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NESTING ASSOCIATIONS OF LEAST BITTERNS AND BOAT-TAILED GRACKLES[1]

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Abstract. Interspecific nesting assemblages may result from independent settlement by individuals or groups of each species in the same limited habitat, or association with other species may be actively sought. Although Least Bitterns (*Ixobrychus exilis*) often nest solitarily, in a South Carolina impoundment they frequently associated with colonies of Boat-tailed grackles (*Quiscalus major*). Bittern nests inside and outside colonies occupied the same microhabitats. However, more bitterns nested in grackle colonies than in equal-sized areas of equivalent habitat in the same marsh. In one of two years, colonial bitterns had higher reproductive success than bitterns nesting outside colonies. We conclude that Least Bitterns actively associate with grackles. Possible reasons for the association of bitterns with grackles are as follows (1) Critical density effect: at high population densities, the advantages of dispersed (cryptic) nesting are lost. Bitterns switching to nest in groups may experience little reduction in reproductive success, relative to those nesting solitarily. (2) Vigilance and mobbing: grackles provide early warning, and actively exclude predatory birds from colonies. Bitterns nesting among grackles appeared to incur few costs, such as may result from competition for food or from intracolony predation.

Key words: Ixobrychus exilis; Quiscalus major; *interspecific coloniality; nest site selection; reproductive success.*

INTRODUCTION

Possible benefits of colonial nesting are protection from predators and improved food delivery. Possible costs are decreased feeding rates (Nettleship 1972, Hoogland and Sherman 1976, Coulson et al. 1982, Gaston et al. 1983), competition for space and losses from parasitism and intracolony predation (Hoogland 1979, Wittenberger and Hunt 1985). Colonial-nesting species benefit from the anti-predator behavior of conspecifics (Hoogland and Sherman 1976, Wiklund and Andersson 1980, Gotmark and Andersson 1984, Haas 1985, Robinson 1985, Brown and Brown 1987). In some cases a less aggressive species may gain by associating with a more aggressive one, and the relationship may benefit one or both parties (Clark and Robertson 1979, Dyrcz et al. 1981, Nuechterlein 1981, Wiklund 1982, Burger 1984). Losses may also be caused by conspecifics and other species nesting in the same colonies; e.g., theft of nest material (Siegfried 1972), egg destruction (Pettingill 1939, Yom-Tov 1975, Shields and Parnell 1986) and cannibalism (McIlhenny 1937, Yom-Tov 1975, Burger and Gochfeld 1981).

Least Bitterns (*Ixobrychus exilis*) have most often been reported nesting solitarily (Weller 1961, Hancock and Elliott 1978, Bowman and Bancroft 1989). In a South Carolina marsh impoundment, we found pairs or groups of bitterns frequently nesting in colonies of Boat-tailed Grackles (*Quiscalus major*). Bitterns may nest in grackle colonies because of limited suitable habitat, or may actively associate with grackle colonies. The active association hypothesis predicts that if habitat quality is the same for both colony and non-colony sites, (1) bitterns will concentrate in sites occupied by the grackles and (2) bitterns nesting inside grackle colonies will have better reproductive success than those nesting outside.

STUDY AREA AND METHODS

The study was conducted during 1985–1991 in a 30-ha cattail marsh at Magnolia Gardens, South Carolina. The outer part of the marsh is surrounded by a channel ≤3 m deep. Away from the channel, water depth in open water areas averages 1 m. Open water covers 75% of the site, and cattails (*Typha* spp.) cover 25%. Additional descriptions are presented in Post and Seals (1991) and Post (1992).

A 13-ha study area was marked with wooden stakes placed at 25 m intervals. Nests were marked with numbered flags, and their positions were plotted on maps. Inter-nest distances were

