BREEDING SUCCESS AND TERRITORIAL BEHAVIOR OF MALE BOAT-TAILED GRACKLES

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OF all parameters investigated in an attempt to relate breeding success with various behavioral characteristics of adult male Boat-tailed Grackles (*Cassidix mexicanus*), the following showed appreciable correlation with number of young fledged: number of nests, territory size, overall performance level (sum of ranking values for each item of individual males—corresponding parameters of the nine males being ranked from highest to lowest values), average number of flights (act of flying between two points) per hour, median number of terminal phrases per song, and fledging success per nest. Because of the importance of full song and territorial behavior in mating activities, as is generally accepted, behavioral attributes such as percentage time spent on the territory, average number of songs per hour and average song duration (as measured on spectrographs), are also discussed. Results are interpreted in terms of individual and sexual selection as developed by Lack (1954, 1966, 1968).

The fact that grackles have a promiscuous mating system (Selander and Giller, 1961; Selander and Dickerman, 1963; Selander and Hauser, 1965) makes them a good object for study because sexual selection is particularly important in species that form no or only temporary pair bonds. Also Boat-tailed Grackles are plentiful and relatively tame in the Austin area, south central Texas, so that individuals could readily be livetrapped and watched at close quarters in their natural environment. Furthermore a considerable amount of background information, which greatly facilitates the analysis and interpretation of data, is available on the behavior (McIlhenny, 1937; Williams, 1952; Nero, 1956a, 1956b, 1964; Bent, 1958; Ficken, 1963; Wiens, 1965), vocalizations (Selander and Giller, 1961; Orians and Christman, 1968; Kok, 1971) and ecology (Orians, 1960, 1961a, 1961b; Selander and Nicholson, 1962; Willson, 1966) of grackles and other members of the family Icteridae.

METHODS

Observations were made at three colonies (A, B, C) in the Austin region, Travis County, south central Texas, selected on the basis of their suitability for intensive observation. At colony A, Evergreen Cemetery (Figure 1), and colony B, Municipal Auditorium area (Figure 2), the dominant vegetation consisted of relatively small cultivated cedars (*Juniperus cultivar*). Colony C was the open grounds of the Austin Parks and Recreation Department bordering the southern side of the Colorado River (Figure 3). All nests in the latter were in two American elms (*Ulmus americana*) surrounded by a few scattered chinaberry (*Melia azedarch*), weeping willow (*Salix* sp.), and mimosa (*Mimosa* sp.) trees.
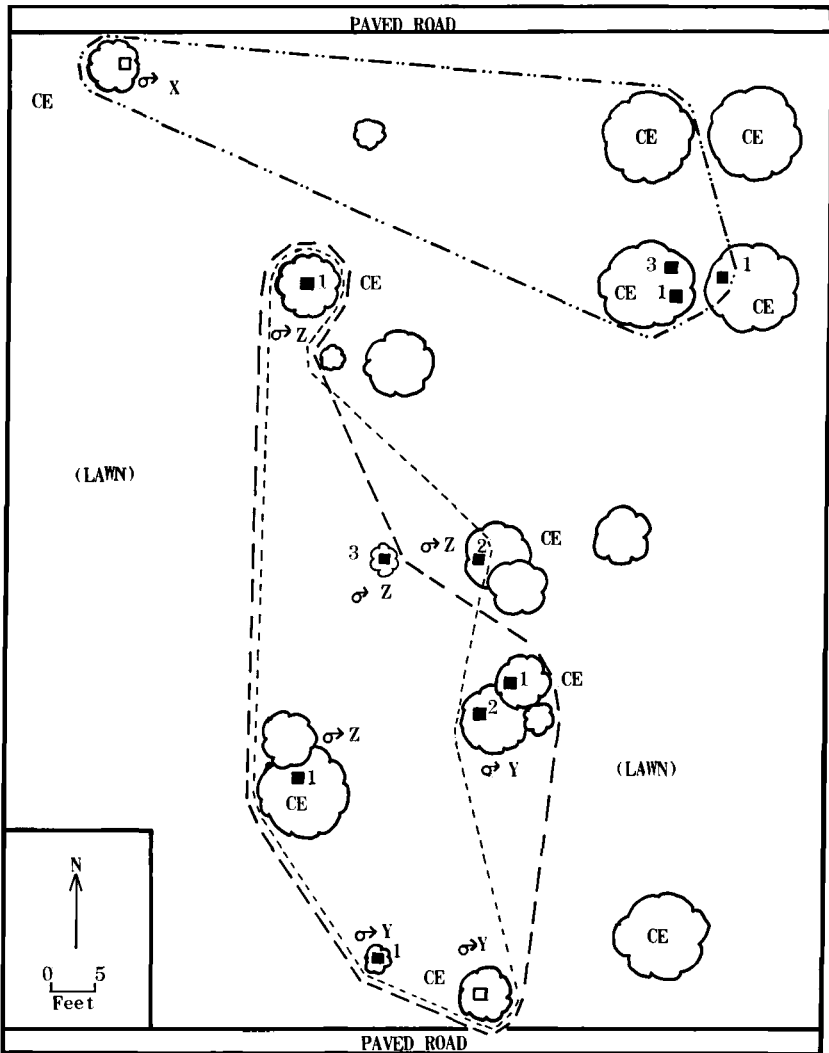
Figure 1. Diagram of approximate territories of *C. mexicanus* males at colony A, 1–9 April 1969. Numbers next to solid squares show fledglings per nest; open squares, deserted nest; ― ·· ―, territorial boundary ♂ X; ― ― ―, same ♂ Y; - - - -, same ♂ Z; CE, cedar.

