

ADVANTAGES OF COLONIALITY IN FEMALE BOAT-TAILED GRACKLES

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ABSTRACT.—In a South Carolina cattail marsh, female Boat-tailed Grackles (*Quiscalus major*) concentrated to nest on predator-safe islands patrolled by American alligators (*Alligator mississippiensis*). I examined several hypotheses regarding colonial nesting behavior of Boat-tailed Grackles. (1) I reject the null hypothesis that colony-nesting and solitary females do not differ in reproductive success. Solitary-nesting females had lower reproductive success (37%) than colony females (63%), a difference perhaps attributable to males' defense of colonies from predatory birds. (2) I reject the hypothesis that the physical characteristics of sites used for colonies differ from those that are not used. Islands occupied by colonies were the same as unoccupied islands in measurements of water depth and vegetation structure. Colony site use is therefore not a result of habitat heterogeneity. (3) I reject the hypothesis that breeding success does not differ between contemporaneous colonies. In two of four years, I found significant variation among colonies in percentage of nests that produced young. Nesting success was independent of colony size. (4) I accept the hypothesis that the reproductive success of colonial females is related to extrinsic factors rather than to differences in female quality. Predation was the main cause of nest mortality, and varied between colony sites, but its intensity was not related to colony size. Although clutch size remained constant over the nesting period, number of fledglings per nest decreased, mainly as a result of the increased proportions of nests lost to predators. Starvation, the second most important cause of mortality, did not vary according to colony size nor to time of breeding. Early synchronized nesting of the whole population may reduce the effects of predation by both a "head-start" effect, and by predator satiation. Received 23 Aug. 1997, accepted 30 July 1998.

The number of mates that a male can monopolize depends on the spatial and temporal distribution of females (Emlen and Oring 1977), and on the male's competitive abilities (resource-holding potential of Parker 1974). Polygyny often occurs in colonial, non-territorial populations (Lack 1968) in which males have little influence on female distribution, and male-male competition limits access to females (harem polygyny of Wittenberger 1979). Harem polygyny has been found in many mammals, but rarely in birds (Emlen and Oring 1977, Wittenberger 1979). Among birds, it has been described for populations of large, sexually dimorphic oropendolas and grackles (Icteridae; Chapman 1929, Schäfer 1957, Tashian 1957, Drury 1962, Post 1992, Webster 1994). An understanding of how this mating system is maintained may be gained by considering the behavior of males and females separately, as each sex appears to act independently of the other until females actually choose colony sites.

Nesting female Boat-tailed Grackles (*Quiscalus major*) in South Carolina congregate in predator-secure sites, such as marsh islands

patrolled by American alligators (*Alligator mississippiensis*; Post and Seals 1991, Post et al. 1996). Females build nests and rear young unaided by males. Males, which are 1.9× heavier than females, defend colonies from predatory birds. Females settle in colonies independently of male activities, but males adjust their behavior to maximize closeness to females. In each colony, an alpha male defends most receptive females from other males, and the clustering of females allows these males extreme reproductive advantage (Post 1992). Although the aggregation of females is advantageous to some males and may thus promote polygyny, the question of why females group in the first place should be addressed (Campagna et al. 1992). To examine this question, I consider the following hypotheses: (1) females nesting in colonies do not differ in reproductive success from females nesting alone; (2) the physical characteristics of sites used for colonies differ from those that are not used; therefore, aggregations may simply be a response to habitat heterogeneity; (3) as a corollary, if colony sites vary in quality, breeding success should vary between contemporaneous colony sites; (4) further, reproductive success should be related to extrinsic factors such as accessibility to predators,

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rather than to characteristics related to female quality, such as ability to gather food for young.

STUDY AREA AND METHODS

The study was conducted in a 30-ha impounded cattail (*Typha* spp.) marsh at Magnolia Gardens on the Ashley River 10 km north of Charleston, South Carolina. The outer part of the marsh was surrounded by a channel up to 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%. Further descriptions of the study area are in Post and Seals (1991) and Post (1992).

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 begins with the penultimate egg, lasts 13 days), or from age of nestlings, determined by criteria in Bancroft (1984).

