

## REPRODUCTION OF FEMALE BOAT-TAILED GRACKLES: COMPARISONS BETWEEN SOUTH CAROLINA AND FLORIDA

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Abstract.—Over 7 yr, nesting success, nest mortality and reproductive behavior of female Boat-tailed Grackles (*Quiscalus major*) nesting in a freshwater impoundment in South Carolina were examined. Most (96% of 1368) nests were built in colonies on cattail (*Typha* spp.) islands. Average colony size ranged from 7 to 10 nests; maximum size ranged from 20 to 37 nests. Average distance between nearest-neighbor colony nests was 3.5 m. Breeding was synchronized, and at least 50% of all nests in the population were started within 12–16 d of the first. Females used dead (overwintering) vegetation for nesting, but colony sites did not appear to be limited. The breeding biology of Boat-tailed Grackles in South Carolina differs little from that reported for a population nesting in cattail marshes in central Florida, 600 km SW. In each region, 61% of nests produced at least one fledgling. Daily mortality rates of eggs were slightly lower in South Carolina, but mortality rates of nestlings were the same. Unlike in Florida, no difference was found between the survival of two-egg and three-egg clutches. In both regions, predation was the main cause of nest loss. Starvation was the second most important mortality factor in South Carolina, where it was relatively more important than in Florida. Most predation in South Carolina was by snakes. In Florida rodents were most important. In both areas, predation appears to be the main selective force molding females' nesting behavior.

### COMPARACIÓN DE LA REPRODUCCIÓN EN HEMBRAS DE *QUISCALUS MAJOR* ENTRE CAROLINA DEL SUR Y FLORIDA

Sinopsis.—Se examinaron el éxito en anidar, la mortalidad al anidar y el comportamiento reproductivo de hembras de *Quiscalus major* anidantes en un anegado en Carolina del Sur por más de 7 años. La mayoría (96% de 1368) de los nidos se construyeron en colonias en islotes de *Typha* sp. El tamaño promedio de las colonias varió entre 7 y 10 nidos; las colonias más grandes tenían entre 20 y 37 nidos. La distancia promedio entre nidos adyacentes de una colonia fue de 3.5 m. La reproducción fue sincronizada y por lo menos 50% de todos los nidos en una población se comenzaron entre 12 y 16 días a partir del primero. Las hembras usaron vegetación muerta (postinvernal) para anidar, pero el tamaño de las colonias no pareció ser limitado. La biología reproductiva de *Quiscalus major* en Carolina del Sur difiere un poco de los reportes de una población que anida en las ciénagas de *Typha* en el centro de Florida, 600 km al SO. En cada región, 61% de los nidos produjo por lo menos un volantón. Las tasas de mortalidad diarias de huevos fueron ligeramente inferiores en Carolina del Sur, pero las tasas de mortalidad de pichones fueron idénticas. No se encontraron diferencias entre la supervivencias de camadas de dos huevos y las de tres huevos, a diferencia de la Florida. En ambas regiones la depredación fue la causa principal de la pérdida de nidos. La inanición fue la segunda causa importante de mortalidad en Carolina del Sur, con más peso relativo que en Florida. Las culebras fueron los depredadores más importantes en Carolina del Sur. En Florida, los roedores fueron los depredadores principales. La depredación parece ser la fuerza selectiva principal modificando el comportamiento reproductivo de las hembras en ambos lugares.

Boat-tailed Grackles (*Quiscalus major*) nest in or near tidal areas from New York to central Texas. The species is characterized by its large size, conspicuous displays and pronounced sexual dimorphism. Females nest

in large, dense colonies, a dispersion pattern that allows individual males to monopolize many females (Post 1992). Its mating system (harem polygyny; Emlen and Oring 1977) also has been found in the oropendolas of the American tropics (Webster 1994), but not in any other North American passerine. The colonial nesting behavior of the female grackle is critical for the occurrence of harem polygyny in this species (Post 1992). For this reason, information on the reproductive behavior of females is useful for an understanding of this unusual mating system. The breeding biology of the species has been studied extensively in Florida (Bancroft 1983, 1986, 1987; Dunham 1988, 1990). Although no individually-marked population has been studied in Florida, the species appears to be harem polygynous in that region also (Bancroft 1987). Therefore, comparative data on female nesting ecology from different regions may provide insights into the factors favoring the evolution of harem polygyny.