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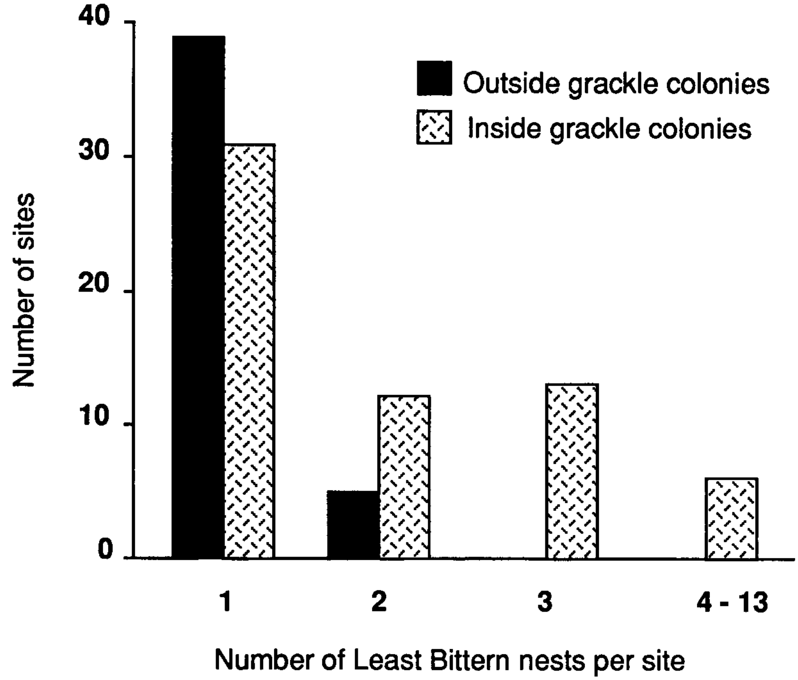

FIGURE 1. Comparison of numbers of Least Bitterns that nested inside and outside Boat-tailed Grackle colonies, 1986–1989 ($n = 106$ sites; 160 Least Bittern nests). Larger nesting groups were located more frequently in Boat-tailed Grackle colonies than in equivalent areas outside colonies ($\chi^2 = 20.8$, $P < 0.001$, df = 3).

taken from the maps. Bittern colonies were defined as groups of two or more nests occurring within grackle colonies, and with maximum nearest neighbor distance of 15 m. As Least Bitterns renest if their first nesting attempt fails, we calculated their population densities by determining the maximum number of nests that were simultaneously active in a given area during the nesting season. The study site was visited at least three times per week 1 April–1 July, and each nest was checked at least once per five days. We used the Mayfield (1975) method, as modified by Johnson (1979), to calculate nest success, and used associated statistical tests given in Hensler (1985). Least Bittern nest survival was calculated for the period that eggs were in the nest (22 days), and from the time the first egg hatched until the first young left the nest (>6 days).

We measured characteristics of nest sites by placing a 1 × 1 m quadrat around each nest. The vegetation at the four corners of the quadrat and at one side of the nest was sampled by positioning a 6-mm diameter metal rod vertically in the vegetation. The number of contacts that residual (overwintering) and new vegetation made with each decimeter of the rod was tallied (Wiens 1969). Vegetation density was defined as the average number of contacts made at the 5 points of the quadrat. Vegetation heterogeneity is defined for each quadrat as maximum number of contacts at any corner point minus minimum number of contacts at any corner point, divided by the mean number of contacts at all 4 corner points (Wiens 1974). At the 4 corner points and at the nest, we measured water depth. We also measured height of eggs above water and distance of the nest from the nearest open water.

RESULTS

Nest site characteristics. Least Bitterns nested throughout the study area at varying densities, both inside and outside Boat-tailed Grackle colonies. All nests were built over water on cattail islands surrounded by water containing American alligators (*Alligator missippiensis*). No ground predators were found on the study islands. The islands were all about the same distance from a tree-lined dike (see figure in Post 1992). The largest bittern groups occurred in grackle colonies (Fig. 1). Grackle colonies were aggregations of

TABLE 1. Characteristics (Mean ± 1 SD) of isolated and colonial Least Bittern nests. Data collected 20–30 May 1991.

Parameter[a]	Isolated nests ($n = 13$)[b]	Nests in colonies ($n = 15$)
Distance to open water (m)	3.5 ± 2.6	3.8 ± 2.0
Height of eggs above water (cm)	56.9 ± 20.3	64.3 ± 22.4
Water depth (cm)	32.5 ± 8.9	26.0 ± 14.9
Maximum height of vegetation (dm)	22.2 ± 2.3	22.8 ± 3.0
Height of maximum vegetation density (dm)	6.2 ± 2.9	7.5 ± 4.4
No. of vegetation contacts/point	7.57 ± 2.57	8.75 ± 2.68
Ratio of residual to green vegetation	0.83 ± 0.48	0.96 ± 0.62
Heterogeneity	1.05 ± 0.52	0.84 ± 0.35

[a] Parameters defined in methods.

[b] Number of nest-centered quadrats. To determine water depth, height of maximum vegetation density, number of vegetation contacts/point and ratio of residual to green vegetation, five samples were taken per quadrat. Heterogeneity is based on the four outer points of the quadrat (subpoint at nest not included).

5–37 nests (mean distance between nearest neighboring grackle nests = 2.52 ± 2.44 (SD) m; $n = 342$) that occurred in discrete patches of cattails on islands within the impoundment.