Nests were usually visited every three days. Estimates of nest survival probabilities are based on the time that nests were exposed to risk (Mayfield 1975, Johnson 1979). Only nests whose fates were known were included in the statistical analysis. The incubation period (13 days) and nestling period (13 days) were analyzed separately. To test for differences in nest success between solitary nests and colonial nests, I calculated the variance of the daily survival rate using the formula of Johnson (1979) and Hensler (1985). The Z-statistic was then used to test for differences between nesting success estimates (Hensler 1985).

Sources of mortality to nests were determined by examining the condition of depredated nests and their contents (Bancroft 1986). For example, a nest destroyed at night was assumed to have been taken by a snake or rodent. If the nest was disheveled and egg shell pieces were found, I inferred rodent predation. If the nest was intact and all signs of contents missing, I inferred snake predation. Daytime nest searches revealed the presence of snakes, which often rested in nests. Rodents left the marsh during the day, but fresh feces could be found in depredated nests. Starvation was inferred from the condition of a nestling; e.g., it was often listless, and showed little apparent weight gain in comparison to nestmates. Dead nestlings under six days old were removed by the females; older ones were left in the nest. Partial losses of nest contents to avian diurnal predators was possible, but smaller predatory birds (e.g., Blue Jays; *Cyanocitta cristata*), were not seen in the study area and large birds such as Fish Crows (*Corvus ossifragus*) would have taken the entire contents of nests (pers. obs.).

To address the question of whether areas used for nesting colonies differed from those not used, I followed these procedures: during 10–16 April 1992, I chose 10 islands, 5 of which had colonies with more than 10 nests and 5 which had no nests, but which had been used as colony sites in the previous year. At the end of the nesting season (July) I confirmed that no

female grackles had nested in the latter sites. The islands all were about the same size (300 m²) and were the same distance from the upland edge of the marsh and from open water. I placed ten 1-m quadrats in each site along a transect through the long axis of the island. I positioned the quadrat by throwing a meter-stick over my back and then putting the quadrat over the center of the point where the stick fell. After taking three paces, I repeated the procedure. I made four measurements: water depth, maximum height of vegetation, number of residual (overwintering) cattail stems per m², number of green cattail stems per m².

To determine whether females followed each other in and out of colonies, I used observation points from which I could see females approaching or leaving each colony for at least 100 m in any direction. A female was classified as being followed if, during the period it was in view within the 100-m radius, another female from its colony used the same flight path.

To gather information about food that females brought to nests in April–May of 1985–1986, I placed pipe cleaner ligatures (Orians 1966) around the necks of all nestlings in a series of randomly chosen nests. After 0.5 h, I retrieved all food from nestlings' throats and from the nest cup, and removed the pipe cleaners. Each nest was sampled once.

Females nested in groups of 2–37 (Post 1974). For purposes of analysis, groups of five or more simultaneously active nests, with no nest farther than 12.5 m from any other, were classified as colonies. Solitary females nested more than 25 m from any other female.

RESULTS

Breeding success of solitary vs colonial females.—Each year a small percentage of females nested outside colonies. Isolated females nested on cattail islands similar to those occupied by colonies, but nested more than 25 m from other females. I studied 58 solitary nests over five years (1986–1990). I detected significant differences in the daily nest survival rates between isolated and colonial females in two years: daily nest survival during the nestling stage was significantly lower for isolated females in 1988 ($Z = 2.21$, $P < 0.05$, $n = 19$ nests in each group) and 1989 ($Z = 1.76$, $P < 0.05$, $n = 12$). Differences in nesting success were due to predation, which accounted for 46% of mortality to eggs or nestlings of solitary females, versus 32% for progeny of colony females, a significant difference ($\chi^2 = 8.5$, $P < 0.01$, $df = 1$).

Colony site characteristics.—Most nests (96% of 1354) were in colonies (groups of five or more nests) on small cattail islands or narrow peninsulas in open water occupied by

TABLE 1. Nest survival rates of lone and colonial females.

Year	<i>n</i> ^a	Percentage of nests surviving during:					
		Egg period (13 d)		Nestling period (13 d)		Total period (26 d)	
		Lone	Colony	Lone	Colony	Lone	Colony
1986	8	64.4	72.0	58.8	85.1	37.7	61.3
1987	11	51.9	79.0	100.0	100.0	51.9	79.0
1988	19	51.1	77.9	36.4 ^b	81.7	18.6	50.3
1989	12	49.9	45.5	64.4	100.0	32.1	45.5
1990	8	52.2	100.0	82.7	76.5	43.2	76.5

^a The number of nests in each category.^b Daily nest survival significantly higher for colony nests (1988: $Z = 2.21$; $P = 0.014$; 1989: $Z = 1.76$; $P = 0.039$).

alligators. The mean area of 10 colony sites was $310.4 \pm (\text{SD}) 144.8 \text{ m}^2$.