#### METHODS

The study was conducted near Charleston, South Carolina, in 1985–1991. The study site was a 30-ha impounded cattail (*Typha* spp.) marsh at Magnolia Gardens, 10 km north of Charleston, on the Ashley River (32°52'N, 80°5'W). The outer part of the marsh was surrounded by a channel  $\leq 3$  m deep. Away from the channel, water depth in open water areas averaged 1 m. In 1985 open water covered 75% of the site, and cattails covered 25%. More detailed descriptions are in Post and Seals (1991). Over 7 yr (1985–1991) I studied 1368 nests, located in 60 different colony sites. In 1986–1989, I tried to locate all nests within the study area: a mean of  $293 \pm 36$  (SD) nests was found in each of the 4 yr, and a mean of  $28 \pm 3.6$  colony sites was occupied each year.

Most nests were found during construction or egg-laying. I determined the date of clutch initiation of other nests by extrapolating from either date of hatching (one egg is laid each day; incubation, which usually begins with the penultimate egg, lasts 13 d), or from age of nestlings, determined by criteria in Bancroft (1984). In all 7 yr for which I gathered these data, grackles in the study area nested in two distinct cycles, the first starting in late March–early April, and the second in mid-May. For each colony, I plotted the distribution of clutch initiation dates to define graphically each cycle. Each nesting attempt was then assigned to one of the periods. Nests were usually visited every 3 d, and at least once per 5 d. Estimates of nest survival probabilities are based on the time that the nests were exposed to risk (Mayfield 1975, Johnson 1979); only nests whose fates were known were used. The incubation period (13 d) and nestling period (13 d) were analyzed separately. To test for differences in nest success between different groups, I used statistical methods given in Hensler (1985).

I used wooden stakes to establish 6.25-m grids within colony sites. When a nest was first found, it was marked with a numbered flag, and its Cartesian coordinates in relation to the nearest marker were recorded. Nest positions were then plotted on a map of the colony site, and interest

distances were measured from the map. Nearest neighbor distance is defined as the distance between a newly-established nest and the nearest viable, previously-established nest; i.e., only one distance was calculated for each nest.

I sampled vegetation following the methods of Wiens (1969). At each nest a  $1 \times 1$  m cross was placed, the ends of which acted as the corners of a quadrat. At each of the four corner sub-points, a 6-mm rod (2 m high) was placed vertically. The contacts that green and dead plants made with each 10-cm interval of the rod were tallied. One additional sub-point was established at the side of the nest. Vegetation density is defined for each quadrat as the average number of contacts made at the five points. For each sampled nest, I measured number and type (dead or green) of stems supporting the nest.

Grackles were captured in wire funnel traps and Potter traps baited with bread and maize, in mist-nets placed next to nests, or in clap nets baited with mounted female decoys. By 1990, 225 males and 658 females were individually color-banded.

Throughout, standard deviation is the statistical measure of dispersion.

#### RESULTS AND DISCUSSION

*Breeding phenology.*—The mean date of the first clutch started in each year during the period 1986–1991 was 29 March  $\pm$  5 d, range 20 March–4 April. Older ( $>2$  yr) females started clutches in the first 10 d of the cycle. Many of the early-nesting females had bred in the same colony sites in previous years. Of 20 marked females that nested in one colony in 1990, 60% returned to breed there in 1991. Second-year females started nesting after the first peak of clutch initiation, accounting for a slight (secondary) peak about 2 wk later.

A third peak of clutch initiation occurred  $34.0 \pm 4.1$  d after the first ( $n = 10$  colonies, 1986–1988). The third peak consisted of females which had fledged young earlier, and those which were renesting after a failed nesting attempt. The height of nesting activity, defined as the week with the most nests containing eggs and young, was 26 April–2 May in 1986–1989. The mean date of the last clutch initiated in each of the 6 yr was 20 June  $\pm$  11 d; range, 6 June–3 July. The mean length of the breeding season (interval between initiation of first and last clutches) was  $83.7 \pm 16.4$  d; range, 64–106 d ( $n = 6$  yr, 1986–1991).

