California gull. Condor, 58:134–162; 206–221.

Kalela, O.
1958. Über ausserbrutzeitliches Territorialverhalten bei Vögeln. Ann. Acad. Sci. Fenn., ser. A, IV. Biol., 42:1–46.

Lockie, J. D.
1956. Winter fighting in feeding flocks of rooks, jackdaws and carrion crows. Bird Study, 3:180–190.

Marshall, A. J.
1952. The interstitial cycle in relation to autumn and winter sexual behaviour in birds. Proc. Zool. Soc. London, 121:727–740.
1961. Breeding seasons and migration. *In* Biology and Comparative Physiology of Birds, edited by A. J. Marshall. Vol. 2 (Academic Press, New York), pp. 307–339.

Marshall, A. J., and Coombs, C. J. F.
1957. The interaction of environmental, internal and behavioural factors in the rook, *Corvus f. frugilegus* Linnaeus. Proc. Zool. Soc. London, 128:545–589.

McIlhenny, E. A.
1937. Life history of the boat-tailed grackle in Louisiana. Auk, 54:274–295.

Morley, A.
1943. Sexual behaviour in British birds from October to January. Ibis, 85:132–158.

Nero, R. W.
1964. Comparative behavior of the yellow-headed blackbird, red-winged blackbird, and other icterids. Wilson Bull., 75:376–413.

Nice, M. M.
1937. Studies in the life history of the song sparrow. I. A population study of the song sparrow. Trans. Linnaean Soc. New York, 4:vi + 1–247.

Orians, G. H.
1960. Autumnal breeding in the tricolored blackbird. Auk, 77:379–398.

Pielowski, Z., and Pinowski, J.
1962. Autumn sexual behaviour of the tree sparrow. Bird Study, 9:116–122.

Selander, R. K.
1958. Age determination and molt in the boat-tailed grackle. Condor, 60:355–376.
1960. Sex ratio of nestlings and clutch size in the boat-tailed grackle. Condor, 62:34–44.
1961. Supplemental data on the sex ratio in nestling boat-tailed grackles. Condor, 63:504.
1965. On mating systems and sexual selection. Amer. Nat., 49:*in press*.

Selander, R. K., and Giller, D. R.
1961. Analysis of sympatry of great-tailed and boat-tailed grackles. Condor, 63:29–86.
Selander, R. K., and Nicholson, D. J.
1962. Autumnal breeding of boat-tailed grackles in Florida. Condor, 64:81–91.
Snow, D. W.
1955. The abnormal breeding of birds in the winter 1953–54. Brit. Birds, 48:120–126.
Summers-Smith, D.
1963. The house sparrow (Collins, London).
Threadgold, L. T.
1956*a*. The annual gonad cycle of the male jackdaw *Corvus monedulus*. Qualitative aspects. La Cellule, 58:19–42.
1956*b*. The annual gonad cycle of the male jackdaw *Corvus monedulus*. Quantitative aspects. La Cellule, 58:45–54.
1960. A study of the annual cycle of the house sparrow at various latitudes. Condor, 62: 190–201.
Wolfson, A.
1942. Regulation of spring migration in juncos. Condor, 44:237–263.
Wright, P. L., and Wright, M. H.
1944. The reproductive cycle of the male red-winged blackbird. Condor, 46:46–59.

Department of Zoology, The University of Texas, Austin, Texas, June 18, 1964.