Many apparently suitable colony sites were not occupied. The non-colony islands were about the same size as colony islands and equidistant from the edge of the marsh (figure in Post 1992). For the characteristics that I measured, colony sites did not differ significantly from unoccupied islands [water depth: colony: $24.5 \pm 1.5 \text{ cm}$, unoccupied: $28.3 \pm 1.5 \text{ cm}$, $t = 1.8$, $P > 0.05$; vegetation height: colony: $153.2 \pm 3.2 \text{ cm}$, unoccupied: $148.2 \pm 2.9 \text{ cm}$, $t = 1.1$, $P > 0.05$; vegetation density (stems/m²): colony: 30.2 ± 1.2 , unoccupied: 31.9 ± 1.1 , $t = 1.0$, $P > 0.05$; ratio of residual to green vegetation: colony: 1.10 ± 0.06 , unoccupied: 0.98 ± 0.05 , $t = 1.6$, $P > 0.05$; $n = 50$ for each site category for each measure].

Reproductive success and sources of mortality in different colonies.—Although areas used for colonies did not appear to differ from each other physically, nest success (percentage of nests producing at least one fledgling) differed between colony sites. The mean annual difference between the most successful and least successful colony over six years was 49.2%. In three of the six years, I found sig-

nificant overall variation in success between colony sites (Table 2).

Most mortality to nest contents was from predation (33.6% of 2202 destroyed eggs or young; Table 3). Next in importance was starvation (26.4%), followed by nest abandonment (14.1%), hatching failure (9.4%) and collapse of nest support (7.7%; Table 3). Nest abandonment and collapse of nest were partly related to predator activity; some females deserted nests when snakes moved into a colony, and some nests were knocked down by alligators climbing into colonies to bask. Not all colonies were found by snakes, which contributed to significant variation in colony success (Table 2). For example, the years with lowest nesting success, 1985 and 1989, had the highest mortality from predation. In these years water levels were low enough to expose mudflats over which snakes could move into colonies. The low success of nests in 1988 was related to both predation and starvation, mortality factors which are not independent, as females may desert nests with young when colonies are invaded by snakes. Male grackles invariably attacked predatory birds near colonies and females occasionally joined in mob-

TABLE 2. Variation in reproductive success among colonies.

Year	No. of colonies (No. of nests)	Average success/colony (%) ^a				
		$\bar{x} \pm \text{SD}$	Range	χ^2	P	df ^b
1985	5 (164)	54.0 ± 15.9	29.5–71.4	13.5	<0.01	4
1986	15 (239)	75.9 ± 17.5	30.0–100.0	30.4	<0.01	14
1987	14 (248)	66.8 ± 14.4	50.0–90.9	18.2	>0.05	13
1988	15 (273)	58.8 ± 22.2	22.7–92.3	41.7	<0.001	14
1989	8 (148)	55.8 ± 16.2	33.3–74.1	12.7	>0.05	7
1990	5 (119)	65.7 ± 12.6	48.0–80.0	4.9	>0.05	4

^a Success is percentage of nests fledging at least one bird.^b df is one less than the number of colonies.

TABLE 3. Sources of mortality to Boat-tailed Grackle eggs and young, 1985–1991.

Mortality source	Eggs (<i>n</i> = 1085) ^a		Young (<i>n</i> = 1117)	
	Mean ^b ± SD	Range	Mean ± SD	Range
Unhatched	18.7 ± 5.8	14.0–29.1	—	—
Abandoned	20.6 ± 9.6	9.5–38.5	7.7 ± 4.1	2.1–14.8
Depredated	42.1 ± 15.5	13.6–58.0	25.3 ± 7.4	14.3–34.5
Starved	—	—	52.1 ± 8.5	40.3–60.0
Nest collapsed	7.1 ± 4.0	0–10.5	8.3 ± 5.7	0–12.8
Other ^c	11.5 ± 7.2	0.7–23.5	6.5 ± 4.7	0–11.7

^a Sample sizes refer to numbers of failed eggs and young.^b Means are percentages, averaged over seven years.^c Included losses from alligators basking in cattails, eggs removed by females, death from parasites, and eggs or young destroyed by human observers.

bing (13% of 67 mobbing incidents). Predators ranged in size from Fish Crows to Great Blue Herons (*Ardea herodias*).

