Florida Field Naturalist

PUBLISHED BY THE FLORIDA ORNITHOLOGICAL SOCIETY

VOL. 15, NO. 1 FEBRUARY 1987 PAGES 1-28

MATING SYSTEM AND NESTING PHENOLOGY OF THE BOAT-TAILED GRACKLE IN CENTRAL GLORIDA

G. THOMAS BANCROFT

Department of Biology, University of South Florida, Tampa, Florida 33620
(Current address: Ornithological Research Unit, National Audubon Society, 115 Indian Mound Trail, Tavernier, Florida 33070)

Abstract.—The mating system of Boat-tailed Grackles (*Quiscalus major*) varied from territorial polygyny to male dominance depending upon availability of suitable nesting sites. At colonies where available nesting habitat was less than 500 m², no male successfully defended a territory. At larger, dispersed colonies, some males attained territories. Grackles in Florida nested from March to July and averaged 2.64 eggs per clutch. Over 50% of the clutches were laid during March and the first half of April. Clutch size did not vary within season or between study areas. The start of nesting was probably influenced by the ability of females to reach physiological condition for laying eggs; and the cessation of nesting at various locations was influenced by water levels, predation rates, availability of suitable nesting sites, and possibly the number of males and females in the area.

Boat-tailed Grackles (*Quiscalus major*) are an abundant bird in peninsular Florida throughout the year (Howell 1932). Despite their abundance surprisingly little is known about their nesting biology in Florida. Boat-tailed Grackles are sexually size dimorphic and apparently exhibit a polygynous-promiscuous mating system (McIlhenny 1937, Selander and Giller 1961). In central Florida, they nest annually in the spring (Selander and Nicholson 1962) and occasionally in the fall (Selander and Nicholson 1962, Kale 1975, Riddle 1976). Clutch size appears to vary from two to four eggs (Selander and Nicholson 1962). This study was undertaken to provide more detailed information on the nesting biology of Boat-tailed Grackles in central Florida.

METHODS

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

I located grackle colonies early in the spring before egg laying began or soon after the first few clutches had been laid. I visited some colonies daily and others every second to third day. I found most nests during construction and individually marked all nests with numbered flags. I marked eggs with a permanent marker and young shortly after hatching by clipping one claw.

I examined the chronology of nesting by determining the date of completion of the first and last clutch in a colony. I used the time required for 50% of the clutches to be laid as an indication of the synchrony of nesting within a colony. To determine the timing and intensity of nesting during the reproductive season, I tabulated the number of clutches completed, number of nests with eggs, and number of nests with young for each week in the season.

I calculated incubation time as the number of days between the laying of the last egg and the hatching of that egg. For the calculation of hatching spread, I used a technique similar to that of Bryant (1978). Clutches that hatched entirely between visits where the spread could have been between one hour and 24 hours, were termed "synchronous hatching." Clutches that required more than one visit to find all eggs hatched were considered to have hatched asynchronously. For calculations, the hatching spread was considered to be 0.5 days if all eggs hatched between two visits and 1.5 or 2.5 days if all eggs hatched over two or three visits. Only data from the East Lake and Courtney colonies are used for these analyses because only these two colonies were visited daily throughout the breeding season.

RESULTS

Mating System and Colony Structure.—The behavior of male Boat-tailed Grackles differed with colony size. At colonies with less than 500 m^2 of suitable nesting habitat, the males present never attained sole ownership of a section of cattails. In these situations, males moved throughout the colony and interacted with other males in frequent dominance confrontations. Some of the males frequented the main part of the colony while others fringed the outer radius of the foraging area. For example, at East Lake most nests were found in a cattail clump 30 by 10 m on a small island. Generally, four to six males were on the island during the height of the nesting season, while 6 to 10 others were dispersed in suburban yards and other cattail stands up to 500 m from the nesting area. These males did not visit the colony but displayed and called at these peripheral locations.

At large colonies (greater than 500 m^2 of suitable nesting space) where nesting occurred in several different cattail patches, at least one male became dominant at a site and excluded all other males from it. Thus, these males succeeded in defending the limited resource, nesting sites. For example, at North Lake during 1981 a section of cattails about 60 m long and from 1 to 10 m wide was patrolled by three males early in the nesting season. They chased each other frequently and appeared to be separating the strip of cattails into three sections. Three or four other males, who stayed around the outer edge of the strip, made several passes per hour through the area and were chased. Thirty nests were

begun here in the first two weeks of nesting. By the second or third week of the nesting season one male became dominant and successfully excluded all other males. A total of 71 clutches was laid here during the 16-week laying period. At other sites in the North Lake colony no single male ever became dominant, and several males displayed throughout the nesting season.

At Alligator Lake in March of 1982, I watched male behavior during the start of nesting. In one site a single definitive-plumage male (Selander 1958, Selander and Giller 1961) defended a patch of cattails 5 m by 10 m. Definitive-plumage males are approximately two-years old or older (Selander 1958, Selander and Giller 1961). The patch had eight to 10 nests under construction and had several with eggs. Four definitive-plumage males called and displayed in the cattails and willows peripheral to this area. Few or no nests were under construction in their areas. These males frequently flew over the cattails where nests were under construction giving song and ruff-out display (Selander and Giller 1961). The resident male vigorously chased any of these males that landed in the cattails. Several additional definitive-plumage males occasionally landed in the cattails around the nests. These males rarely called and usually were not chased by the resident male. Between 8 and 10 first-year males (in first-basic plumage and about one-year old, Selander 1958, Selander and Giller 1961), including six that had been color banded as nestlings, flew into the cattails, and rarely were they chased. The one first-year male that displayed and called frequently was chased regularly by the resident adult.

At North Lake and Alligator Lake, males that became dominant at some locations mobbed me vigorously when I approached the nests. Several males struck me on my back or head with their bill or feet when I handled young or eggs. At locations where no male was dominant, no male vigorously defended the nests. Rather, males either sat off to the side and gave alarm calls or occasionally continued displaying and calling.