It is possible that nest microhabitats used by colonial Least Bitterns were different from those of isolated pairs. To test this, we compared the characteristics of 14 solitary nests with those of 15 colonial ones ($n = 8$ colonies). None of the eight variables that we measured differed between the two dispersion patterns (Table 1).

Association between bitterns and grackles. The mean yearly (1986–1988) density of Least Bitterns in the 13-ha study area was 2.90 pairs/ha, SD = 0.31 (Post and Seals 1991). In relation to the vegetated (25%) area of the marsh, mean density was 11.56 ± 1.25 pairs/ha. During 1986–1989, 70% of 163 Least Bittern pairs nested in colonies of nesting Boat-tailed Grackles, which were usually on islands (mean area = 310.4 ± 144.9 m^2, $n = 10$).

Within the colonies, bitterns started nesting after the grackles. The average delay between the initiation of the first grackle nest and the first bittern nest during four years (1986–1989) was 21.7 ± 19.9 days ($n = 18$ colonies), 21.2 ± 11.5 days (17), 29.2 ± 12.3 days (16), 28.7 ± 13.9 days (9). The average clutch initiation date of colonial bitterns (13 May ± 15 days, $n = 11$) did not differ ($t = 0.87$, $P > 0.05$; df = 25) from that of non-colonial bitterns (16 May ± 7 days, $n = 16$).

Most frequently, three pairs of bitterns nested in the grackle colonies (13 cases; Fig. 1). The largest number of contemporary bittern nests in one colony, 13, was found on a 621 m^2 island that also had 32 grackle nests containing eggs or young. A mean of 1.9 ± 1.3 bitterns nested in grackle colonies ($n = 60$ colonies). By contrast, a mean of 1.1 ± 0.3 bittern pairs nested in equal-sized areas of equivalent habitat (continuous, discrete stands of cattails on islands; $n = 44$) outside the grackle colonies, and only 10 of 49 pairs nested within 15 m of each other (five groups of two; Fig. 1). Significantly larger groups of Least Bitterns nested with grackles (Fig. 1). In addition, the numbers of bitterns nesting in each grackle colony was correlated with the numbers of grackles nesting there ($r = 0.584$, $P < 0.001$, df = 34).

All colonial bittern nests were closer to grackle nests than to each other. During 1986–1998, at the time of bittern clutch start, the distance of bittern nests to nearest neighboring grackle nests was 3.3 ± 2.0 m ($n = 21$). For the same nests, the distance to the nearest bittern nest was 9.4 ± 5.2 m. These distances are significantly different (two-tailed paired-sample $t = 5.89$, $P < 0.001$, df = 20). This is expected, however, based on the higher density of grackle nests. In the same colonies, the mean distance between nearest neighboring grackle nests at the time of their first egg was 4.4 ± 3.2 m (n = 18), which indicates that bitterns are able to nest as close to grackles as grackles are to each other.

Female grackles, which are larger (109.0 ± 13.3 g, $n = 100$) than bitterns (78.0 ± 4.9 g, n

TABLE 2. Nesting success of Least Bitterns nesting inside or outside Boat-tailed Grackle colonies, 1988–1989.

	Daily survival rates (%) of nests:			
	Outside grackle colonies		In grackle colonies	
Year	Egg stage	Nestling stage	Egg stage	Nestling stage
1988	93.57 ± 2.07[a]	97.30 ± 16.22	98.56 ± 0.83[a]	100.00 ± 0
	(n = 15)		(n = 17)	
1989	97.27 ± 1.55	100.00 ± 0	97.30 ± 0	100.00 ± 0
	(n = 10)		(n = 9)	

[a] Z = 2.24; P = 0.0125.

= 9) mobbed bitterns that approached their nests. Male grackles (198.1 ± 15.7 g, n = 100) joined females in mobbing bitterns, but did not defend nest sites from bitterns. Bitterns sometimes took over grackle nest sites, usually by using grackle nest platforms as bases for their own nests.

Reproductive success. We asked whether bitterns that nested with grackles had the same success as those nesting away from them. Because of small numbers of non-colonial bittern nests, we could make this comparison for two years only. In 1988, daily nest survival during the egg stage was significantly higher for bitterns nesting in grackle colonies (Table 2). In 1989, colonial and non-colonial bitterns had the same daily nest survival during the egg stage. In both years nest survival during the nestling stage did not differ between nests that were either inside or outside grackle colonies (Table 2). We found no partial (within brood) losses during the nestling stage for the 41 nests, and no evidence that young starved when they were less than seven days old. As young bitterns leave the nest 6–7 days after hatching (Weller 1961, this study), it is possible that some young may have been lost after fledging.

