NESTING SUCCESS AND MORTALITY OF THE BOAT-TAILED GRACKLE

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ABSTRACT.—Of 605 Boat-tailed Grackle (*Quiscalus major*) nests with complete clutches, 60.5% fledged young. Survival of nests to the hatching stage averaged 78.7%, and survival from hatching to fledging averaged 76.9%. Nesting success between localities varied from none to almost all nests fledging some young. Fledging success for 3-egg clutches averaged 64.8% and was significantly higher than the 50.8% success rate that 2-egg clutches averaged. Individual survival of eggs from laying through hatching was lower in 2-egg clutches than in 3-egg clutches, but from hatching to fledging nestling survival was higher. Thus, in contrast to nest survival, equal proportions of eggs in 2- and 3-egg clutches produced fledglings.

Predation was the greatest source of mortality, with predators taking 14.8% of the 1,605 eggs and 13.1% of the 1,145 nestlings. Of eggs that survived to the hatching stage, 9.2% failed to hatch. Starvation (13.4%) was the most common source of nestling mortality. Nest abandonment accounted for the death of 5.7% of the eggs and 2.9% of the young. The sources of mortality varied spatially and temporally in an unpredictable way. This uncertainty has resulted in the flexible nesting biology of grackles. *Received 30 November 1984, accepted 15 July 1985.*

NATURAL selection operates in part on the variability in reproductive success. The observed reproductive pattern of a species must be considered an evolved life-history trait that will maximize the fitness of the individual (Williams 1966a, b; Lack 1968; Stearns 1976). Frequently, reproductive success varies temporally and spatially for a species. Knowledge of the variation in success and the sources of mortality are critical to evaluating the evolution of the observed life-history tactic (Stearns 1976).

Altricial birds lay their eggs in nests and care for the dependent young (Nice 1962; Lack 1966, 1968). The egg and nestling stages of the life cycle often are the period of greatest mortality (Ricklefs 1969a, 1973). Little is known about the microgeographic variation in reproductive success of individuals. Species must be adapted to this variation in success as well as to an overall average rate (Stearns 1976).

Boat-tailed Grackles (*Quiscalus major*) are polygynous-promiscuous and are extremely sexually size dimorphic (Bancroft 1983, 1984a). In central Florida they nest colonially from March through July (Bancroft 1983). Clutch size averages 2.64 eggs (range 1-4 eggs) and does not vary with the season (Bancroft 1983). Females that begin nesting in March lay smaller eggs that presumably contain less nutrients (Bancroft 1984b, 1985). Reproductive success should have played an important role in determining the observed pattern of reproduction. This study was undertaken to quantify reproductive success and its spatial and temporal variability. I analyze sources of egg and nestling mortality to understand the types of selective pressures that lead to the reproductive pattern of a highly polygynous-promiscuous species.

METHODS

I studied Boat-tailed Grackle colonies at seven locations during four field seasons, 1978-1981. All colonies were in western Hillsborough Co., Florida, except the Alligator Lake colony, which was near Safety Harbor, in the eastern part of adjacent Pinellas Co., Florida. All grackle colonies were located in cattail (*Typha latifolia*) stands in and around bodies of water. Detailed descriptions of the study areas appear in Bancroft (1983).

I located grackle colonies early in the spring prior to egg-laying or soon after the first few clutches were laid. I visited some colonies daily and others every 2-3 days. I found most nests during construction and marked all nests individually with numbered flags. I marked eggs with a permanent marker and young shortly after hatching by clipping one claw.

Generally, I recorded the contents of each nest at least every third day. I recorded the fate of each egg

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TABLE 1. Location, year, and nesting success of Boat-tailed Grackles in central Florida.

Location	Year	No. of clutches	No. of nests with nestlings	No. of nests with fledglings	Percentage of nests hatching	Percentage of nests fledging	Percentage of nestlings fledging[a]
Alligator Lake	1980	116	96	76	82.8	65.5	79.2
	1981	87	79	70	90.8	80.5	88.6
Univ. South Florida campus	1978	12	11	9	91.7	75.0	81.8
Courtney	1978	9	7	7	77.8	77.8	100.0
	1979	11	9	1	81.8	9.1	11.1
East Lake	1978	50	44	36	80.0	72.0	81.8
	1979	16	10	9	62.5	56.2	90.0
	1980	29	27	23	93.1	79.3	85.2
	1981	9	1	0	11.1	0.0	0.0
North Lake	1981	245	181	128	73.9	52.2	70.7
Hillsborough River	1980	11	4	3	36.4	27.3	75.0
University Mall	1980	10	7	4	70.0	40.0	57.1
Total		605	476	366	78.7	60.5	76.9

[a] Percentage of nests with nestlings that fledged.

laid. I considered eggs or young that were cold, wet, and dead in nests to have been abandoned. I considered single eggs that disappeared from nests that had other eggs still remaining to have been taken by a predator. When all eggs or all healthy young disappeared between visits, I recorded it as predation. I usually weighed young several times during the nestling period. I recorded young that were growing normally and disappeared between visits as being taken by a predator. If a nestling was not growing normally or was losing weight, or if I had no knowledge of its condition, I assumed it starved. I recorded the age of mortality as the day between visits unless more exact information was known.

RESULTS

Reproductive success.—Of 605 Boat-tailed Grackle nests with complete clutches, 60.5% fledged some young (Table 1). Success between sites ranged from no nests reaching fledging at one small colony, which was destroyed by mammalian predators, to almost all nests fledging young. For colonies larger than 20 nests (Alligator, East, and North lakes), fledging success ranged from 52.2 to 80.5%. Alligator Lake had significantly higher fledging success in 1981 than in 1980 ($\chi^2 = 4.78$, $P < 0.05$). The East Lake colony also showed significant variation in nesting success between years ($\chi^2 = 21.04$, df = 3, $P < 0.0001$). Nesting success at East Lake did not vary significantly from 1978 to 1980, but in 1981 success was significantly lower than in the previous 3 yr. Significant variation occurred in fledging success between Alligator Lake, East Lake, and North Lake ($\chi^2 = 17.27$, df = 2, $P < 0.0001$). Fledging success was not significantly different between Alligator Lake and East Lake ($\chi^2 = 1.10$, $P > 0.25$), but birds at these colonies were more successful than those at North Lake ($\chi^2 = 17.27$, $P < 0.005$; $\chi^2 = 4.60$, $P < 0.05$). Furthermore, the Alligator Lake colony during both years was more successful at fledging young than North Lake ($\chi^2 = 4.56$, $P < 0.05$; $\chi^2 = 19.16$, $P < 0.01$).