Definitive-plumage males were the most common males in colonies. However, contrary to the findings of McIlhenny (1937), first-year males did attend colonies. At both East Lake and Alligator Lake, I saw males, whom I had color-banded as nestlings, the spring after they fledged on the same ponds from which they fledged. They frequently passed through nesting areas and were not chased by definitive-plumage males, possibly because the first-year males did not represent a breeding risk to them. At Alligator Lake, one first-year male that was color-banded, regularly called and displayed from a large oak tree at the edge of the lake, less than 200 m from the islands where most females nested.

Females did all nest building, incubation, and care of nestlings. In over 200 hours of observation at colonies, I never saw males participating in these activities. Frequently while a female was building the nest a

male displayed to her from directly above the nest and followed her on flights for gathering nest material (McIlhenny 1937, pers. obs.). Only two males were observed caring for fledglings. At East Lake in 1978 a definitive-plumage male did all the feeding of three fledglings that flew well. Over a two-week period this male, but no female, repeatedly fed the young who followed him begging. At Alligator Lake in 1984 a definitive-plumage male, but no female, was observed feeding a well grown male fledgling during one afternoon.

At many locations the density of nests was high. Nests were often less than 1 m apart and on several occasions they were less than 0.3 m apart. At Alligator Lake during 1980 several cattail clumps had four to five nests in a 2-m strip. One cattail island at Alligator Lake consisted of an oval patch of cattails 20 m long by 10 m wide. Cattails were dense in a 1-m wide band around the circumference of this oval, and most nests were constructed there. During the course of the nesting season, I found 61 clutches in this section. Two nests were reused and five others had new nests built on top of old ones. Fledglings from some of these nests were still being fed when the second nest was constructed and the eggs laid. This delay suggests that grackles were using all of the best nest sites, and some females were delaying nesting in order to attain prime sites.

I saw no agonistic behavior between females in these densely populated areas. I saw females that were apparently not nesting move in cattails that contained active nests. Only if they came within 1 m of an active nest were they chased by the nesting female.

Chronology of Breeding.—In central Florida, Boat-tailed Grackles nested from early March through late July (Fig. 1). I found the earliest nest with three eggs on 13 March (1980); the eggs hatched on 15 March. Allowing 13 days for incubation (see below), and incubation starting when the second egg was laid (see below), the first egg was laid on 1 March. Peak egg laying occurred in the third and fourth weeks of March when 215 clutches were completed (Fig. 1). These clutches in the third and fourth weeks represented 30.6% of the 703 clutches. Half of all new clutches were laid during a 4-week period from the beginning of the third week of March to mid-April. The number of new clutches decreased steadily from late March to mid-July. The last clutch was started on 10 July (1981).

No second peak of nesting occurred in June, and this suggests that Boat-tailed Grackles probably attempted only one successful nest a year. The steady decrease in the number of new clutches suggests that these clutches represented either late-nesting individuals starting their first clutch, or individuals renesting after their first attempt failed. More females than active nests were present in colonies early in the nesting

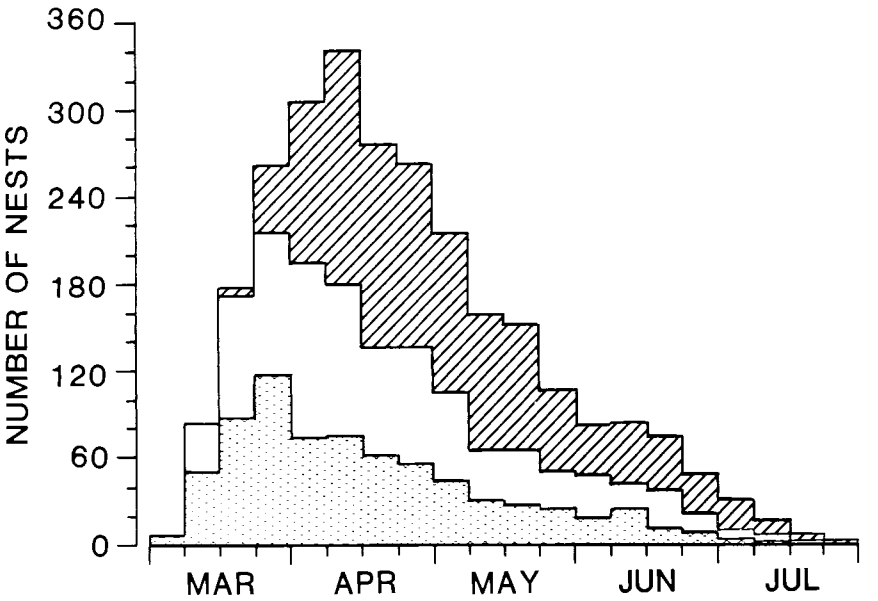

Figure 1. The breeding schedule of Boat-tailed Grackles based on data collected at 10 locations in central Florida between 1978 and 1981. The bar graphs represent the total number of active nests per week, the cross-hatched area within represents the number of clutches completed each week, the cross-hatched area plus the open area represents the number of nests with eggs each week, and the area with diagonal lines represents the number of nests with young each week.

season, suggesting that not all females began to nest during the first few weeks of the season. In 1980 at Alligator Lake, new nests were started less than 1 m from nests that had recently fledged young; these new nests had eggs in them while the fledgings were still being fed by the parent. This information suggests that new nests after the initial peak were partly a result of late nesting females and renesting attempts.