To test for seasonal variation in nest success, I divided the breeding period into seven 2-week periods. Mean clutch size did not change significantly over the season ($F = 1.26$; $df = 7, 1392$; $P > 0.05$). However, mean number of fledglings per nest varied significantly over the breeding season ($F = 3.70$; $df = 7, 1392$; $P = 0.001$). While clutch size remained the same, the average number of fledglings decreased as the season progressed (Fig. 1)

The proportion of nests lost to predators was low at the start of the nesting season, but the proportion increased as the season progressed (Fig. 2). In the first three weeks of the 1986–1989 nesting seasons (29 March–18 April), 1.6% of 959 nests were depredated. In the middle of the nesting season (17 May–6 June), 8.2% of the 943 remaining nests were depredated (Fig. 2). In three of the four years, the proportion of nests depredated varied significantly between months (1986: $\chi^2 = 1.0$, $P < 0.05$, $df = 3$; 1987: $\chi^2 = 11.3$, $P < 0.01$, $df = 3$; 1988: $\chi^2 = 26.0$, $P < 0.001$, $df = 3$).

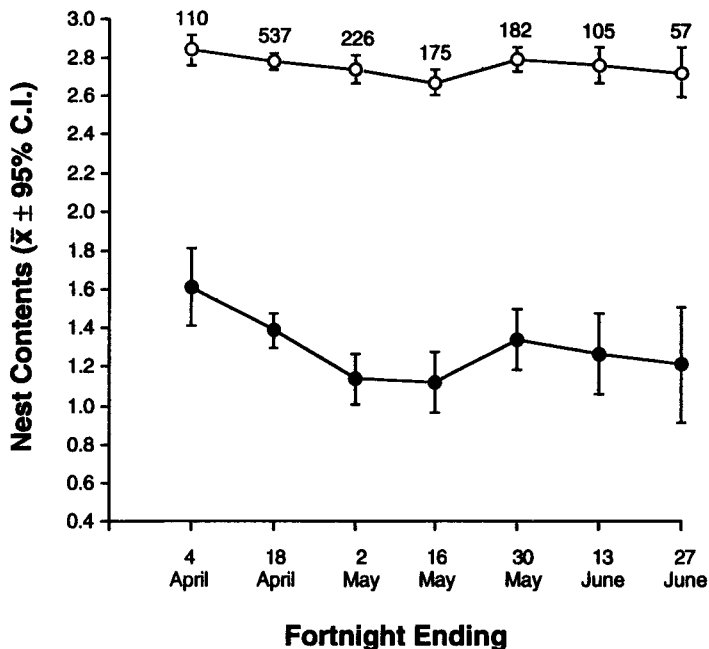


FIG. 1. Seasonal variation in clutch size (open circles) and number of fledglings (closed circles) per nest, 1985–1991. Sample size for each fortnight is given at top of figure. Sample size = 1392 nests.