Survival of all nests to the hatching stage averaged 78.7% (Table 1). Survival at larger colonies ranged from 73.9 to 90.8%. Significant variation occurred in survival to hatching between Alligator Lake, East Lake, and North Lake ($\chi^2 = 10.36$, df = 2, $P = 0.006$). The Alligator Lake colony had significantly more nests that survived to hatching than the North Lake colony ($\chi^2 = 9.60$, $P < 0.05$), primarily because of the greater hatching success at Alligator Lake during 1981. All other comparisons showed no significant differences.

For all nests with young, fledging success was 76.9% (Table 1). Success at larger colonies ranged from 70.7 to 88.6%. Significant variation occurred in fledging success of nests with young at three colonies ($\chi^2 = 10.34$, df = 2, $P = 0.0006$), with both Alligator Lake and East Lake similar and having higher success than those at North Lake ($\chi^2 = 7.41$, $P < 0.01$; $\chi^2 = 4.52$, $P < 0.05$). The Alligator Lake colony was more successful than North Lake primarily because of their higher success in 1981.

TABLE 2. Nesting success of Boat-tailed Grackles relative to clutch size and colony location.

	Alligator Lake[a]		East Lake[b]		North Lake[c]	
	2 eggs	3 eggs	2 eggs	3 eggs	2 eggs	3 eggs
No. of clutches	60	139	36	67	78	157
No. of nests with nestlings	50	121	24	58	45	126
No. of nests that fledge young	42	101	18	50	32	89
Percent nests that hatch eggs	83.3	87.1	66.7	86.6	57.7	80.3
Percent nests that fledge young	70.0	72.7	50.0	74.6	41.0	56.7
Percent nests with young that fledge	84.0	83.5	75.0	86.2	71.1	70.6

[a] Data from 1980–1981 combined.
[b] Data from 1978–1981 combined.
[c] Data from 1981 only.

Clutch-size variation.—Nesting success (i.e. success at fledging any young) averaged 64.8% ($n = 401$) for 3-egg clutches, which was significantly higher than the 50.8% ($n = 189$) success rate for 2-egg clutches ($\chi^2 = 8.82$, $P < 0.01$). Three-egg clutches (83.3%) had an average higher proportion of nests hatch some eggs than did 2-egg clutches (67.7%; $\chi^2 = 16.76$, $P < 0.01$). Once a nest had nestlings, however, clutch sizes of 2 and 3 eggs had the same success in fledging some young (75.0 and 77.8%, respectively; $\chi^2 = 0.05$, $P > 0.05$). Two of 3 4-egg clutches and 8 of 12 1-egg clutches fledged young.

Nesting success at colonies with more than 20 nests ranged from 56.7 to 74.6% for 3-egg clutches and from 41.0 to 70.0% for 2-egg clutches (Table 2). At all three sites, 3-egg clutches had higher nesting success than 2-egg clutches, but only at the East Lake and North Lake colonies did a significantly higher proportion of 3-egg clutches fledge young ($\chi^2 = 5.28$, $P < 0.03$; $\chi^2 = 4.5$, $P < 0.05$). Success at hatching eggs was higher for 3-egg clutches than for 2-egg clutches at both East and North lakes ($\chi^2 = 4.55$, $P < 0.04$; $\chi^2 = 12.27$, $P < 0.01$), but success at raising nestlings to fledging was similar ($\chi^2 = 0.82$, $P > 0.36$; $\chi^2 = 0.02$, $P > 0.89$).

At Alligator Lake, Boat-tailed Grackles were more successful fledging young from 3-egg clutches in 1981 than in 1980 ($\chi^2 = 4.15$, $P < 0.05$). No significant difference occurred between years in fledging success of 2-egg clutches or in hatching success and raising nestlings of either clutch size at Alligator Lake. Significant variation occurred in fledging success with locality for both 2-egg ($\chi^2 = 11.6$, $P < 0.003$) and 3-egg clutches ($\chi^2 = 11.1$, $P < 0.004$). Compared with North Lake, nesting success at Alligator Lake was higher for both 2-egg ($\chi^2 = 10.3$, $P < 0.01$) and 3-egg clutches ($\chi^2 = 7.5$, $P < 0.01$). These differences resulted from grackles having higher success at Alligator Lake during

TABLE 3. Fledging rate of Boat-tailed Grackles relative to clutch size at three colonies.

	2-egg clutch		3-egg clutch				
	n	$\bar{x}$	n	$\bar{x}$	Combined $\bar{x}$	K-W[a]	P
Alligator Lake							
1980	28	1.11	84	1.49	1.39	2.53	NS
1981	32	1.28	53	1.77	1.59	4.80	<0.029
Combined	60	1.20	137	1.60	1.48	6.21	<0.013
East Lake							
1978	20	0.90	29	1.90	1.49	9.31	<0.001
1979	3	0.67	13	1.46	1.31	0.89	NS
1980	9	0.67	20	2.10	1.66	8.54	<0.004
1981	5	0	4	0	0	—	
Combined	37	0.70	66	1.76	1.38	17.29	<0.001
North Lake							
1981	78	0.77	157	1.11	1.00	4.54	<0.032

[a] Kruskal-Wallis test.

1981. For 3-egg clutches, success in fledging young was higher at East Lake than at North Lake ($\chi^2 = 5.68$, $P < 0.05$).

Fledgling production.—Boat-tailed Grackles averaged 1.23 ± 1.13 (SD) fledglings per nesting attempt ($n = 605$). Three-egg clutches averaged significantly more fledglings per nest (1.42 ± 1.19, $n = 401$) than 2-egg clutches (0.87 ± 0.92, $n = 189$; Kruskal-Wallis $\chi^2 = 23.04$, $P < 0.001$). The average number of young fledged per nest varied with clutch size and location (Table 3). At Alligator Lake, 3-egg clutches fledged more young than 2-egg clutches in 1981, but averaged the same number of fledglings in 1980. The fledgling production was the same for both clutch sizes in 1980 because many 3-egg clutches were abandoned or the nest structure collapsed, whereas for 2-egg clutches nest abandonment and nest structure failure were rare. Grackles at Alligator Lake produced the same number of fledglings per nest attempt in 1980 and 1981 (K-W $\chi^2 = 0.91$, $P = 0.34$), despite a decrease in average clutch size between the years (Bancroft 1983). Success was slightly lower in 1980 because more nests were abandoned and more nests suffered support failures. In 1978 and 1980 at East Lake colony, 3-egg clutches produced more fledglings than 2-egg clutches. Significant variation between years at East Lake occurred in the fledging rate per nest (K-W $\chi^2 = 13.52$, $P = 0.004$). Success was low in 1979 because five nests were abandoned during two days of heavy rains in May, and low in 1981 because all nest contents were taken by predators. Three-egg clutches at North Lake also produced more fledglings than 2-egg clutches (K-W $\chi^2 = 4.59$, $P = 0.032$).