The chronology of breeding varied between Alligator Lake, East Lake, and North Lake (Fig. 2). The peak in the completion of new clutches per week occurred during the third week of March at Alligator Lake and East Lake. At North Lake, nesting had only just begun during the third week of March and peak completion of new clutches occurred during the fourth week of March. An extended period when many new clutches were completed occurred at North Lake because new females were recruited to the colony and because renesting occurred by females

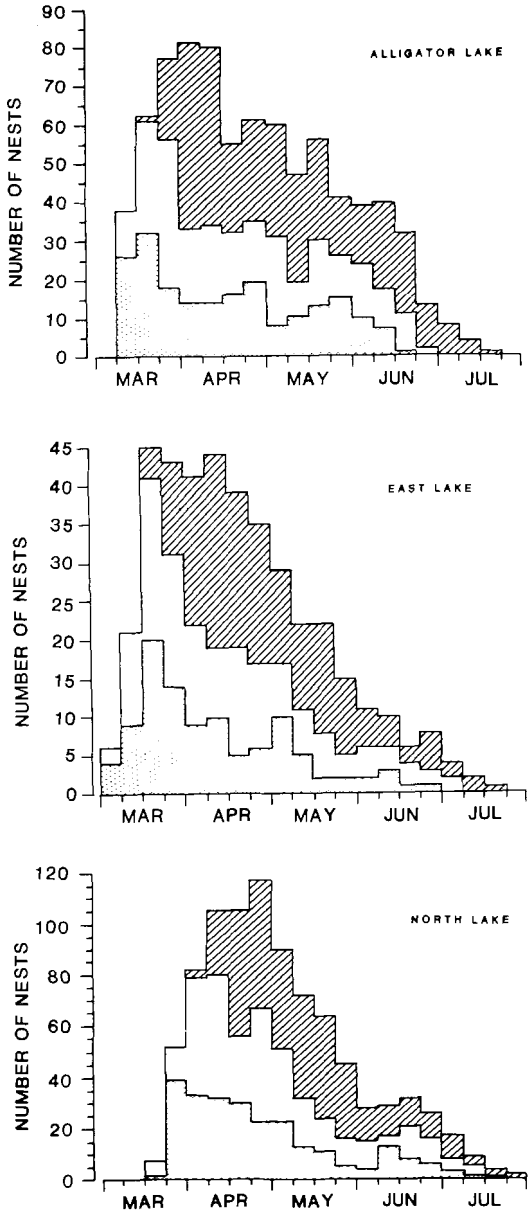

Figure 2. The breeding schedule of Boat-tailed Grackles at three colony sites in central Florida. The bar graphs represent the total number of active nests per week, the cross-hatched area within represents the number of clutches completed each week, the cross-hatched area plus the open area represents the number of nests with eggs each week, and the area with diagonal lines represents the number of nests with young each week.

that lost their first clutch to predators. One section of this colony experienced high rates of predation (Bancroft 1986). Total number of active nests per week reached a peak between late March and mid-April at Alligator and East Lakes. Because nesting began later at North Lake, the peak in number of active nests occurred in mid- to late April.

After the peak in nesting activity, the relative number of active nests per week was higher through the remainder of the season at Alligator Lake than at East Lake or North Lake. Nesting activity decreased rapidly at East Lake because in 1979 no new nests were begun after two days of heavy rain in early May and in 1981 all nests were destroyed by predators during early April, causing the birds to move from the area. At North Lake the number of active nests per week decreased to a low in late May and early June before showing a small rise in mid-June. Many nests failed during May because young starved and predation rates on eggs and nestlings were high during May and June. Alligator Lake maintained a relatively high number of active nests throughout the season partially because both predation and starvation rates were low (Bancroft 1986).

Variation in the onset of nesting occurred between localities and between years (Table 1). The first completed clutch at different colonies varied from 3 March to 1 April. The date of the earliest clutch was determined for 16 colony-year combinations: one was started during the first week of March, eight during the second week of March, five during the third week of March, and one each in the fourth week of March and the first week of April. The best indication of the synchrony of the onset of nesting at each colony is the time span taken for all individuals to begin their first nesting attempt. However, few females were color marked and it was difficult to determine which marked female belonged to which nest because of the density of nesting and the inability to view the nests from a distance. Therefore, I used the time required for 50% of the clutches to be completed as an indication of nesting synchrony (Table 1). At some small colonies, 50% of the nests were started in less than one week. Alligator Lake in 1981 and East Lake in 1980 required the most time, 39 days, to reach 50% of the clutches. At North Lake, the largest colony, 50% of the clutches were completed in a 29-day period between 20 March and 18 April. For all colonies combined 50% of the clutches had been laid by 11 April.

Duration of the nesting season varied between sites and years (Table 1). New clutches were found over a two-week period at University Mall in 1980 and East Lake in 1981 (Table 1). New clutches were found at East Lake in 1980 and North Lake in 1981 over a 16-week period. The length of the nesting season was correlated with the number of clutches

Table 1. Parameters of nesting for all study colonies of Boat-tailed Grackles in central Florida

Location	Year	No. of clutches	Dates of Clutches			Range (days)
			first	last	median	
Alligator Lake	80	116	9 Mar	10 Jun	5 Apr	93
Alligator Lake	81	87	9 Mar	18 Jun	17 Apr	101
Campus	78	12	1 Apr	25 Apr	10 Apr	24
Courtney	78	9	21 Mar	1 Apr	24 Mar	11
Courtney	79	11	23 Mar	28 Mar	25 Mar	5
East Lake	78	50	16 Mar	11 Jun	1 Apr	87
East Lake	79	16	15 Mar	5 May	29 Mar	51
East Lake	80	29	1 Mar	23 Jun	11 Apr	112
East Lake	81	9	10 Mar	22 Mar	11 Mar	12
I75	81	30	10 Mar	24 Apr	23 Mar	45
North Lake	81	245	20 Mar	10 Jul	18 Apr	112
Poncho	80	31	8 Mar	2 Jun	24 Mar	86
Poncho	81	17	11 Mar	17 Apr	4 Apr	37
River	80	11	18 Mar	22 Mar	20 Mar	4
Sinclair Lake	80	15	13 Mar	18 Apr	28 Mar	36
Sinclair Lake	81	5	14 Mar	7 Apr	18 Mar	24
University Mall	80	10	16 Mar	24 Mar	18 Mar	8

($r = 0.65$, $p < 0.05$). Thus, at large colonies new clutches tended to be initiated over a longer period of time than at smaller colonies.