Breeding synchrony was high. In 1986, 50% of all clutches ( $n = 282$ ) had been completed by 12 April, 16 d after the first clutch was completed; in 1987 ( $n = 281$ ), by 26 April (14 d), and in 1988 ( $n = 297$ ), by 23 April (12 d). Intracolony standard deviation of clutch initiation dates, another measure of breeding synchrony (Gochfeld 1980), was  $\pm 7.0$  d ( $n = 32$  nesting cycles for colonies  $\geq 10$  nests). Degree of synchrony appeared to be about the same in Florida: the time between initiation of the first nest and the median nest was 18 d (Dunham 1988). The length of the breeding period, as defined by dates on which first and last eggs were laid, was also about the same. During 1986–1991, the longest breed-

ing period that I recorded was 106 d (1990), compared with 112 d in Florida (East Lake colony in 1980 and North Lake colony in 1981; Bancroft 1983).

*Nesting dispersion and nest site characteristics.*—Most nests (96% of 1354) were in colonies on small cattail islands or peninsulas (mean size =  $310 \pm 144$  m<sup>2</sup>,  $n = 10$ ). Mean colony size was  $8.4 \pm 7.1$  nests; range, 2–37 ( $n = 122$  colonies, 1986–1989). Maximum sizes ranged from 20 (1987) to 37 simultaneously active nests (1986). Solitary nests ( $n = 58$ ) were more than 25 m from a colony, but were in sites similar to those occupied by colonies. Nests in colonies were close together, some in contact with each other (see also Bancroft 1987). Mean nearest-neighbor distance between successive nests was  $3.5 \pm 2.3$  m ( $n = 240$  nests, 7 colonies).

To determine if early-nesting females in cattails used different sites from late-nesting ones, I compared nests started early in the growing season with ones started later. For early nests (18–27 April), the density of residual (overwintering vegetation) was  $3.67 \pm 2.99$  ( $n = 128$ ) contacts per point, as compared to  $3.58 \pm 2.76$  (125) for late nests (25 June–22 July), a non-significant difference ( $t = 0.09$ ). Density of green vegetation around early nests was  $2.29 \pm 1.90$  (128) contacts per point, versus  $4.76 \pm 4.20$  for late nests (125), a significant difference ( $t = 5.88$ ;  $P < 0.01$ ). A mean of  $3.53 \pm 1.17$  (19) dead cattail stems was used to support early nests as compared to  $2.23 \pm 1.41$  (22) late in the season, a significant difference ( $t = 2.28$ ;  $P < 0.05$ ). Number of green stems used for nest support early in the season was  $0.11 \pm 0.32$  (19), versus  $1.86 \pm 1.39$  (22) later, also a significant difference ( $t = 5.30$ ;  $P < 0.01$ ).

In both South Carolina and in Florida, female Boat-tailed Grackles congregate at specific sites to avoid predators (Bancroft 1986, Post 1992). Bancroft (1983, 1986) hypothesized that in early spring females in Florida have limited appropriate nesting areas, and that they delay breeding until such sites are available. Several other studies have demonstrated that the distribution of marsh-nesting species is influenced by limited suitable habitat, related to the need to avoid predators and floods (Bongiorno 1970; Post 1974, 1981). In this study, however, sites used for colonies did not differ from those not used (unpubl. data). Further, throughout the breeding season, females used nest sites with a high ratio of dead (overwintering) vegetation to green vegetation. The most common nest supports throughout the summer were also overwintering cattail stems. The availability of overwintering vegetation does not increase during the growing season, but tends to decrease. Thus, the largest number of suitable sites should be available early in the season. Although some colony sites were flattened by winter storms, or were flooded, females responded by shifting to different sites in the same marsh, and nesting chronology varied little between years. Females appeared to be flexible in their choice of colony and nest sites. The first requirement for successful nesting is the availability of an area secure from ground predators (Post 1992). Settling females appeared to use past experience, and the presence of other females, as a cue to site suitability (unpubl. data). They did not appear to

TABLE 1. Survival of Boat-tailed Grackle nests and nest contents in a cattail marsh at Magnolia Gardens, South Carolina, 1985–1991.