Comparison of the combined fledging rate among the three localities with large samples showed significant variation in success (K-W $\chi^2 = 20.02$, $P < 0.0001$), with North Lake fledging fewer young per nest than either Alligator Lake or East Lake colonies (Table 3). Comparison of fledging success for clutches of 2 and 3 also showed significant variation among localities (2-egg: K-W $\chi^2 = 8.22$, $P = 0.016$; 3-egg: K-W $\chi^2 = 18.36$, $P < 0.0001$).

The mean number of young fledged per nest varied significantly by half-month periods in the nesting season (K-W $\chi^2 = 28.6$, df = 9, $P < 0.0008$; Fig. 1). The general trend was for mean fledging success to decrease through the season ($r = -0.78$, $P = 0.012$). Mean fledging success was highest during the first half of March, decreased through April, and increased again in May. Mean fledging success varied significantly between half-month periods at Alligator Lake (K-W $\chi^2 = 17.70$, df = 8, $P < 0.029$) and at North Lake (K-W $\chi^2 = 22.16$, df = 8, $P = 0.0046$). However, fledging success did not vary significantly with season at East Lake (K-W $\chi^2 = 3.76$, df = 8, $P = 0.88$). None of the three sites showed a significant decrease in mean fledging success through the season (Fig. 2).

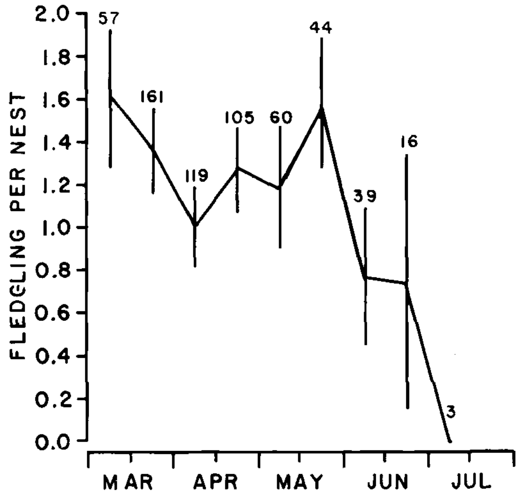

Fig. 1. Mean number of fledglings per nesting attempt relative to the half-month when the clutch was completed for Boat-tailed Grackles in central Florida. Vertical lines represent 95% confidence limits around the mean, and numbers above the lines are the numbers of clutches during each half-month.

Fledging dates for 366 successful clutches occurred between 29 March and 30 July, with 2 fledging in March, 149 in April, 131 in May, 63 in June, and 21 in July. The number of young fledging per week peaked in the fourth week of April, when 16% of all young fledged (Fig. 3). Of all fledglings produced, 50% came from clutches started during the first third of the nesting season.

At East Lake in 1978 and 1980, color-banded fledglings were followed closely to determine survivorship during the fledgling period. The East Lake colony was located on a small island, and young could not leave the area until they could fly well (about 30 days after hatching). As fledglings became more mobile, they would perch in willows bordering the cattails, and when in these trees their color bands were easy

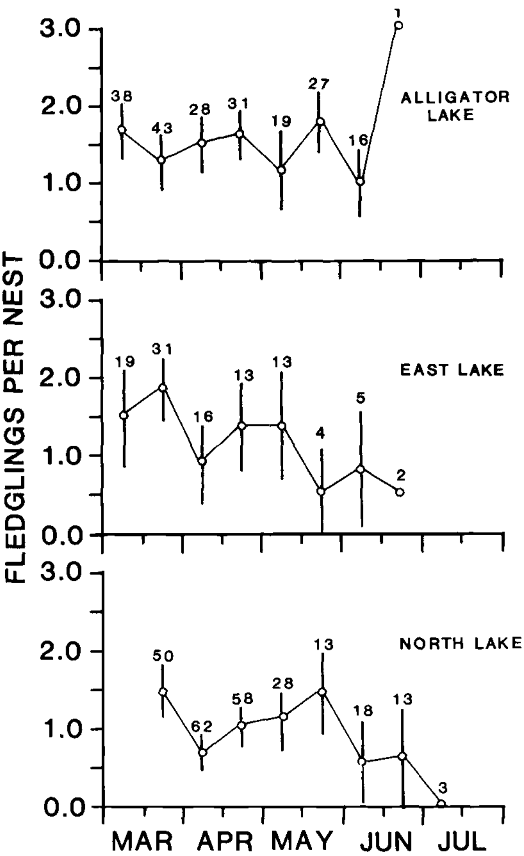

Fig. 2. Colony location and mean number of fledglings per nesting attempt relative to the half-month when the clutch was completed for Boat-tailed Grackles in central Florida. Vertical lines represent 95% confidence limits around the mean, and numbers above the lines are the numbers of clutches during each half-month.

to read. Of the 107 fledglings followed, 45% were seen 25 days after hatching or later. This represents a minimum estimate of survivorship for the first 10–12 days after fledging.

Age-specific survivorship.—Age-specific survivorship of eggs and nestlings is negatively skewed, indicating that mortality increases as the nesting period progresses (Fig. 4). Of the 1,605 eggs in complete clutches, 71.3% produced nestlings and 46.4% produced fledglings. The initial decline in the curve is attributable to the high rate of egg predation and nest abandonment early in the nesting cycle. The distinct drop in survivorship at hatching is the result of hatching failure. Unhatched eggs included infertile eggs and eggs in which the

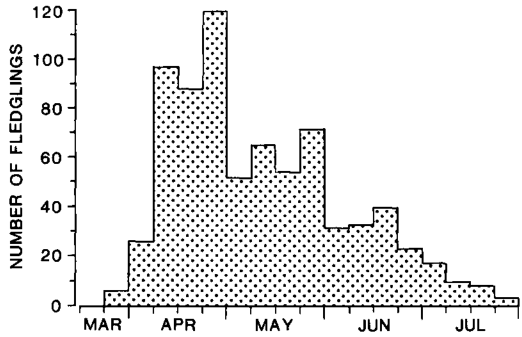

Fig. 3. Number of fledglings produced during each quarter-month of the nesting season for Boat-tailed Grackles.

embryo died. As the exact cause or age of this mortality was not known, the age of mortality was assigned to the hatching period. The increase in the slope of the survivorship curve after hatching indicates that the mortality rate is higher during the nestling period than during the incubation period.