Sequence of Hatching.—The eggs in clutches at the East Lake and Courtney colonies hatched simultaneously or up to three days apart. At other colonies in a few instances, when a day was skipped during egg laying, the three young hatched over a 4-day period. Of 20 2-egg clutches, nine hatched synchronously, ten hatched over two visits and one over three. Of 48 3-egg clutches, one hatched synchronously, 35 hatched over two visits, and 12 over three visits. The mean hatching spread for 2-egg clutches was 1.1 days (s.d. = 0.6, n = 20) and was significantly shorter than the 1.7 days (s.d. = 0.5, n = 48) that 3-egg clutches required to hatch (Kruskal-Wallis $\chi^2=11.19$, df=1, $P<0.0008$).

The eggs hatched asynchronously presumably because incubation began before the clutch was complete. Eggs always hatched in the same order they were laid. Generally, for 3-egg clutches the first two eggs hatched on the same day and usually with several hours between the hatching of the first and second. The mean number of days between the laying and hatching of the third egg of 37 3-egg clutches was 13.1 days (s.d.=0.5). The third egg usually hatched one day after the first two. If incubation started when the first egg was laid then each egg hatched on successive days. The female began feeding the nestlings when the first one hatched. If not disturbed, young typically fledged 13 to 15 days after hatching.

Table 2. Clutch sizes relative to localities and year for Boat-tailed Grackles in central Florida

Location	Year	Clutch Size				Total	Mean
		1	2	3	4		
Alligator Lake	80		28	86	2	116	2.78
Alligator Lake	81	2	32	53		87	2.59
Campus	78		1	11		12	2.92
Courtney	78		2	7		9	2.78
Courtney	79		5	6		11	2.55
East Lake	78	1	20	29		50	2.56
East Lake	79		3	13		16	2.81
East Lake	80		9	20		29	2.69
East Lake	81		5	4		9	2.44
I75	81	1	7	22		30	2.72
North Lake	81	9	78	157	1	245	2.61
Poncho	80		14	17		31	2.55
Poncho	81	1	6	10		17	2.56
River	80		3	8		11	2.73
Sinclair Lake	80		10	5		15	2.33
Sinclair Lake	81		1	4		5	2.83
University Mall	80		4	6		10	2.60
TOTAL		14	228	458	3	703	2.64

Clutch Size.—The mean clutch size for 703 Boat-tailed Grackle nests was 2.64 (Table 2). Fourteen nests had one egg, 228 had two eggs, 458 had three eggs, and three had four eggs. Some of the presumed 1-egg clutches may have contained additional eggs which disappeared before I discovered the nest. However, two of the nests with 1-egg clutches were followed through nest building and egg laying, and it seems likely that some were single-egg clutches.

For those colonies that had more than 20 nests, clutch size varied from a mean of 2.55 per nest at Poncho in 1980 to a mean of 2.78 per nest at Alligator Lake in 1980 (Table 2). Mean clutch size at Alligator Lake decreased from 1980 to 1981 (Kruskal-Wallis $\chi^2=3.84$, $P<0.05$, $df=1$). The mean clutch size between years at East Lake did not change significantly (Kruskal-Wallis $\chi^2=3.24$, $P=0.34$, $df=3$). More than 100 clutches were observed during the study at three locations: Alligator Lake, East Lake, and North Lake. Mean clutch size between these three locations did not differ significantly (Kruskal-Wallis $\chi^2=1.35$, $P=0.51$, $df=2$).

Seasonal trends in clutch size were examined by comparing mean clutch size during half-month periods of the nesting season (Fig. 3). Excluding the first half of July, mean clutch size varied from 2.76 to 2.61. No significant variation in clutch size during the season was detected (Kruskal-Wallis $\chi^2=8.35$, $df=9$, $P>0.50$). Excluding half-months with less than ten clutches, mean clutch size at Alligator Lake, East Lake,

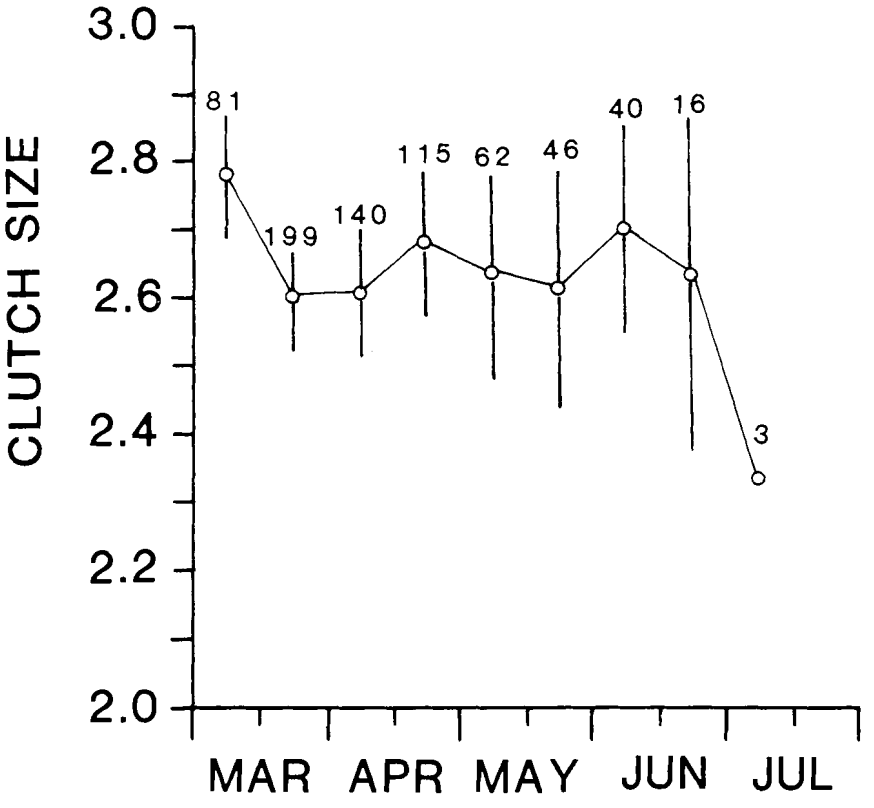

Figure 3. Mean clutch size relative to season for Boat-tailed Grackles in central Florida. The vertial lines represent the 95% confidence limits around the mean, and the number above the lines is the number of clutches during that half month.

and North Lake varied from 2.50 at North Lake to 2.84 at Alligator Lake (Fig. 4). No significant seasonal trends in clutch size occurred at any of the different localities.