Grackles were captured with mist nets, traps, and bait treated with 1.5 percent alpha-chloralose. In all 113 birds (74 males and 39 females) were caught and individually marked with a combination of colored aluminum leg bands. Not all banded birds remained on the study area, nor were all resident on the study areas marked.

With the aid of 7 × 35 binoculars and a 20× spotting scope, activities of nine adult males were recorded during daily observation periods lasting at least 10 hours.
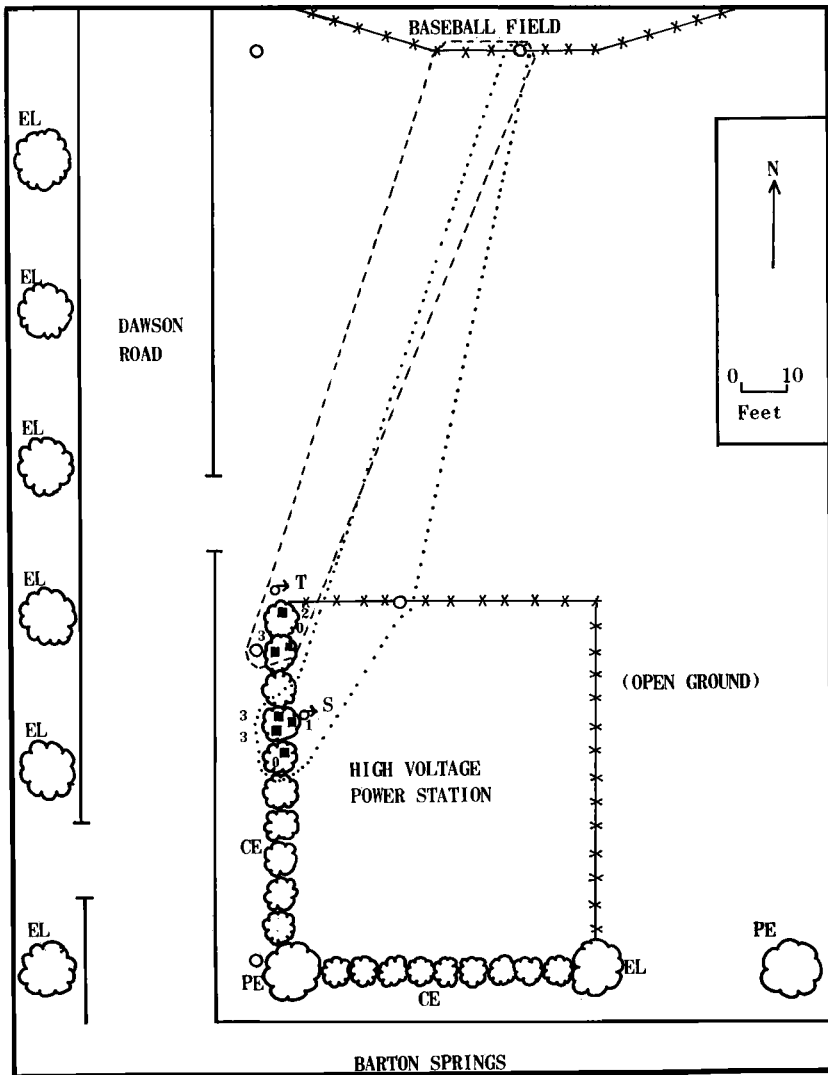
Figure 2. Diagram of approximate territories of *C. mexicanus* males at colony B, 10–15 April. Numbers next to solid squares show fledglings per nest; ...., territorial boundary ♂ S; - - - -, same ♂ T; CE, cedar; EL, elm; PE, pecan.