The age-specific survivorship curves were considerably different among localities (Fig. 4). More eggs produced fledglings at Alligator Lake (54.8%) and East Lake (51.8%) than at North Lake (38.0%). All three curves were negatively skewed, indicating that mortality increased at all locations as the nesting cycle progressed.

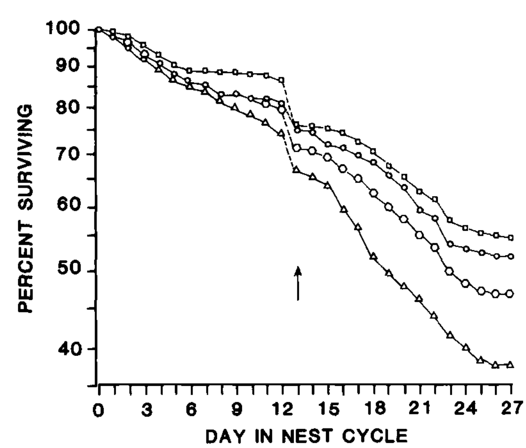

Fig. 4. Age-specific survivorship of eggs and nestlings during the nesting cycle for the total sample and for three colonies. Hexagon = total sample, square = Alligator Lake, circle = East Lake, triangle = North Lake. The arrow indicates the day eggs hatch.

TABLE 4. Sources of mortality of Boat-tailed Grackle eggs and nestlings in central Florida.

	Eggs				Nestlings			
Source	n	Percent of egg mortality	Percent of total mortality	Percent of eggs laid	n	Percent of nestling mortality	Percent of total mortality	Percent of nestlings
Unhatched	116	25.2	13.5	7.2				
Abandoned	91	19.9	10.6	5.7	33	8.2	3.8	2.9
Depredated	238	51.7	27.7	14.8	150	37.5	17.4	13.1
Starved					153	38.2	17.8	13.4
Nest collapsed	8	1.7	0.9	0.5	24	6.0	2.8	2.1
Other	7	1.5	0.8	0.4	40	10.0	4.7	3.5
Total	460	100.0	53.5	28.7	400	100.0	46.5	34.9

Survivorship was similar through the first half of incubation and then began to change at the three locations. At Alligator and East lakes, survivorship during the nestling period was similar. Therefore, the different fledging rates were a result of the difference in survival during the later part of incubation and the first few days of the nestling period. At North Lake, mortality was higher than at Alligator Lake and East Lake late in incubation and during the nestling stage. This resulted in many fewer eggs producing fledglings at North Lake than at either Alligator Lake or East Lake.

Sources of mortality.—Predation was the greatest single source of mortality, with predators taking 238 (14.8%) of the 1,605 eggs (Table 4). Egg predators accounted for 51.7% of all the egg mortality and 27.7% of all mortality. Of the 1,605 eggs observed, 116 (7.2%) did not hatch. Causes included infertility and embryonic death (Caccamise 1976). Failure to hatch affected 9.2% of the eggs in nests that reached the hatching stage. Nest abandonment represented the third most common source of egg mortality (5.7% of all eggs). A few additional eggs were abandoned in nests before the clutches were complete. Abandonment presumably included females that deserted their nests and females that died. The "other" category for eggs includes those that I cracked or accidentally broke (4) and those lost to high water levels.

Starvation represented the most common (153 nestlings, 13.4%) and nest predators the second most common source of nestling mortality (150 nestlings, 13.1%; Table 4). Abandonment, failure of nest structure, and other sources accounted for less than 4% each of fates of nestlings; when combined, they accounted for less than 9% of all nestlings (Table 4). Of the 33 abandoned young, 18 were 8 days old or older. Failure of nest structures generally occurred as a result of storms. Cattails collapsed (17) or became uprooted (5), and the bottoms of nests built in willows were torn out (2). The "other" category for young includes nestlings that drowned (6), fell out of the nest (2), or presumably were poisoned by food from recently sprayed yards (22). Poisoned young did not form fecal sacs and became covered with fecal material. They also appeared to pass more fluids than normal and became dehydrated. Usually, they lost weight for a few days and then died.

Timing of mortality in the nest cycle.—Mortality from the various sources varied with stage of the nest cycle (Fig. 5). The number of eggs abandoned peaked soon after egg-laying began and then decreased through the incubation period. Egg predation peaked on day 3 and then decreased through the incubation period. Depredation of nest contents may be more likely during inattentive periods. Some females may be less attentive, and females in general may be less attentive at the start of incubation. These factors would contribute to the early peak in egg predation.

Starvation and predation of young showed bimodal peaks during the nestling period (Fig. 5). The first peak of predation occurred on the third day of the nestling period and the first peak for starvation occurred on the fifth day. The second peak for both sources occurred on day 10 in the nestling period (day 23 overall). The first peak in predation occurred soon after all young hatched. Starvation first peaked just before the point of maximum weight gain for nestlings and peaked again when some male nestlings were still gaining weight rapidly and feather development was progressing rapidly.

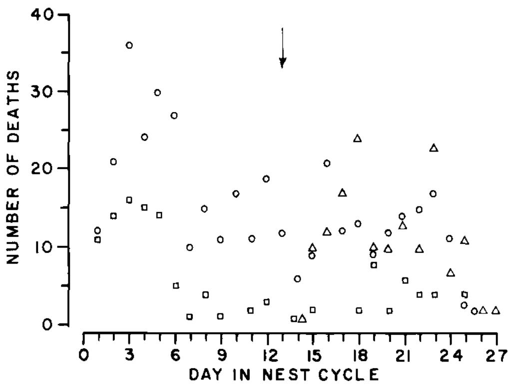

Fig. 5. Number of eggs and nestlings that die from predation (circles), abandonment (squares), and starvation (triangles) on each day of the nest cycle for Boat-tailed Grackles in central Florida. The arrow indicates the day eggs hatch.

Motor activity of the young increased at this time.