DISCUSSION

Mating System.—The mating system of Boat-tailed Grackles varies from territorial polygyny to a system based on male dominance. At colonies where available nesting habitat is less than 500 m^2, no male successfully defends a territory. At larger, dispersed colonies, some males attain territories. Boat-tailed Grackles and Great-tailed Grackles (*Quiscalus mexicanus*) nesting in marsh habitats in Louisiana and Texas show similar mating systems (McIlhenny 1937, Selander and Giller 1961). When these two species nest in more upland habitat their mating system be-

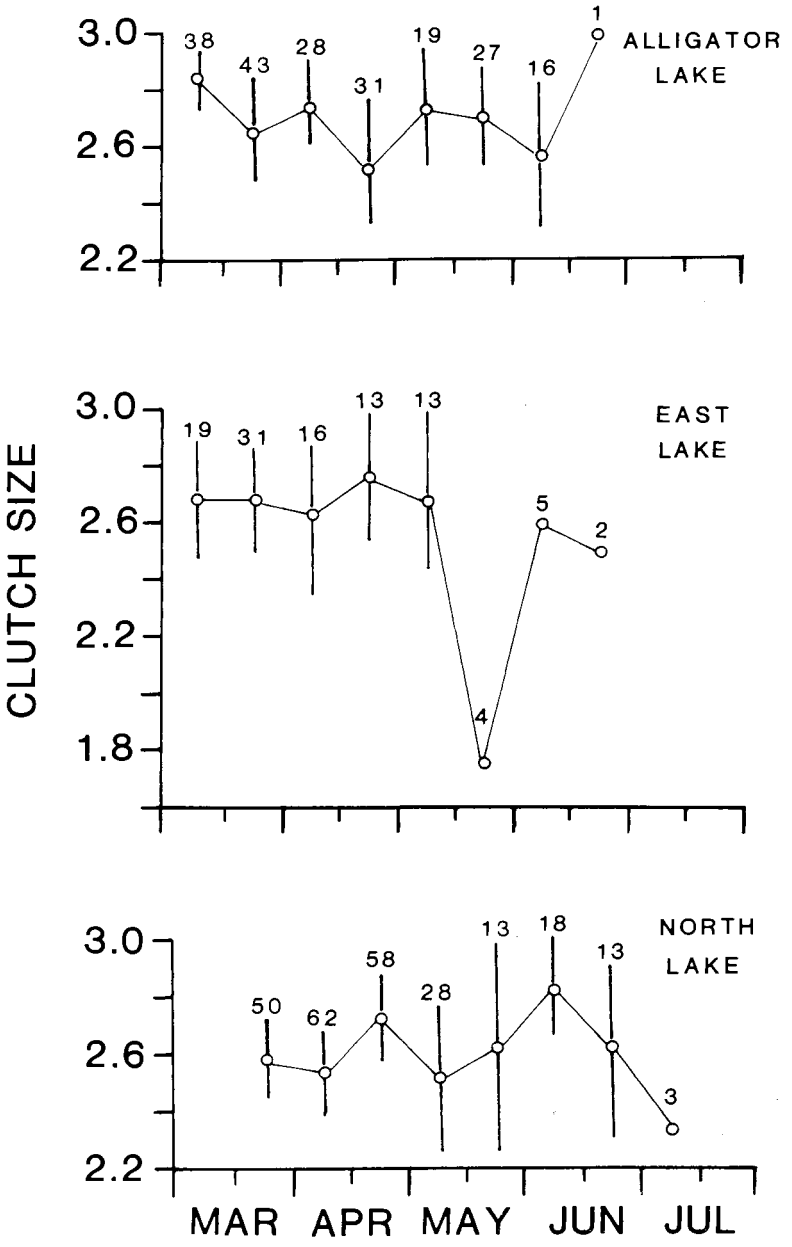

Figure 4. Mean clutch size relative to season at three colonies for Boat-tailed Grackles in central Florida. The vertical lines represent the 95% confidence limits around the mean, and the number above the lines is the number of clutches during that half month.

comes more typically territorial (Selander and Giller 1961, Kok 1972), although frequently males still do not obtain inter-male exclusive territories (Kok 1972). Selander (1960) did not describe the status of male Great-tailed Grackles at a large tree where he found over a hundred nests. Possibly under this circumstance of extremely high nesting density no male could successfully defend the site.

McIlhenny (1937) stated that Boat-tailed Grackle males in Louisiana gathered and displayed in the vicinity of large nesting sites, but only an occasional male actually visited the colony. He stated that only at small colonies were males in regular attendance. I found males displayed and called within nesting areas regardless of colony size. McIlhenny also found that small colonies were established late in the breeding season and then usually as subsets of larger colonies. In contrast, I found small colonies being established at the same times as larger colonies and fully independent of the large colonies.

It seems that coloniality in Boat-tailed Grackles is centered around the availability of nesting sites protected from predation. The delay in the start of nesting by some females (e.g. Alligator Lake) in order to attain places on the islands suggests that predation may be an important factor selecting for coloniality. Many cattail patches on the shore of Alligator Lake appeared as good as the islands but were used rarely, and when they were most of the eggs were depredated. The complete or almost complete destruction of colonies at East Lake, Hillsborough River, Courtney, and University Mall attest to the effect of predation (Bancroft 1986). Other authors also have suggested that predators are important in influencing where marsh-nesting birds place their nests (Lack 1968, Kale 1965, Post 1981). The very high nesting success of grackles at locations that were not affected much by predators indicates the possible advantages in finding ideal nesting locations (Bancroft 1986).