Although the activities of these males were followed throughout the breeding season of 1969, detailed observations were made only in April, in order to minimize the effect of temporal changes in behavior.

Vocalizations were recorded with a Nagra 3B portable recorder at a tape speed of 7½ inches per second, using an Altec 633A microphone mounted on a 24-inch parabolic
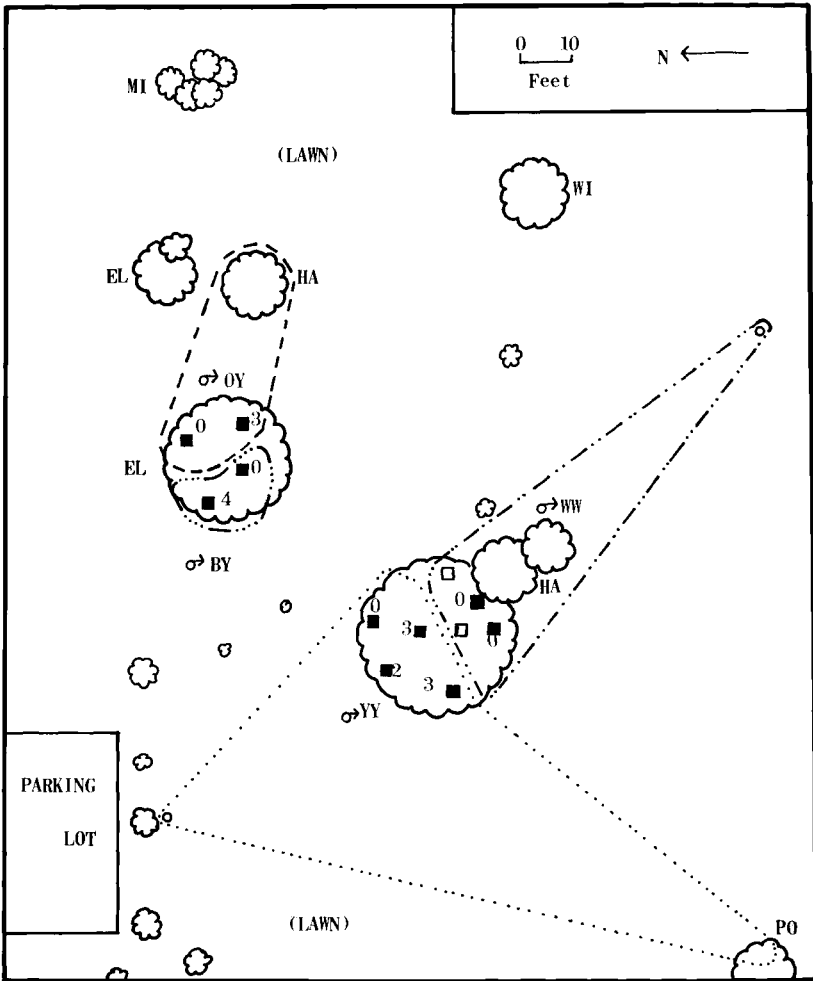
Figure 3. Diagram of approximate territories of *C. mexicanus* males at colony C, 18–30 April. Numbers next to solid squares show fledglings per nest; open squares, deserted nest; ——·····—, territorial boundary ♂ BY; —— ——, same ♂ OY; ·····, same ♂ YY; ——··—, same ♂ WW; EL, elm; HA, hackberry; MI, mimosa; PO, poplar; WI, Willow.

mirror. Sound spectrographs were made on a Kay Electric Company Sonograph, using the wide-band and "high-shape" filter settings.