Locality variation in sources of mortality during the egg period.—Principal factors responsible for egg mortality varied significantly with locality ($\chi^2 = 104.3$, df = 8, $P < 0.001$; Table 5). Between 6.3 and 11.1% of the eggs given the opportunity failed to hatch (Table 5). Grackles at Alligator Lake had the highest proportion of unhatched eggs (39.7% of the egg mortality at that location). Unhatched eggs accounted for 20.9% of egg loss at East Lake and 19.2% at North Lake.

At East Lake the greatest egg mortality was due to abandonment (49.3%; Table 5). Heavy rains in May 1979 caused much of the abandonment (11 of 27 eggs). Presumably, females could not stay with the eggs constantly during the two days of rain, and, once soaked, the eggs were abandoned. Egg abandonment accounted for 27.5% of the egg mortality at Alligator Lake and 6.1% at North Lake. Most of the nests abandoned at Alligator Lake occurred in 1980, when 7 nests with eggs and 5 nests with young were abandoned early in the season. Egg abandonment accounted for only 6.6% and 2.0% of the total eggs laid at Alligator Lake and North Lake, whereas it accounted for 12.0% of the eggs laid at East Lake.

Egg predation was the major mortality factor at North Lake, where 72.8% of the eggs that did not reach hatching were lost to predators. This represented the most numerous source of mortality of eggs and young at North Lake, with 39.0% of all mortality attributable to this factor. Egg predation was the second most common source of egg loss at East Lake (29.9%) and the third most common at Alligator Lake (24.4%). Almost 25% of all eggs laid at North Lake were taken by predators, compared with only 5.9% and 7.3% at Alligator Lake and East Lake.

Locality variation in sources of mortality during the nestling period.—Factors responsible and their relative importance for nestling mortality varied with locality ($\chi^2 = 155.5$, df = 8, $P < 0.001$; Table 6). Starvation was the most common source of nestling mortality at Alligator and East lakes and the second most common source at North Lake (Table 6). However, approximately the same proportion of all nestlings starved at East Lake (18.4%) and North Lake (15.9%), whereas only 10.6% of the nestlings at Alligator Lake died from this cause. Thus, although starvation was the most common source of mortality at Alligator Lake, a smaller proportion of all nestlings died from this cause at Alligator Lake than at the other two localities (Table 6). This lower starvation rate at Alligator Lake was partially responsible for the greater nesting success there compared with the other two localities.

The most common source of nestling mor-

TABLE 5. Sources of mortality of Boat-tailed Grackle eggs at three localities.

	Alligator Lake			East Lake			North Lake		
	Mortality		Percent of eggs	Mortality		Percent of eggs	Mortality		Percent of eggs
Source	*n*	%	laid	*n*	%	laid	*n*	%	laid
Unhatched	52	39.7	9.5	14	20.9	5.1	41	19.2	6.4
Abandoned	36	27.5	6.6	33	49.3	12.0	13	6.1	2.0
Depredated	32	24.4	5.9	20	29.9	7.3	155	72.8	24.2
Nest fell	8	6.1	1.5						
Other	3	2.3	0.5				4	1.9	0.6
Total	131	100.0	23.9	67	100.0	24.5	213	100.0	33.3

TABLE 6. Sources of mortality of Boat-tailed Grackle nestlings at three localities.

Source	Alligator Lake			East Lake			North Lake		
	Mortality		Percent of nestlings	Mortality		Percent of nestlings	Mortality		Percent of nestlings
	n	%		*n*	%		*n*	%	
Abandoned	22	19.0	5.3	5	7.7	2.4	4	2.2	0.9
Depredated	15	12.9	3.6	5	7.7	2.4	107	58.2	25.1
Starved	44	37.9	10.6	38	58.5	18.4	68	37.0	15.9
Nest fell	22	19.0	5.3	2	3.1	1.0			
Other	13	11.2	3.1	15	23.1	7.2	5	2.7	1.2
Total	116	100.0	27.9	65	100.0	31.4	184	100.0	43.1

tality at North Lake was predation (58.2% of all nestling mortality; Table 6). Predation was a minor cause of nestling mortality at Alligator Lake (12.9%) and East Lake (7.7%). The magnitude of nestling predation at North Lake is revealed when one considers the proportion of total nestlings lost to predators. Predators took just over 25% of the nestlings at North Lake, but less than 4% at Alligator and East lakes. Thus, starvation and predation together accounted for the low fledging success at North Lake compared with the other two localities.

Nest abandonment and failure of nest structure were important sources of nestling mortality at Alligator Lake. Both sources of mortality were common in 1980 but rare in 1981 and account for the differences in nesting success between the two years at Alligator Lake. Many of the abandoned nestlings were several days old.

Of the 15 nestlings that died in the category of "other" at East Lake, 11 presumably died from insecticide poisoning. Six young died from this cause at Alligator Lake in 1980 and 3 at North Lake in 1981. Several young recovered from poisoning after losing weight, but fledged below average weight.

During storms some cattail clumps supporting nests collapsed and some nests in willows were torn apart. Storms accounted for 19.0% of the nestling mortality at Alligator Lake, most of which occurred in 1980 and contributed to the observed difference in nesting success between years.

Seasonal variation in sources of mortality.—The intensity of different mortality factors varied with the season and the number of active nests (Fig. 6). Egg predation peaked when nests were most numerous, which was slightly later than the peak in the number of active nests with eggs. The first peak in egg predation resulted from almost total predation of eggs at the Hillsborough River and University Mall colonies in 1980 and at East Lake colony in 1981. In these cases, eggs in many nests were eaten during a 2-night period. Egg predation was least frequent in May and peaked again in late June. Nestling predation peaked just after the peak in active nests and at the same time as maximum number of nests with young. Nestling predation also reached a low during May and then peaked a second time in late June. The second peak in egg and nestling predation in late June resulted from high predation at North Lake. This peak coincided with the formation of an icterid and European Starling (*Sturnus vulgaris*) roost in many of the cattails that contained active nests.

Egg abandonment remained fairly constant through mid-May and did not change with the number of active nests. Young abandonment peaked in the first quarter of April and remained low through May. Neither egg nor young abandonment was correlated with the number of active nests. Some nests with eggs were abandoned when cattails supporting the nests became tipped. Many nests abandoned with young remained intact for several days to a week after the young had died. The frequency of hatching failure, which peaked at the same time as the number of nests with eggs, remained high through late April before decreasing in parallel with the number of active nests.