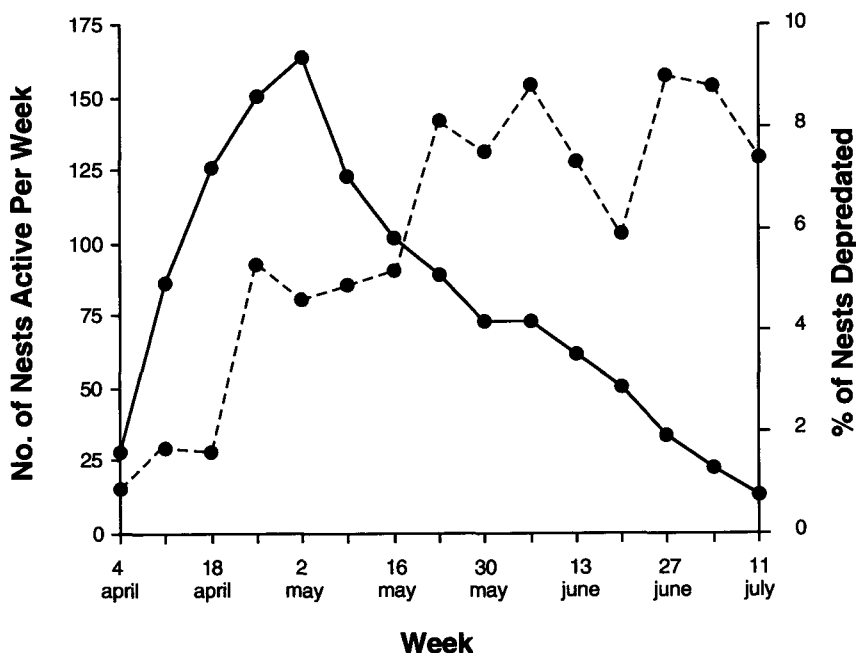


FIG. 2. Number of nests active per week (solid line), compared with proportion of nests depredated (dashed line), 1986–1989. Sample size (total no. of weeks that nests were exposed to losses) = 1902.

Foraging of colony-nesting females.—Females foraged away from the colonies, during low tide in adjacent river marshes, and during high tide in suburban and urban habitats 0.5–2.0 km away. Females did not follow each other to feeding areas, as indicated by associations between individuals leaving and entering the colonies. During 14.5 h of observation of five colonies, I recorded 718 foraging flights by individual females (401 leaving and 317 flights entering colonies). Only 20 flights out involved groups (19 pairs, one trio; 10% of all individual flights out). Similarly, I saw only 16 group flights into colonies (all involving pairs; 10% of all individual flights in).

As would be the case if females were foraging independently of each other, most of the food items brought to nests were arthropods that were widely dispersed in and around the study area. The most important (by frequency occurrence) dietary items collected from nestlings ($n = 290$ items from 43 nests, 25 Apr–1 Jun) were: adult Odonata, mainly Libellulidae, 16%; adult Diptera, mainly Stratiomyidae, 14%; Arachnida, mainly Lycosidae, 15%; Odonata naiads, 7%; adult Coleoptera, 8%;

Orthoptera, mainly Acrididae, 7%; fish (*Menidia* and *Fundulus*), 4%; larval Diptera, mainly Stratiomyidae, 4%. Nestlings also received frogs (*Hyla cinerea* and *Rana utricularia*) and skink (*Eumeces* sp.) egg masses. Although not picked up in the samples, *Anolis* lizards were seen delivered to nests.

I found no correlation between number of young in a colony and percentage of young starving (1986: $r = 0.32$, $n = 16$ colonies; 1987: $r = 0.35$, $n = 13$; 1988: $r = 0.11$, $n = 17$; 1989: $r = 0.29$, $n = 11$; $P > 0.05$ for each year).

DISCUSSION

The hypothesis that colony nesting and solitary females have the same reproductive success (RS) is rejected. At least in some years, the RS of female Boat-tailed Grackles is enhanced by colony nesting. Over a 5-year period (1986–1990) colony nesting females had an average nest success (percentage of nests with at least one fledgling) of 63%, compared to 37% for contemporaneous solitary nesting females. Males only associated with solitary females during the 3-day period of sexual receptivity. After that, when an avian predator

approached their nests, these females often attacked alone. Males were always in attendance at colonies (Post 1992). At least in some years, male mobbing may be advantageous to colony females. Further, the protection that colony females gained from male mobbing appeared to have an all-or-nothing effect; RS was independent of colony size (Post 1994). An alternative explanation for the different RS of colony and solitary females is that the latter differ from the former in some trait such as food gathering ability. However, nestling starvation, which could be used as a measure of female quality, accounted for a larger proportion of nestling mortality in colonies than it did among solitary females: 27% of mortality in colonies was assigned to starvation vs 16% for solitary females ($\chi^2 = 5.84$, $P < 0.05$, $df = 1$).

It is possible that female Boat-tailed Grackles nest together because appropriate nest sites are limited (Bancroft 1987). In Florida cattail marshes, where rodent predation was the main cause of nest mortality, the vegetative structure (microhabitats) of depredated and successful grackle nest sites differed (Dunham 1990). But, in the cattail habitat I studied, appropriate macrohabitats (colony sites) were in surplus. Cattail islands having the same structural characteristics as contemporaneous colony sites were unoccupied. The idea that nesting habitat was not limited is further supported by findings that female grackles do not compete for nest sites (Post 1994).