RESULTS

Figure 1 shows the size and spacing of the three territories at colony A, 1–9 April. Note that nests of polygamous males may be located in several

trees. A few days after male Y copulated with a female, a major portion of his territory was taken over by male Z. The latter, a bird with an extremely loud voice, thereafter dominated male Y on all occasions in the area of territorial overlap, and later obtained four successive females (copulations observed) from whose nests seven young were fledged altogether. Male Y eventually copulated with three additional females, one in the area of territorial overlap, the others in the area of nonoverlap. The former female deserted at an early stage of nest construction, possibly because of interference from male Z.

At colony B two males held adjacent territories that overlapped in one corner (Figure 2). During the 6 days of observation, 10–15 April, prolonged agonistic encounters between the two territorial males took place repeatedly. Because of the sudden onset and ensuing confusion of battles between the males, the identity of the one that initiated the fights could not always be determined, but male S appeared to be the more dominant of the two. No copulating was ever seen at this particular breeding site.

Four adult males were studied carefully at colony C, 18–30 April (Figure 3). Nesting activities at this site began rather late, probably because of the late leafing out of the two elms involved. Male YY was the only bird that regularly visited this site earlier in the season. Later he not only managed to hold the largest territory (Figure 3), but also dominated all other males in the neighborhood.

A remarkable case of an intrusion occurred when male WW quickly occupied the exact territory of a resident male that was trapped for banding. Following the release of the banded individual, prolonged aggressive encounters and fierce fighting took place. The next day the former owner was completely dominated and forcibly driven off by the newcomer, never to be seen in the area again. Nero (1956b) and Orians (1961a) report similar cases among Red-winged Blackbirds (*Agelaius phoeniceus*). At the time of the expulsion, the former resident had already copulated with a female, and was paying much attention to a second female that had started building. Both females eventually deserted. Male WW, abnormal in the sense that he never gave full song nor "clacked," succeeded in attracting two additional females, but they likewise deserted, one while in the nest building stage, the other after having laid two eggs.

As was usually the case, copulations involving males OY and BY took place without interference near the nests in their respective territories. Frequent copulatory attempts on the neutral grounds at some distance from the colony, by contrast, were rarely successful because of the spirited and prompt interference by rival males.

Values for the different territorial activities of the nine individual males are summarized in Table 1. Employing the data given in this table (male

TABLE 1

SUMMARY OF TERRITORIAL ACTIVITIES OF NINE *C. MEXICANUS* MALES

	Colony A males			Colony B males		Colony C males			
	X	Y	Z	S	T	OY	BY	YY	WW
Number of young fledged	5	4	7	7	5	3	4	8	0
Number of nests	3.50	3.50	4.00	4.00	3.00	2.00	2.00	4.00	1.50
Number of fledglings per nest	1.43	1.14	1.75	1.75	1.67	1.50	2.00	2.00	0.00
Territory size (square feet)	241	326	355	190	185	83	25	420	149
Percentage time on territory	60	80	86	89	77	71	54	65	74
Average number of flights/hour	20	26	10	21	12	10	7	29	16
Average number of songs/hour	17	9	17	12	10	17	3	5	0
Average song duration (seconds)	5.80	5.81	7.03	5.44	4.96	5.67	6.88	5.23	3.41[1]
Median number of terminal phrases/song	1.20	1.03	1.43	1.01	1.01	1.00	1.03	1.24	3.33
Overall performance level[2]	27	22	14	24	37	39	44	25	40