Nestling starvation peaked in late April, slightly later than the peak in number of active nests with young, and remained high through the third quarter of May. The intensity of mortality from this factor was attributable to the female's ability to gather enough food for the developing young. The second peak in starvation in May coincided with the end of the dry season. It may be that insect abundances suit-

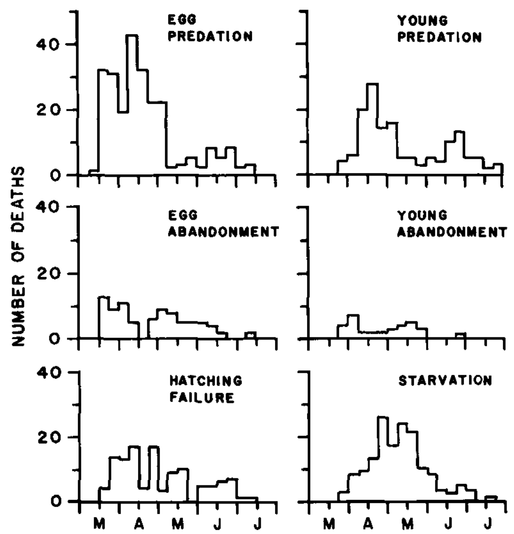

Fig. 6. Number of eggs and young that die from each source of mortality during each quarter-month of the nesting season for Boat-tailed Grackles in central Florida.

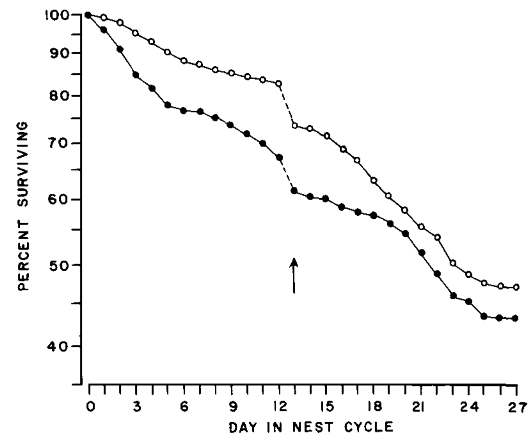

Fig. 7. Clutch size and age-specific survivorship of eggs and nestlings during the nesting cycle for Boat-tailed Grackles in central Florida. Closed circles = 2-egg clutches, open circles = 3-egg clutches. The arrow indicates the day eggs hatch.

able for grackles were low at this time and this increased the difficulty of females fledging all their young.

Age-specific survivorship and sources of mortality of 2- and 3-egg clutches.—Of the 378 eggs in 2-egg clutches, 61.9% hatched, whereas 74.0% of the 1,203 eggs in 3-egg clutches hatched. However, similar proportions of eggs produced fledglings from each clutch size (43.4% from 2-egg, 47.2% from 3-egg). The survivorship curves of eggs and young showed a different pattern of survivorship for each clutch size during the nesting cycle (Fig. 7). The survivorship of eggs during incubation was constant for each clutch size. The mortality rate of eggs, however, was much higher in 2-egg clutches, which accounted for the observed difference in proportion of eggs hatching. Hatching failure caused the survivorship curves to drop steeply. The proportion of eggs that failed to hatch did not vary with clutch size ($\chi^2 = 1.41$, $P > 0.10$; Table 7). Immediately after hatching the survivorship of young in 2-egg clutches was much higher than in 3-egg clutches. Consequently, by the fifth or sixth day of the nestling period equal proportions of young from each clutch size had survived. Mortality rates were the same from day 6 to fledging for both clutch sizes. Hence, equal proportions of young fledged from the two clutch sizes.

The different survivorship curves for each clutch size came from differences in the intensities of the mortality factors (Table 7). For 2-egg clutches, 21.4% of the eggs were taken by predators and 11.1% were abandoned, compared with only 13.1% and 4.0% for 3-egg clutches. The proportions of young taken by predators did not differ with clutch size. In 3-egg clutches 14.9% of the young starved; in 2-egg clutches only 8.1% starved. The higher predation and abandonment rates during incubation for 2-egg clutches accounted for the lower proportion of eggs that hatched in 2-egg clutches. The higher rate of nestling starvation in 3-egg clutches accounted for the similar proportions of eggs producing fledglings from each clutch size.

The timing of mortality during the nest cycle varied with the cause of mortality and with clutch size (Fig. 8). Egg predation was highest early in the nest cycle for both clutches. Throughout incubation, predation remained high for 2-egg clutches but decreased for 3-egg clutches. Egg abandonment principally occurred early in incubation and was more frequent for 2-egg clutches. This different pattern of egg predation and egg abandonment accounted for the observed difference in the survivorship curves for the clutch sizes. For 3-egg clutches, predation of young and starvation showed significant peaks early in the nestling period. Predation of young remained high throughout the nestling period, and starvation

TABLE 7. Sources of mortality of Boat-tailed Grackle eggs and nestlings in clutches of 2 and 3 eggs.

	2-egg				3-egg			
Source	*n*	Percent of eggs laid	*n*	Percent of nestlings	*n*	Percent of eggs laid	*n*	Percent of nestlings
Unhatched	18	4.8			97	8.1		
Abandoned	42	11.1	12	5.1	48	4.0	21	2.4
Depredated	81	21.4	31	13.2	157	13.1	116	13.0
Starved			19	8.1			133	14.9
Nest fell	2	0.5	2	0.9	6	0.5	18	2.0
Other	1	0.3	6	2.6	5	0.4	34	3.8
Total	144	38.1	70	29.9	313	26.0	322	36.2

peaked a second time late in the period. For 2-egg clutches, both young predation and starvation were low until late in the nestling period, when they peaked. The low starvation and predation rates of young in 2-egg clutches during the first half of the nestling period were responsible for the higher survival rate that resulted in equal proportions of eggs producing young that were alive at day 6. The similar predation and starvation rates late in the nestling period for both clutch sizes were the cause of equal proportions of eggs producing fledglings.

DISCUSSION

One can speculate on how long it would take a female to replace herself in the breeding population, if one assumes the following. A female has only one successful brood per year, but she can have three attempts to produce it. A successful attempt averages two fledglings, and 60% of the attempts will produce fledglings. With these assumptions, an average of 1.87 fledglings should be produced by each breeding female per year. The hatching sex ratios of grackles are not significantly different from one, and male and female survivorship does not vary significantly during the nestling and fledgling periods (Bancroft 1983). My data suggest that only half of the fledglings survive to independence; if only 50% of the independent young survive to breeding age, five breeding seasons would be required to produce one female and one male offspring that would survive to age 1 yr. If survival of fledglings was less, then a longer period would be required. Adult survivorship for the closely related Great-tailed Grackle (*Quiscalus mexicanus*) averages 75% for females (Searcy and Yasukawa 1981). This indicates that a female that reached reproductive age would average between four and five breeding seasons during her lifetime (Krebs 1972).