As predicted, RS varied significantly between colonies. Over the six year period, the mean annual difference between the most successful and least successful colony was 49%. Variation in RS between colonies was mainly due to differences in predation rates. Reproductive success within colonies was not related to nest density, colony size, nor to intervals between nest starts (Post 1994). This lack of correlation may be due to the density independent effect of ground predators and the effectiveness of male grackles in deterring avian predators. Males are able to exclude diurnal avian predators from colonies, but they cannot protect nests from ground predators, which are active at night. When a colony was invaded by snakes, many females abandoned their nests and joined other colonies. The all-or-

nothing effect of predation contributed to intercolony variation in RS.

In most colonies, large numbers of females were simultaneously receptive and overall synchrony within colonies was high (Post 1994). Numbers of nests peaked early in the season and, as numbers decreased, increasingly higher proportions of nests were depredated. This pattern suggests that predators found colonies gradually. By nesting early, grackles may be able to get a head start on predators (Wiley and Wiley 1980) or predators may initially be satiated (Hoogland and Sherman 1976). Alone or in combination, these factors would favor temporal clumping of nests. Other mortality factors, though independent of nest density, also favor early nesting. Nests built in April had fewer live support stems than those built in July (0.1 vs 1.9; Post 1995). Nests that are attached to living cattails stems are more likely to tilt because of different growth rates of stems (Bancroft 1987). Further, later nests were higher than early ones (88.7 cm vs 32.9 cm), which made them more likely to be blown down in storms (Post and Seals 1991). Herons roosted on some colony islands in late June and many grackle nests in these localities were destroyed by the herons (see also Bancroft 1987). Late nests were also subject to interference by grackle fledglings from earlier nests. Until they could fly, fledglings moved around island colony sites up to 30 days after leaving the nest (Bancroft 1987). Fledglings perched on nests, and trampled and defecated on eggs and small nestlings.

If female quality varied significantly among colonies, it would be expected that in at least some years, starvation, which is a measure of females' food-gathering ability, would vary between colonies. Starvation, however, varied little between colony sites. Food available for nestlings is probably not a determinant of breeding chronology. Initiation of breeding may be related primarily to females' ability to build up enough protein reserves for egg formation (Perrins 1970, Greenlaw 1978). It is unlikely that female grackles would be able to modify their reproductive behavior to reduce the effects of starvation.

Colonies do not appear to be formed as a means of improving foraging efficiency (Horn 1968, Bayer 1982). Female grackles fed nestlings prey that appeared to be evenly dis-

persed in and around the study area. It is unlikely that females foraging for such prey would benefit by following each other, as they would if they were feeding at concentrations of food (Horn 1968). Further, it is unlikely that females were exchanging information on the location of food, as only 10% of them left colonies together on feeding flights. In addition, the findings that starvation rates did not vary according to colony size and did not change over the season, indicate that food availability is not a critical factor in determining nest dispersion. Finally, females nesting together do not coordinate their breeding activities, such as might be the case if they benefitted from cooperative feeding (Post 1994).

Female Boat-tailed Grackles nest on marsh islands or isolated trees over land (Post et al. 1996), which are relatively safe from snakes and mammals. In addition to grackles, other species of large, sexually dimorphic blackbirds (oropendolas and caciques, *Psaracolius* and *Cacicus*) aggregate in isolated trees, apparently as a means of avoiding predators (Chapman 1929, Schäfer 1957, Drury 1962, Robinson 1985, Fraga 1989, Webster 1994). As in Boat-tailed Grackles, female caciques appear to have a surplus of appropriate nest sites, and site selection is more influenced by site tenacity than by physical differences between sites (Feekees 1981).

The behaviors related to coloniality in female Boat-tailed Grackles appear to occur as a response to predation. Colony sites are not limited, but females apparently follow each other to settle in appropriate (predator-safe) sites. Within colonies, females do not coordinate their breeding activities or foraging behavior. However, as a result of early breeding by females and, possibly, their common attraction to colony sites, overall synchrony of breeding is high. The temporal and spatial aggregation of female grackles allows individual males to sequester entire colonies.

Although males do not appear to influence where females settle to breed (Post 1994), the spacing and timing of breeding allow dominant males to monopolize entire colonies. The fitness of an individual male is determined mainly by the size of the female group that he sequesters, and the overall RS of that group. This may be critical for the evolution of harem polygyny in this species.

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