[1] Actually incomplete songs, since introductory phrases were always omitted.
[2] Sum of ranking values of each item, with the exception of number of young fledged and number of fledglings per nest, per individual.
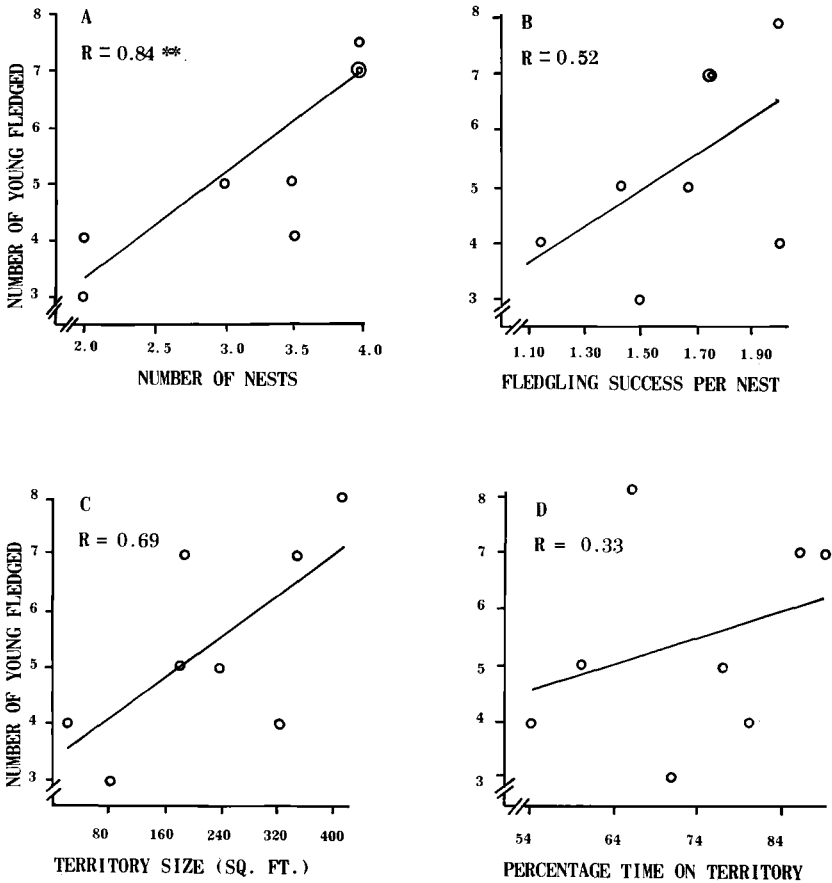
Figure 4. Regression of fledgling success on various territorial activities of 8 *C. mexicanus* males. R, linear product-moment correlation coefficient; **, significant at the 1 percent level.

WW not included because of his abnormal behavior), a multiple regression analysis was performed. The number of fledglings was used as the dependent variable, while territory size, percentage time spent on the territory, average number of flights per hour, average number of songs per hour, average song duration, and median number of terminal phrases per song were treated as independent variables. The extremely high regression coefficient obtained (R = 0.99) should not be considered as significant, because R approaches unity as the number of independent variables approaches sample size, even though the variates are uncorrelated (Morrison, 1967).

As breeding success is the ultimate measure of fitness, fledgling pro-
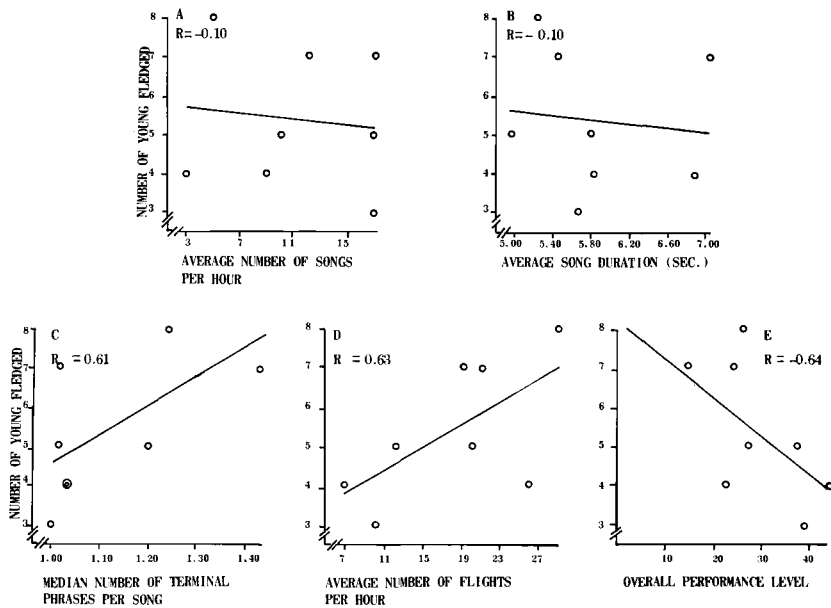
Figure 5. Regression of fledgling success on various activities of 8 *C. mexicanus* males. R, linear product-moment correlation coefficient.