The factors that reduce the production of young most are those that apply the greatest selective pressures for modification of breeding. Predation was the most severe mortality source (45.1% of all egg and nestling mortality). Of this total, 27.7% was egg predation and 17.4% was nestling predation. Starvation represented the second most important factor (17.8% of all mortality). Hatching failure and nest abandonment accounted for about equal proportions of the total mortality (14–15% each). Some of the nest abandonments may have resulted from the death of the breeding female. For many marsh-nesting icterids, predation represents the source of greatest mortality for eggs and young (Orians 1961, 1973, 1980; Willson 1966; Robertson 1972, 1973b; Holm 1973; Caccamise 1976). During the nestling period, the relative intensity of predation and starvation varies with the species and the nesting location. Starvation frequently accounts for the greatest number of nestling deaths (Robertson 1972, 1973a, b). Starvation is a very significant cause of nestling death for a great many passerines (Lack and Lack 1951; Snow 1958; Ricklefs 1965, 1969a; Howe 1976, 1978; O'Connor 1978a). For most passerines, however, predation is the major mortality source of nest contents (Ricklefs 1969a, Clark and Wilson 1981 and references therein).

As the largest source of mortality, predation would provide the greatest selective pressure to evolve mechanisms to decrease its effect. Mammals and birds represent the two main groups of organisms that prey upon nest contents of grackles. The high variance between

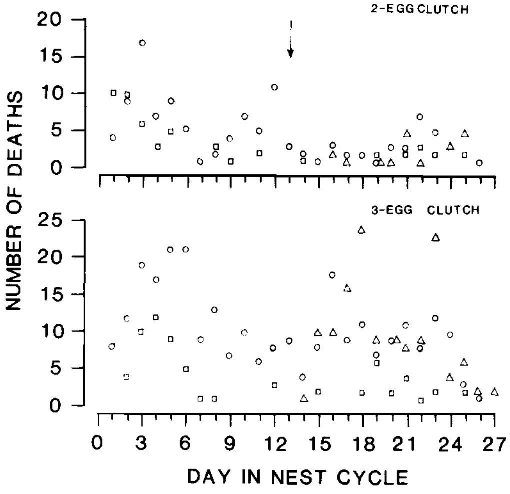

Fig. 8. Clutch size and the number of eggs and nestlings that die from predation (circles), abandonment (squares), and starvation (triangles) on each day in the nest cycle for Boat-tailed Grackles. The arrow indicates the day eggs hatch.

colonies in the effect of predators on reproductive success illustrates the advantage of finding a predator-free nesting site.

Rice rats (*Oryzomys palustris*) were a primary predator, usually depredating colonies during the night. When rats moved into a colony, they destroyed most grackle nests in a few nights. Broken eggshells were frequently found in the nests, and twice partially eaten adult females were on the nest. Occasionally, rats domed over grackle nests to use for their own nests. Rice rats are found throughout the distribution of Boat-tailed Grackles (Hall and Kelson 1959). Grackles responded to the invasion of rice rats by abandoning their colonies (e.g. at Courtney, East Lake, Hillsborough River, University Mall). The Courtney colony was invaded by rats in 1979 and was abandoned by grackles. This site was not used by grackles in either 1980 or 1981, presumably because rats were still present. Rice rats influence the distribution of Seaside Sparrows (*Ammodramus maritimus*) in Florida because of predation and competition for safe nest sites (Post 1981). Rice rats are known predators of Marsh Wren (*Cistothorus palustris*) and Red-winged Blackbird (*Agelaius phoeniceus;* Kale 1965, Orians 1973) nests. The most effective way for grackles to deal with rats and other mammalian predators is to nest in areas free of these predators, such as islands. The large variation in nesting success between localities partly reflects the effectiveness of finding a predator-free location.

Birds also represent potential predators of nest contents. Herons, Fish Crows (*Corvus ossifragus*), and Blue Jays (*Cyanocitta cristata*) were common near all nesting colonies. Although predation was not observed, all of these species were actively mobbed by grackles. Mobbing was commonly observed at Alligator Lake, where a heronry occurred in the willows near the grackle nests. Great Blue Herons (*Ardea herodias*) and Great Egrets (*Casmerodius albus*) were mobbed by both male and female grackles whenever they landed within several meters of a grackle nest. Male Boat-tailed Grackles also are mobbed vigorously by female grackles at some nesting localities. McIlhenny (1937) reported male grackles as an important predator of eggs and nestlings in Louisiana. At two parts of the North Lake colony where no single male was dominant, loud mobbing was observed on several occasions and was ended by several females vigorously chasing males from these nesting areas. I found one whole egg and three healthy nestlings from different nests floating in the water short distances from their nests, suggesting they were dropped when taken as a food item by a predator being mobbed.

The higher mortality rate of individuals during the nestling period compared with the incubation period may be related to the need of the nestlings to be fed. Foraging for nestlings requires the female to be gone from the nest more than during the incubation period, which leaves the nest unprotected. The increased activity of the female around the nest plus the begging of the nestlings may indicate the location of the nest to certain predators (Skutch 1949). The percent daily loss of whole nests caused by predators did not, however, vary significantly between incubation and nestling periods (Bancroft unpubl. data). The individual mortality rate is higher during the nestling period than during the incubation period because young starve.

Vigilance at or near the nest would protect the contents from avian predators. This, however, may not permit the female to forage. Females often travel 0.5 km on feeding trips. The higher starvation rate of nestlings at North Lake may in part result from females spending more time guarding the nest from avian predators. Nests at the North Lake colony experienced high predation from presumed avian predators. Vigilance at or near the nest is thought to be an important mechanism of improving nesting success in the Florida Scrub Jay (*Aphelocoma coerulescens;* Woolfenden 1978, Woolfenden and Fitzpatrick 1984). At North Lake, 2-egg clutches experienced much higher predation rates. Much predation was concentrated early in incubation. Clutches of 3 eggs were depredated less often. In several other icterids, clutch size is on average smaller for first-year breeders (Crawford 1977). As Boat-tailed Grackles typically lay clutches of only 2 or 3 eggs, a major portion of the females that lay 2-egg clutches may be yearlings. The greater predation rate on 2-egg clutches thus may reflect the lack of experience of these females. First-year females of several icterids have lower nesting success than older individuals (Crawford 1977). In addition to being less effective in protecting their nests, young, inexperienced females may have poorer nesting sites than older females, which would also decrease their success.