Year	# nests	Survival probability of whole nest during:			Survival probability of individual contents of nest during:			
		Egg period (13 d)	Nestling period (13 d)	Total period (26 d)	# eggs	Egg period (13 d)	Nestling period (13 d)	Total period (26 d)
1985	164	0.643	0.725	0.466	441	0.603	0.523	0.315
1986	244	0.851	0.911	0.775	663	0.747	0.778	0.582
1987	248	0.761	0.862	0.656	672	0.671	0.786	0.527
1988	273	0.759	0.981	0.745	731	0.658	0.617	0.406
1989	139	0.659	0.829	0.546	363	0.585	0.639	0.374
1990	119	0.728	0.807	0.587	316	0.604	0.667	0.403
1991	181	0.707	0.685	0.484	473	0.631	0.775	0.480
Total	1368	0.730	0.829	0.608	3659	0.643	0.684	0.441

compete for nest microhabitats within colonies (Post 1994), and nests were occasionally built in contact with each other. The second requirement is substrate high enough so that the nest will not be flooded (Dunham 1990). Amount of cover above the nest did not appear to be a critical requirement (Dunham 1990), which may be related to the effective mobbing of male grackles (Post 1992, Post and Seals 1993).

*Reproductive success and mortality.*—During the 7-yr study period, 60.8% of nests produced at least one fledgling, and 44.1% of eggs produced fledglings. Whole-nest success ranged from 48% (1991) to 78% (1986). In every year except 1991, whole-nest survival was greater in the nestling than in the egg stage. Analyzed from the point of view of individuals within nests, however, survival probabilities during the egg and nestling stages were nearly equal in most years (Table 1).

A mean of  $1.32 \pm 1.08$  ( $n = 1265$  nests) fledglings was produced from

TABLE 2. Annual variation in Boat-tailed Grackle nesting success in cattail marsh at Magnolia Gardens, South Carolina, 1985–1991.

Year	# nests	Nest contents ( $\bar{x} \pm 1$ SD)		
		Eggs	Nestlings	Fledglings
1985	147	2.80 $\pm$ 0.45	1.88 $\pm$ 1.24	1.01 $\pm$ 1.03
1986	261	2.74 $\pm$ 0.47	2.16 $\pm$ 1.02	1.63 $\pm$ 1.04 <sup>a</sup>
1987	252	2.77 $\pm$ 0.47	1.96 $\pm$ 1.14	1.52 $\pm$ 1.16 <sup>b</sup>
1988	271	2.73 $\pm$ 0.49	1.97 $\pm$ 1.07	1.17 $\pm$ 1.03
1989	111	2.77 $\pm$ 0.47	1.85 $\pm$ 1.17	1.16 $\pm$ 1.02
1990	76	2.66 $\pm$ 0.53	1.90 $\pm$ 1.09	1.28 $\pm$ 1.04 <sup>b</sup>
1991	147	2.71 $\pm$ 0.47	1.89 $\pm$ 1.10	1.16 $\pm$ 1.04
Total	1265	2.75 $\pm$ 0.48	1.97 $\pm$ 1.11	1.32 $\pm$ 1.08

<sup>a</sup> # fledged/nest higher than in all other years except 1987 (Tukey HSD;  $P < 0.05$ ).

<sup>b</sup> # fledged/nest higher than 1985 (Tukey HSD;  $P < 0.05$ ).

all nests. This value represents 48% of the mean number of eggs laid. Average numbers of fledglings produced per nest ranged from 1.0 (1985) to 1.6 (1986). Success was significantly higher in 1986, 1987 and 1990, compared with several other years (Table 2). The mean number of fledglings produced per successful nest was  $1.97 \pm 0.67$ .