duction can be used, in the absence of data on the ultimate destiny of the offspring, to illustrate the selective advantage of one male over another. As discussed by Fisher (1958), female responsiveness to the morphological and/or behavioral characteristics that reflect the fitness of males must be under strong selection pressure, because females mating with more successful males will leave offspring that are more fit on the average than those resulting from matings with less successful males. Behavioral characteristics of

TABLE 2
VARIATION IN AVERAGE PERFORMANCE LEVEL OF MALE TERRITORIAL
ACTIVITIES PER LOCALITY

|	Colony A 1–9 April	Colony B 10–15 April	Colony C 18–30 April
Number of males	3	2	3
Number of young fledged	5.3	6.0	5.0
Number of nests	3.7	3.5	3.7
Territory size (square feet)	307	188	176
Percentage time on territory	75	83	63
Average number of flights/hour	22	17	15
Average number of songs/hour	14	11	8
Average song duration (seconds)	6.21	5.20	5.93
Median number of terminal phrases/song	1.22	1.01	1.09
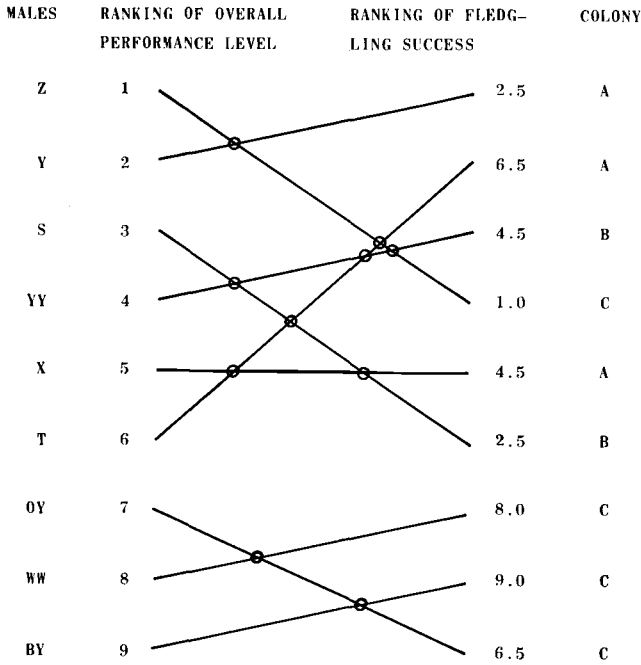
Figure 6. Relationships between overall performance level and fledgling production of 9 adult *C. mexicanus* males. Overall performance level per individual refers to the sum of the ranking values for each item used in the comparison of the males' territorial activities.

males most effective in influencing a female's choice of a mate should be correlated with reproductive success. By comparing various behavioral parameters with the number of young fledged per male, it should be possible to determine the relative importance of features that might operate in this regard. The separate linear regressions of the number of young fledged on each category, with the exception of those referring to male WW, are illustrated in Figures 4 and 5. Note that only number of nests shows a correlation above the 5 percent significance level.

Figure 6 demonstrates the fact that the males considered to be dominant at the three different breeding colonies, males Z, S, and YY, are high in the ranking of overall performance level, as well as fledgling success. It also appears as if the males that breed later in the season are of lower rank, but this may partly result from a general change in behavior through time. Obvious decreasing trends, for instance, are apparent for territory size and the average number of songs and flights per hour over the 1-month period (Table 2). In the case of the former, added pressure probably results from

newcomers that establish territories, while the decrease in the number of songs and flights per hour presumably relates to the lesser amount of visual and vocal stimuli provided by the breeding females.

DISCUSSION

Darwinian theory, as modified and developed by Lack (1954, 1966, 1968), holds that natural selection favors those individuals that contribute the greatest number of individuals to the next generation. Reproductive rates of any species or population will therefore tend to represent the maximum effort possible under the average prevailing conditions. As discussed by Orians (1969), it is also generally accepted that in birds, females select mates from among available males.