DISCUSSION

The predictions of the active association hypothesis were confirmed. (1) Although macrohabitats (marsh islands) and nest microhabitats did not differ between colony and non-colony sites, more bitterns nested in grackle colonies than outside. Further, bitterns congregated in some colonies more than in others, and numbers of bitterns using equal-sized areas were correlated with numbers of grackles using them. (2) In one year, bittern pairs nesting in colonies had higher egg survival than solitary pairs. In a second year, colonial and non-colonial bitterns had the same nest survival rates. We conclude that nesting Least Bitterns actively associate with grackle colonies.

Most bitterns grouped together with grackles on small, predator-free islands, some of which may have been preferred to others. Although a mean of two pairs of bitterns nested in each colony, some colonies had as many as 13 pairs. Similarly, Kushlan (1973) found a group of 11 Least Bittern nests in a 260 m^2 sawgrass (*Cladium jamaicense*) stand, and he speculated that the bitterns aggregated because of locally abundant food. As in the present study, it is possible that while food abundance facilitated aggregation, the sawgrass provided a safe haven from predators.

Nest defense may be achieved by concealment or by using inaccessible sites (Lack 1968). At lower population densities, nest dispersal and reliance on concealment might offer more protection from predators than would clumping together in safe sites. Bitterns may join grackle colonies because their density is too high for dispersed nesting to be advantageous (critical density effect of Wittenberger and Hunt 1985). The density of bitterns (3 pairs/ha for the 13-ha study area, and 12 pairs/ha for the 3.3-ha area of cattails) is higher than reported from one other study of a comparable sized area (2 nests/ha in 34 ha; Weller 1961).

Group defense is a deterrent to predators (Kruuk 1964, Patterson 1965, Horn 1968, Wiley and Wiley 1980, Robinson 1985). Boat-tailed Grackles mobbed predators such as Fish Crows (*Corvus ossifragus*) within 100 m of colonies. Away from the vicinity of their nests, Least Bitterns did not respond aggressively to predators. Mutual vigilance would benefit members of breeding colonies by providing adults and young warning of the approach of predators. Adults would not be surprised at the nest (Feekes 1981, Nuechterlein 1981), and also could join mobbing groups while young hide (Crook 1964). As Least

Bitterns nest in low, dense vegetation, they may be vulnerable to a rapidly approaching aerial predator, and may benefit from warning calls of grackles. Both young bitterns and young grackles leave the nest prematurely (bitterns at age 5–6 days; grackles at 11–12 days) when disturbed by a predator.

A potential cost of nesting in colonies is loss of nesting material, eggs or young to other colony members (reviewed in Wittenberger and Hunt 1985). Male Boat-tailed Grackles depredate nests of their own and other species (McIlhenny 1937). We did not see grackles take eggs or young of any birds during 1986–1991 (>600 hr of timed observations of colony sites during April–July). Further, during the egg stage, nests in grackle colonies had equal or higher success than those outside the colonies. We also found no partial (within-brood) losses during the bittern nestling stage, when the young are small and would be most vulnerable. Bitterns nested closer to grackles than to other bitterns, and they nested closer to grackles than grackles did to each other. Bitterns occasionally usurped grackle nest sites, but not vice versa. Possibly, bitterns competed with female grackles for nest sites within the colonies.

Colony-nesting bitterns would obtain a net energy gain, compared with solitary-nesting birds, if they obtained information about the location of food (Ward and Zahavi 1973), or if nesting in a colony put individuals closer to food (Horn 1968). It is unlikely that bitterns obtain information about food location from grackles: 85.2% of food items delivered to young grackles were arthropods; 90% of Least Bittern food was fish (Post, unpubl. data). Both species feed solitarily during the breeding season, and we did not see bitterns following each other or grackles to or from colonies. Using natural variation in reproductive success, it is not possible to infer if colony-nesting bitterns had improved reproductive success by being closer to their food: partial losses during the nestling stage, which indicate starvation (Ricklefs 1969), were not found.

In summary, information on the spatial distribution of bitterns supports the hypothesis that bitterns actively associate with grackles. Information on Least Bittern reproductive success give only weak support to the active association hypothesis, but these data do demonstrate that bitterns are not penalized by associating with grackles. Although the reasons for the association cannot yet be identified, we suggest that interspecific coloniality in Least Bitterns is related to predator avoidance; possible contributing factors are (1) critical density effect: higher population density reduces the value of dispersed (cryptic) nesting. (2) Bitterns benefit from grackles' predator mobbing, and their warning about the location of predators.

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