Other species of icterids nest colonially but are monogamous. According to Selander (1965) coloniality may have developed before polygyny or promiscuity in the genus *Quiscalus* because "the morphologically and behaviorally primitive species (e.g. *Q. lugubris*), which are colonial, are primarily monogamous possibly because good nesting locations are more wide spread than they are for Boat-tailed Grackles. The abundant nesting sites cannot be monopolized and therefore male Common Grackles obtain more than one mate less often than Boat-tailed Grackle males (Wiley 1976, Howe 1979). Brewer's Blackbirds (*Euphagus cyanocephalus*) are regularly polygynous in areas where nests are placed in scattered trees (Williams 1952), but are strictly monogamous where nests are placed in abundant sage brush (Horn 1968). Where they nest in sage brush they are also colonial, and Horn suggested this permits better exploitation of a variable food supply. Orchard Orioles (*Icterus*

spurius) normally are monogamous but become highly colonial and polygynous when breeding in scattered trees in marshland in the South (J. V. Dennis *in* Bent 1958). Thus, the mating system becomes polygynous for Brewer's Blackbirds and Orchard Orioles when nesting sites become limiting. Presumably for monogamous marsh-nesting icterids, reproductive success requires help by both parents. Tricolored Blackbirds (*Agelaius tricolor*) are monogamous and nest colonially (Payne 1969). Often both parents forage for the nestlings, up to several kilometers from the nest. Presumably if only one parent attempted to raise the young, reproductive success would be greatly diminished and thus single parenthood would be selected against.

Chronology.—Boat-tailed Grackles in Florida nest from early March to late July with over half of all clutches laid in March and April. This is similar to the egg dates and nesting peaks reported for Florida by Howell (1932) and Selander and Nicholson (1962). The earliest complete clutch reported for Florida was found on 27 February in the Kissimmee Valley (Selander and Nicholson 1962), which is five days earlier than the earliest complete clutch I found slightly farther north in Hillsborough County. Boat-tailed Grackles in Louisiana also have a four to five month nesting season from late March to early July (McIlhenny 1937). Great-tailed Grackles in Texas begin nesting in March and continue nesting into August with peak activity occurring in June (Selander 1960, Tudor 1962, Kok 1972). Common Grackles in Florida begin nesting earlier than Boat-tailed Grackles, with active nests in mid-February (Woolfenden and Rohwer 1969) and nest at least until late May (pers. obs.). Common Grackles in northeastern North America may have a shorter nesting season. New Clutches were reported from April to early June (Petersen and Young 1950, Maxwell and Putnam 1972, Howe 1977).

Some fall nesting occurs in Boat-tailed Grackles in Florida (Selander and Nicholson 1962, Kale 1975, Riddell 1976), where a few females nest successfully in November and December. No evidence of fall nesting was obtained for the populations I followed.

Eggs laid during March weigh less and presumably contain fewer nutrients than those laid later in the season (Bancroft 1984a, 1985). As growth rates and survivorship of young are correlated with egg weight in many species (Schifferli 1973, Davis 1975, Parsons 1975, Nisbet 1978, Lunber and Väisännes 1979, O'Connor 1979, Moss et al. 1981), this suggests that grackles are selected to begin nesting before they can lay the heaviest egg possible. An advantage might be that by beginning nesting early, more time for renesting would be available if the attempt failed. Also, fledging young early allows more time for the young to mature and develop before they enter summer flocks and communal

roosts (Bancroft unpubl. data). Young may begin the first prebasic molt at a particular age, and those out of the nest earlier may have more time to complete molt. Perrins (1965, 1970, 1980) has shown that survival of Great Tit (*Parus major*) fledglings is higher for young from earlier broods in the season. Thus, selection favors females which begin nesting as soon as they reach reproductive condition. Egg weight of Great Tits increases as the season progresses even for individuals laying both early and late in the season. Supplemental provisioning of food allows Great Tits to begin nesting earlier (Källander 1974) which suggests that the start of nesting is determined by when females can accumulate enough nutrients for egg formation (Perrins 1965, 1970, 1980).

Although new clutches were initiated over a 120-day period, many colonies were deserted by late May. Typically larger colonies had a longer period of nesting. This pattern also was observed in colonies of Kittiwakes (*Rissa tridactyla*, Coulson and White 1960) and of Red-winged Blackbirds (Smith 1943, Orians 1961, Robertson 1973). All grackle colonies I studied began nesting at about the same time so the difference in the length of the nesting season was a result of larger colonies remaining active longer. This contrasts with Red-winged Blackbirds in which the longer nesting season at some colonies was caused by females nesting earlier at those sites (Robertson 1973).

The proportion of young present that die from starvation peaks during May (Bancroft 1986). Thus, the probability of young dying from starvation increases as the season progresses. Grackles forage extensively along the water's edge and on lawns. May and June are at the end of the dry season in Florida (Thomas 1974) and possibly insects are not as readily available at this time. The increase in starvation rates may contribute to early termination of nesting activity at some colonies.

Predation rates may shorten the nesting season. Mammalian predators usually destroyed most of the nests in a colony in a few nights after the colony's discovery (Bancroft 1986). I checked nests quickly and with minimal disturbance to minimize my influence on the likelihood of predation. These colonies were normally deserted after predation and represent some of the colonies in my data that had short nesting seasons. At other colonies the proportion of nests depredated may change with the course of the season. At North Lake a higher proportion of the nests later in the season were destroyed by predators. Woolfenden and Fitzpatrick (1984) showed that predation on Scrub Jay (*Aphelocoma c. coerulescens*) nests in Florida increases as the season progresses and suggest that predation may preclude Scrub Jays from nesting beyond June. Blue Jays (*Cyanocitta cristata*) nest into September at this same locality but in a different habitat (Bancroft and Woolfenden 1982).

The availability of suitable nesting sites might influence the length of the nesting season. Smaller colonies typically occur in areas with few nesting sites. Most grackle nests are built in cattails and nests usually are supported by both previous-year growth and new growth. As the season progresses the old cattails gradually are knocked down. Grackle nests rarely are supported entirely by new cattail growth. Possibly new growth does not represent a good support structure as it may continue to grow throughout the nesting season. Smaller colonies may have a greater proportional loss of suitable nesting sites as the season progresses. The importance of the availability of suitable nest sites for development of a nesting colony is illustrated by the number of nests constructed on a small cattail island at Alligator Lake in each year. In 1980 the island had extensive stands of old cattails and 61 nests were constructed during the season. In 1981 very little old growth was available and only 27 nests were constructed. As a result of either drought or heavy rains, water depth around cattails often changed dramatically late in the season, resulting in the loss of suitable nesting sites at several colonies.