Daily mortality rates varied little during the study period. For the entire nesting cycle (26 d), the daily mortality of whole nests (M) was 2.1% (7-yr mean; range, 1.0–2.9%). The comparable figure for individuals in nests (m) was 3.2% (2.1–4.2%). In all years, daily mortality rates of eggs ( $m_e$ ) and nestlings ( $m_n$ ) were nearly equal (3.4% versus 2.9%). In all but 2 yr, mortality rate of eggs was slightly higher than that of nestlings. Daily mortality of whole nests during the egg stage ( $M_e$ ) was higher than that during the nestling stage ( $M_n$ ): 2.4% versus 1.7%.

The nest survival and mortality patterns that I found in South Carolina were similar to those in central Florida. Female grackles in Florida also nested in colonies in cattails (Bancroft 1983, 1987). The Florida population had a total nest success (proportion of nests producing at least one fledgling) of 60.5% ( $n = 605$  nests studied over four seasons), compared with my estimate of 60.8%. The probability that an individual egg would produce a fledgling was 0.464 in Florida, versus 0.441 in South Carolina. The slightly lower value in my study resulted from lower survival of eggs (64.3% survival in SC, versus 71.3% in FL), rather than survival of nestlings, which was about the same in the two regions (SC: 68.4%; FL: 65.1%).

In both regions the daily mortality rate of individuals in nests (m) was higher than that to whole nests (M), an indication that mortality factors such as hatching failure and starvation were more important than predation or flooding (Ricklefs 1969). In South Carolina, mortality rates to individuals were about the same during the egg and nestling stages, whereas in Florida they varied according to clutch size. Florida nests with two eggs had higher mortality in the egg stage than in the nestling stage. This difference was attributed to the inexperience of females laying two-egg clutches (Bancroft 1983).

Predation was the main cause of nest mortality in both South Carolina and Florida (Bancroft 1987). Predation was more important in Florida, during both the egg (51.7%, versus 42.1% in SC) and nestling stages (37.5%, versus 25.3% in SC). Of the main mortality factors, only starvation rates were higher in South Carolina (52.1%, versus 38.2% in FL). Starvation in South Carolina, however, may have been partly related to predation, rather than to food shortage alone. Females deserted young when snakes became residents in colonies. Snakes were either absent or were unimportant predators in Florida grackle colonies, where the main predators were rodents (Dunham 1990). Although female grackles abandoned colonies in response to predation by rodents, such abandonment was not reported to be a major mortality factor (Bancroft 1986, 1987). This may be because rodents did not build nests in Florida grackle colonies, but commuted to breeding areas in adjacent uplands (Dunham

1990). Hatching failure accounted for a higher percentage of egg mortality in Florida (25.2%, versus 18.7% in SC). This difference could be due to the lower success of Florida two-egg clutches, or to the tendency of younger females to abandon nests in the egg stage (Bancroft 1987).

In my study area, predation and nest abandonment (often related to presence of predators) contributed to high intercolony differences in nest success. Starvation did not vary between colonies. The nesting success of Boat-tailed Grackles nesting in Florida cattails varied significantly between different study sites, and was related to different mortality factors. For example, at one site most egg mortality was caused by abandonment; at another, hatching failure; and at a third, predation. It was not reported whether success or mortality factors varied between colonies within the different sites (Bancroft 1986). Differences between sites in Florida may be related to variation in macrohabitat rather than microhabitat (colony) characteristics. The results of my study, however, indicate that within-site variation in reproductive success may be as large as that between sites. As one or a few males accomplish most of the breeding in each colony, such variation has important implications for the fitness of individual males in a given population.

*Clutch size.*—Mean clutch size for the 7-yr period of the South Carolina study was  $2.75 \pm 0.48$  ( $n = 1265$ ). The most frequent clutch size was three (75.2% of 1265 clutches), followed by clutches of two (22.9%), one (1.5%) and four (0.4%). Total nest success (success at fledging at least one young) was 67.8% for two-egg clutches ( $n = 289$ ), and 66.8% for three-egg clutches ( $n = 951$ ), a non-significant difference ( $\chi^2 = 0.12$ ;  $P > 0.75$ ,  $df = 1$ ).