Starvation, the second-largest source of mortality, must apply strong selection for the evolution of mechanisms to reduce its effect. One mechanism is to reduce clutch size. This, however, decreases the possibility of raising more young if the female is successful in finding food. Some have suggested that asynchronous hatching and brood reduction through starvation is a mechanism for birds to adjust brood size to available food when food availability cannot be predicted at egg-laying (Lack 1947, 1954; Howe 1976, 1978; O'Connor 1978a). Another mechanism to reduce starvation is to reduce the rate of growth (Lack 1968; Ricklefs 1969b; O'Connor 1978a, b). Presumably, this would reduce the daily food requirements of the young and, thus, reduce the amount of food that the parent has to bring. Some birds, such as swifts and swallows, do slow their growth rate during periods of food shortage (O'Connor 1978b). Slowing the growth rate lengthens the nestling period, which reduces reproductive success to a greater extent if predation rates are high, as they are for grackles (Ricklefs 1969b, O'Connor 1978a). A reduced growth rate would not provide a major energetic savings to female grackles because during the second half of the nestling period, maintenance energy is the major component of the daily energy budget of nestlings (Bancroft 1983).

Hatching failure results from unfertilized eggs or from death of the embryo during development. Selection would favor mechanisms to ensure that fertilization occurs, possibly through multiple copulations. Embryos might die because of lack of attendance by the female that results in eggs cooling or overheating. Also, embryonic death may result from genetic abnormalities. Grackles and many other passerines have a hatching failure rate of 7–10% (Ricklefs 1969a, Rothstein 1973, Koenig 1982). This rate of hatching failure means that less than 80% of the clutches of 3 eggs that reach hatching age will hatch all eggs. This might favor the laying of an "insurance" egg to ensure the proper brood size (Bancroft 1983).

Nest abandonment occurs when the breeding female dies or stops caring for the eggs or young. The probability of the nest surviving the full cycle may influence whether a nest is abandoned. Some nests abandoned with eggs were built in cattails that became tipped. These nests probably had a low probability of surviving the full cycle. Nests with young that became tipped were not abandoned, although occasionally one young fell out. Some abandoned nests remained intact for several days to a week after abandonment. Abandoned young often were growing normally and after death remained in the nest. In these situations the female probably had died.

Temporally, grackles have considerable variation in nesting success, although clutch size does not vary significantly with season (Bancroft 1983). Grackles that began clutches in early March and late May had the highest success. Success was lower but fairly constant from late March through early May. Clutches laid during June had much lower success. The reason for the May peak in success is not known. The higher success of nests started in early March compared with later times suggests there should be strong selection to begin nesting as early as possible. Egg weight during the first half of March is less than later in the season, suggesting that grackles lay eggs before they have the reserves necessary to lay heavier eggs (Bancroft 1984b). The three-month period (March through May) of relatively constant success indicates that the opportunity to renest and to be successful remains constant for a long time. Most of the nests started in June were at North Lake. A large icterid-starling roost formed in this colony during June, and many nest contents were depredated, presumably by these roosting individuals. Predation of eggs and young had two peaks. One tracked the number of active nests, and the other occurred in June. Starvation increased as the season progressed, with a greater proportion of the young starving in the later part of the season.

Nesting success varied significantly between years at both Alligator Lake and East Lake, but for different reasons. Nesting success was lower in 1980 than in 1981 at Alligator Lake because more nests were abandoned and because more fell apart during storms. Nesting success varied significantly between years at East Lake because all nest contents were destroyed by predators in 1981.

Boat-tailed Grackles showed considerable variation between localities in their nesting success. At some colonies no eggs produced fledglings, whereas at others more than 80% of the eggs produced fledglings. The intensity of each mortality source varied with study colony. More eggs produced fledglings at Alligator and East lakes than were lost to all the mortality factors combined, whereas at North Lake more eggs and young were depredated than fledglings were produced. The rank order as well as the intensity of each mortality factor varied with study colony. At Alligator Lake the four most common mortality factors for eggs and nestlings were abandonment (10.6%), unhatched eggs (9.5%), depredation (8.6%), and starvation (8.0%). At East Lake the factors were starvation (13.9%), abandonment (13.5%), depredation (9.1%), and other sources (5.5%). At North Lake more eggs and nestlings were lost to predators (40.8%) than were lost to the top four mortality sources at Alligator Lake and the top three at East Lake. At North Lake the next three greatest factors were starvation (10.6%), unhatched eggs (6.4%), and abandonment (2.7%). This variation in the intensity and relative importance of each mortality factor means that selection on the observed life-history tactic would vary with locality and time.

Selection for modification of the observed life-history pattern is proportional to the intensity of mortality factors (Ricklefs 1969a, 1977; Stearns 1976). The observed reproductive pattern may be a response to the variability and uncertainty of the mortality factors rather than to their average rates (see Wiens 1977, Real 1980). Because mortality sources and their rates vary spatially and temporally in an unpredictable way, specific evolutionary adaptations are unlikely to be effective. The nesting biology of Boat-tailed Grackles seems to reflect this uncertainty. Females appear highly selective in choosing nest sites. Some individuals apparently delay nesting until a nesting place becomes available on cattail islands (Bancroft 1983). Both male and female breeders return to the same nesting colonies in subsequent years (Bancroft pers. obs.). The limited availability of safe nest sites has resulted in the development of a polygynous-promiscuous mating system and the development of a high degree of sexual dimorphism. Adult males average nearly twice the weight of adult females (Bancroft 1984a). Predation has selected for colonial nesting in grackles and has influenced the rapidity with which females will abandon colony sites if discovered by mammalian predators. In addition, predation probably has influenced the relatively short length of the incubation (13.1 days) and nestling periods (12–15 days; Bancroft 1984a, b). Male and female grackles attain an asymptotic weight before fledging relatively quickly compared with the general passerine pattern (Bancroft 1984a). Furthermore, male and female young attain fledging weights that are only 54.8% and 65.3% of adult weight. Young grackles complete growth out of the nest, where they are somewhat mobile and presumably less vulnerable to predation.

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