The number of male and female Boat-taileds in a colony may influence the probability of new females being recruited (Orians 1961, Hailman 1964). The more birds in the colony the greater the chance of attracting late nesters such as first-year females (Orians 1961, Crawford 1977), and females that unsuccessfully attempted first nests elsewhere. Thus, large colonies may have a tendency to attract new females over a longer period. The number of males present at colonies decreases as the season progresses and at a few colonies no male was around while the last females were still feeding young. Males that do remain may spend less time displaying as the season progresses. If calling and displaying by males are important in attracting females, then the disappearance of males would shorten the season.

Clutch Size and Asynchronous Hatching.—The clutch size of Boat-tailed Grackles in central Florida is similar to those in Louisiana and Georgia (McIlhenny 1937, Burleigh 1958), but average smaller than those in South Carolina (Sprunt 1958). In Guatemala, the closely related Great-tailed Grackle has a mean clutch size similar to Boat-taileds in Florida, whereas Great-taileds in Texas and Common Grackles in Michigan have larger clutches (Skutch 1954, Selander 1960, Tudor 1962, Howe 1978). Eggs of Boat-tailed and Great-tailed grackles have similar incubation periods of 13-14 days (McIlhenny 1937, Skutch 1958, Guillory et al. 1981), and eggs of Common Grackles have an incubation period of 12-13 days (Wiens 1965, Howe 1976). For Boat-tailed, Great-tailed and Common grackles, larger clutches and many smaller clutches hatch asynchronously (McIlhenny 1937, Skutch 1954, Selander 1960, Howe 1976). Hatch-

ing asynchrony results in a size hierarchy between the nestlings which influences the pattern of growth in all three species (Selander 1960, Howe 1976, 1979, Bancroft 1984b).

ACKNOWLEDGMENTS

Field work was supported by grants from the Frank M. Chapman Memorial Fund of the American Museum of Natural History and from the Ding Darling Foundation. Randy Jennings kindly helped with field work. Clarence and Anne Jennings gave me permission to enter East Lake through their property and to use their boat. Ken Shoemaker gave me permission to enter North Lake. Discussions with Lise A. Hanners, Wayne Hoffman, Stephen R. Patton, Glen E. Woolfenden and the ornithology luncheon group at the University of South Florida improved various aspects of this study. Lise A. Hanners, James A. Kushlan, John M. Lawrence, James N. Layne, Stephen R. Patton, and Glen E. Woolfenden read and improved drafts of the manuscript. Finally, I thank my wife, Ann, who provided help with field and laboratory work.

LITERATURE CITED

BANCROFT, G. T. 1983. Reproductive tactics of the sexually dimorphic Boat-tailed Grackle (Aves). Unpubl. Ph. D. diss. Tampa: Univ. South Florida.

BANCROFT, G. T. 1984a. Patterns of variation in size of Boat-tailed Grackle eggs. Ibis 126: 496-509.

BANCROFT, G. T. 1984b. Growth and sexual dimorphism of the Boat-tailed Grackle. Condor 86: 423-432.

BANCROFT, G. T. 1985. Nutrient content of eggs and the energetics of clutch formation in the Boat-tailed Grackle. Auk 102: 43-48.

BANCROFT, G. T. 1986. Nesting success and mortality of the Boat-tailed Grackle in central Florida. Auk 103: 86-99.

BANCROFT, G. T., AND G. E. WOOLFENDEN. 1982. The molt of Scrub Jays and Blue Jays in Florida. Ornithol. Monog. No. 29.

BENT, A. C. 1958. Life histories of North American blackbirds, orioles, tanagers, and allies. U. S. Natl. Mus. Bull. 211: 1-549.

BRYANT, D. M. 1978. Establishment of weight hierarchies in the broods of House Martins *Delichon urbica* (L.). Ibis 120: 16-26.

BURLEIGH, T. D. 1958. Georgia birds. Norman: Univ. Oklahoma Press.

COULSON, J. C., AND E. WHITE. 1961. An analysis of the factors influencing the clutch size of the kittiwake. Proc. Zool. Soc. London 136: 207-217.

CRAWFORD R. D. 1977. Breeding biology of year-old and older female Red-winged and Yellow-headed blackbirds. Auk 89: 73-80.

DAVIS, J. W. 1975. Age, egg-size and breeding success in the Herring Gull *Larus argentatus*. Ibis 117: 460-473.

GUILLORY, H. D., J. H. DESHOTELS, AND C. GUILLORY. 1981. Great-tailed Grackle reproduction in southcentral Louisiana. J. Field Ornithol. 52: 325-331.

HAILMAN, J. P. 1964. Breeding synchrony in the equatorial Swallow-tailed Gull. Amer. Natur. 98A: 79-83.

HORN, H. S. 1968. The adaptive significance of colonial nesting in the Brewer's Blackbird (*Euphagus cyanocephalus*). Ecology 49: 682-694.

HOWE, H. S. 1976. Egg size, hatching asynchrony, sex, and brood reduction in the Common Grackle. Ecology 57: 1195-1207.