Although mean clutch size in South Carolina is close to that reported from Florida (2.64; Bancroft 1987), the distribution of clutch sizes is significantly different between the two regions ( $\chi^2 = 22.8$ ;  $P < 0.001$ ,  $df = 3$ ). The difference is due to the larger proportion of two-egg clutches (32.4% in FL, versus 22.9% in SC), and the corresponding reduction in number of three-egg clutches in Florida (66.1%, versus 75.2% in South Carolina). One- and four-egg clutches were about as frequent in both populations. Despite the different distribution of clutch sizes, the same number of fledglings (2.0) were produced per successful nest in both areas. In both regions, clutch size remained constant over the breeding season, but fledging success decreased. The temporal pattern of success was the same in both areas: a peak at the start of the nesting season, a decline during the next month, and an increase of success 2 mo after the first peak. In both regions, the second peak in nesting success may be related to renestings by older, more experienced females.

The clutch size that I found in South Carolina is very different from that reported by Sprunt (1958), who worked in the same region. Sprunt (1958) stated that clutches of four were the most common, but, apparently, he based his statement on oology records. Oologists may have selectively collected larger clutch sizes, or augmented clutches to increase their trade value (McNair 1987). In addition, as Boat-tailed Grackles nest-

ing in trees have larger clutches than those in cattails (unpubl. data), it is possible that the larger clutches found by oologists were related to their selectively collecting from upland habitats. For example, 158 Boat-tailed Grackle sets collected in South Carolina averaged  $3.66 \pm 0.73$  ( $n = 153$ ), as compared to my average of  $2.75 \pm 0.48$  ( $n = 1265$ ). Clutches of four made up 44% of the South Carolina oology sets (versus 5% for the nests that I observed). In contrast, clutches of two were greatly underrepresented by oologists (3% versus 23%). The frequency distribution of clutch sizes from these two samples is (highly) significantly different ( $G = 392.8$ ;  $df = 3$ ;  $P < 0.001$ ). The same discrepancies are apparent between Bancroft's clutch size data and those of Florida egg collectors (unpubl. data).

#### CONCLUSIONS

In another study comparing the reproduction of marsh-nesting populations in different regions, pronounced differences were found (Post et al. 1983). Seaside Sparrows (*Ammodramus maritimus*) nesting in a New York salt marsh had much higher reproductive success than those nesting in a similar marsh in northern Florida: 3% of eggs in Florida produced fledglings, versus 35% in New York. The compensatory factor appeared to be higher annual adult survival in Florida (86%, versus 55% in New York). Geographic differences shown by Boat-tailed Grackles are somewhat different. Nesting success is high in both regions (about 60% of eggs produce fledglings in both areas). These similarities appear to be based on female use of predator-secure nest areas, usually islands protected by American alligators (*Alligator mississippiensis*; Post and Seals 1991, 1993).

In addition to having high reproductive success, the South Carolina Boat-tailed Grackles have high annual adult survival. The estimated annual survival of Boat-tailed Grackles in South Carolina is 60% for females and 85% for males (unpubl. data). Although no information is available for Florida, it is probable that their survival rates are at least as high as those of the South Carolina population. In both regions Boat-tailed Grackles therefore appear to have both high reproductive potential, and high adult survival.

In summary, the reproductive biology of Boat-tailed Grackles in a South Carolina cattail marsh is very similar to that of a population nesting in the same habitat in central Florida, 600 km SW. Reproductive success, clutch size, habitat selection, pattern of breeding phenology, and patterns of mortality are nearly identical in the two regions. In both areas, most nest mortality was due to predation. The main difference between the two areas was in the relative importance of secondary sources of mortality. In South Carolina, nest abandonment was less important, whereas starvation was more important, than in Florida. The results indicate that the same selective forces operating in two widely separated regions have resulted in very similar responses by nesting female grackles. These results agree with Bancroft's (1983) conclusion, that nest predation has been the



main selective force in molding the breeding behavior of female Boat-tailed Grackles.

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