Polygamy will always be advantageous to a male whenever the successful offspring from all its mates outnumber those that can be produced in a monogamous mating (Figure 4A) even though this may result in lowered reproductive success per nest. In order to be selected for, polygamy must also result in the greatest reproductive success for individual females. A "polygyny threshold" theory has been developed, which contends that differences in the productivity and suitability of males' territories may be sufficient to permit the rearing of more offspring on the better territory, even though this involves the reduction of a male's assistance in rearing the young (Verner, 1964; Verner and Willson, 1966; Willson, 1966). Thus in species where the breeding territory provides a significant proportion of the food for the young, females presumably select males primarily on the basis of territorial quality.

Among promiscuous grackles, however, the territories of males are small and function mainly to provide a nesting site and a space where copulation can occur without interference from rival males. Although territories remain more or less fixed for periods of at least several weeks, resident males may also leave their territories when all females are caring for the young and no longer offer opportunity for mating. Furthermore as polygamous and promiscuous mating systems are especially common in regions where food productivity is high (Verner and Willson, 1966), females alone can readily find enough food for the young. It can thus be expected that the genetic quality of a male *per se*, reflected in the relatively large difference in the number of vocalizations between the sexes as well as the high degree of sexual dimorphism, is more important in mate selection than the quality of his territory, even though the higher correlation between territory size and number of young fledged (Figure 4C) indicates that the two factors are probably interrelated.

As grackles have a nonmonogamous mating system, those males that spend most of their time displaying and vocalizing at breeding colonies are

likely to acquire more mates (nests) and raise more young, at least to the fledgling stage, than their companions. Thus selection will favor continued advertisement for additional mates to an extent that it is selectively disadvantageous for males to devote time to nesting activities or caring for the young (Verner and Willson, 1969). As it is of no advantage to a male if other males successfully inseminate his potential mates, the low correlation between percentage time spent on the territory and ultimate nesting success of individual males (Figure 4D) can be attributed to the fact that they guard the females from the advances of rival males by accompanying them on their trips in search of nesting material and food.

Contrary to the abrupt ending of song upon pair formation in most monogamous bird species, the frequency of singing of male grackles remains fairly constant long after the first copulation has been achieved. This is consistent with the view that, in a polygamous or promiscuous mating system, the males continue to advertise in order to enhance their chances of attracting additional females or of raising second broods. Yet rather surprisingly, average song rates per hour and average song duration show a negative correlation, if any, with fledgling production (Figure 5A–5B). Verner (1963) similarly found an inverse relationship between frequency of singing and pairing success in the Long-billed Marsh Wren (*Telmatodytes palustris*), and interpreted it in terms of a balance between available time and energy. Among grackles, the relationship shown between full song and fledging success may perhaps be due to the strong aggressive motivation of full song as indicated by its frequent occurrence and relative importance in competing bouts between males as well as in other hostile situations. In this regard, average rate of solicitation calls per hour, which indicates a male's interest and readiness to mate, may provide a better measure of breeding success.

Of all the different vocalizations or parts thereof, the median number of terminal phrases given per song shows the highest correlation with number of young fledged (Figure 5C). As this phrase is the loudest sound in the vocal repertoire of grackles, its far-carrying capacity is probably extremely effective in luring females to the male, and consequently in increasing the probability of obtaining matings. The fact that male WW was able to attract and copulate with a female, even though he never gave full song (mostly just the terminal phrase—Table 1) and could not keep females in his territory for long, tends to support this idea. Those males that are aggressive in territorial defense and show strong sexual responses, indirectly reflected by their flying activities, have a somewhat greater likelihood of leaving the largest number of progeny in an average season (Figure 5D).

Although some items of territorial behavior closely approach the 5 percent significance level, no specific behavior pattern of male grackles can be

singled out for a meaningful association with nesting success. Instead, behavior expresses the interaction of a variety of selective forces imposing contradictory demands on the individual. From the above discussion, it therefore becomes increasingly evident that those males with an optimal balance of factors, the dominant individuals, will be the most successful in breeding and will leave on the average the most surviving offspring.

SUMMARY

An attempt was made to determine the relationship between ultimate breeding success and various behavioral characteristics of male Boat-tailed Grackles. While none of these variables could be singled out for close association with nesting success, apparently those males with the optimal balance of factors tend to be the most successful breeders.

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