HOWE, H. F. 1977. Sex-ratio adjustment in the Common Grackle. Science 198: 744-746.
HOWE, H. F. 1978. Initial investment, clutch size, and brood reduction in the Common Grackle (*Quiscalus quiscula* L.). Ecology 59: 1109-1122.
HOWE, H. F. 1979. Evolutionary aspects of parental care in the Common Grackle *Quiscalus quiscalus* L. Evolution 33: 41-51.
HOWELL, A. H. 1932. Florida bird life. New York: Coward McCann, Inc.
KALE, H. W., II. 1965. Ecology and bioenergetics of the Long-billed Marsh Wren *Telmatodytes palustris griseus* (Brewster) in Georgia salt marshes. Publ. Nuttall Ornithol. Club, No. 5.
KALE, H. W. 1975. Additional records of autumnal breeding of Boat-tailed Grackles in Florida. Fla. Field Nat. 3: 5-8
KÄLLANDER H. 1974. Advancement of laying of Great Tits by the provision of food. Ibis 116: 365-367.
KOK, O. B. 1972. Breeding success and territorial behavior of male Boat-tailed Grackles. Auk 89: 528-540.
LACK, D. 1968. Ecological adaptations for breeding in birds. London: Methuen Press.
LUNBER, G. A., AND R. A. VAISÄNNES. 1979. Selective correlation of egg size with chick mortaility in the Black-headed Gull (*Larus ridibundus*). Condor 81: 146-156.
MAXWELL, G. R., II, AND L. S. PUTNAM. 1972. Incubation, care of young, and nest success of the Common Grackle (*Quiscalus quiscula*) in Northern Ohio. Auk 89: 349-359.
MCILHENNY, E. A. 1937. Life history of the Boat-tailed Grackle in Louisiana. Auk 54: 274-295.
MOSS, R., A. WATSON, P. ROTHERY, AND W. W. GLENNIE. 1981. Clutch size, egg size, hatch weight and laying date in relation to early mortality in Red Grouse *Lagopus lagopus scoticus* chicks. Ibis 123: 450-462.
NISBET, I. C. T. 1978. Dependence of fledging success on egg-size, parental performance and egg-composition among Common and Roseate Terns, *Sterna hirundo* and *S. dougalli*. Ibis 120: 207-215.
O'CONNOR, R. J. 1979. Egg weight and brood reduction in the European Swift (*Apus apus*). Condor 81: 133-145.
ORIANS, G. H. 1961. Social stimulation within blackbird colonies. Condor 63: 330-337.
PARSONS. J. 1975. Asynchronous hatching and chick mortality in the Herring Gull *Larus argentatus*. Ibis 117: 517-520.
PAYNE R. B. 1969. Breeding seasons and reproductive physiology of Tricolored Blackbirds and Red-winged Blackbirds. Univ. Calif. Publ. Zool. 90: 1-137.
PERRINS, C. M. 1965. Population fluctuations and clutch-size in the Great Tit *Parus major* L. J. Anim. Ecol. 34: 601-647.
PERRINS, C. M. 1970. The timing of birds' breeding seasons. Ibis 112: 242-255.
PERRINS, C. M. 1980. Survival of young Great Tits, *Parus major*. Pp. 159-174, *In* R. Nöhring (ed.). Acta XVII Congr. Internatl. Ornithol., Berlin: Deutschen Ornithol.-Gesellsch.
PETERSEN, A., AND H. YOUNG. 1950. A nesting study of the Bronzed Grackle. Auk 67: 466-476.
POST W. 1981. The influence of rice rats *Oryzomys palustris* on the habitat use of the Seaside Sparrow *Ammospiza martina*. Behav. Ecol. Sociobiol. 9: 35-40.
RIDDLE, K. 1976. Autumnal breeding of Boat-tailed Grackles at Gainesville, Florida. Fla. Field Nat. 4: 36.
ROBERTSON, R. J. 1973. Optimal niche space of the Red-winged Blackbird: spatial and temporal patterns of nesting activity and success. Ecology 54: 1085-1093.
SCHIFFERLE, L. 1973. The effect of egg weight on the subsequent growth of nestling Great Tits *Parus major*. Ibis 115: 549-558.

SELANDER, R. K. 1958. Age determination and molt in the Boat-tailed Grackle. Condor 60: 355-376.

SELANDER, R. K. 1960. Sex ratio of nestlings and clutch size in the Boat-tailed Grackle. Condor 62: 34-44.

SELANDER, R. K. 1965. On mating systems and sexual selection. Amer. Natur. 99: 129-141.

SELANDER, R. K., AND D. R. GILLER. 1961. Analysis of sympatry of Great-tailed and Boat-tailed Grackles. Condor 63: 29-86.

SELANDER, R. K., AND D. J. NICHOLSON. 1962. Autumnal breeding of Boat-tailed Grackles in Florida. Condor 64: 81-91.

SKUTCH, A. F. 1954. Life histories of Central American birds. Pac. Coast Avif. No. 31: 1-448.

SKUTCH, A. F. 1958. Life history of *Cassidix mexicanus mexicanus* (Gmelin) Boat-tailed Grackle. Pp. 335-350, *In* A. C. Bent, Life histories of North American blackbirds, orioles, tanagers, and allies. U. S. Natl. Mus. Bull. 211.

SMITH, H. M. 1943. Size of breeding populations in relation to egg laying and reproductive success in the eastern Red-wing (*Agelaius p. phoeniceus*). Ecology 24: 183-207.

SPRUNT, A. 1958. Life history of *Cassidix mexicanus torreyi* Harper Eastern Boat-tailed Grackle. Pp. 365-374, *In* A. C. Bent, Life histories of North American blackbirds, orioles, tanagers, and allies. U. S. Nat. Mus. Bull. 211.

THOMAS, T. M. 1974. A detailed analysis of climatological and hydrological records of south Florida with reference to man's influence upon ecosystem evolution. Pp. 82-122, *In* P. J. Gleason (ed.). Environments of South Florida: present and past. Miami Geological Society, Memoir 2.

TUDOR, B. M. 1962. Nesting studies of the Boat-tailed Grackle. Auk 79: 77-84.

WIENS, J. A. 1965. Behavioral interactions of Red-winged Blackbirds and Common Grackles on a common breeding ground. Auk 82: 356-374.

WILEY, R. H. 1976. Affiliation between the sexes in Common Grackles. I. Specificity and seasonal progression. Z. Tierpsychol. 40: 59-79.

WILLIAMS, L. 1952. Breeding behavior of the Brewer Blackbird. Condor 54: 3-47.

WOOLFENDEN, G. E., AND J. W. FITZPATRICK. 1984. The Florida Scrub Jay: Demography of a cooperative-breeding bird. Mono. in Popul. Bio. No. 20. Princeton, N. J.: Princeton Univ. Press.

WOOLFENDEN, G. E., AND S. A. ROHWER. 1969. Breeding birds in a Florida suburb. Bull. Fla. State Mus. 13: 1-83.