COLONIAL NESTING BEHAVIOR OF COMMON GRACKLES

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ABSTRACT

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By

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Colonial nesting is a common feature of the breeding biology of blackbirds, Icteridae. While the Common Grackle (*Quiscalus quiscula*) often nests in groups it may be nest-site limited rather than actively colonial. This investigation addresses the questions: Is this bird nest-site limited? Are any of its display behaviors contagious? Are any of its nesting activities synchronized? The questions were examined in three locations in central Michigan. One of these, the Michigan State University campus, was the site of an intense study of grackle biology in the 1950's and census data from the two studies are compared. In addition, I undertook a study to determine techniques for sexing nestlings based upon external measurements.

Colony groups were observed during the pair formation and nest-building periods. Data were taken concerning the relationship of group size and song-display behavior, nest-site choice, and date of beginning nest building. Seventy nestlings were collected at known ages and wing, tail, tarsus, culmen, innermost primary, and weight measurements were taken. Sex was determined by internal examination of the gonads.

Paul Bernard Hamel

These studies reveal that the Common Grackle is actively colonial. Song-display behavior in groups of grackles is contagious. It stimulates a synchronization of beginning nest building by the females. Nest-site choice is also affected, the modal site within colonies being the site first chosen, independent of relative availability of the sites. The census data showed that nest sites were not in limiting supply at the time of either the 1952 or 1971 census, but that the population has increased six-fold in the interim. Partial reasons for the increase are an increased availability of nest sites with new ornamental plantings of conifers and a decrease in competition for sites with Robins (*Turdus migratorius*).

Tentative criteria for sexing based upon Tarsus and Culmen measurements of 11- and 12-day old young are presented. The possible significance of a previously unrecorded series of three color phases is discussed.

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INTRODUCTION

Coloniality holds a prominent place as a breeding regime among the New World blackbirds, Icteridae. The practice is well documented for the oropendolas (*Psarocolius*) and caciques [*Cacicus* (Skutch, 1954; Chapman, 1928; Schafer, 1957; Dunham, 1971; Meyerreicks, 1958)], southern grackles [*Quiscalus* (McIlhenny, 1937; Tutor, 1962; Selander, 1965; Selander and Giller, 1961)], Brewer's Blackbird [*Euphagus cyanocephalus* (Williams, 1952; Horn, 1968, 1970)], marsh blackbirds [*Agelaius* (e. g. Orians, 1961a, 1961b)], and sometimes even certain orioles [*Icterus* (Thomas, 1946; Dennis, 1948)]. The Common Grackle (*Quiscalus quiscula*) has repeatedly been called colonial (Gibbs, 1903; Peterson and Young, 1950). However, nest-site limitation is a viable alternative explanation for a clumped pattern of nesting in this species. Shrubby marshes and swamps, the grackle's original habitat, have been drastically reduced, forcing adaptation to other nesting sites; clumped plantings of ornamental conifers have thus become favorite alternative sites (Gibbs, 1903; Bent, 1958).

This study is an attempt to ascertain whether breeding aggregations of Common Grackles are colonies in the sense developed by Horn (1970) or are functions of a patchy distribution of nest sites. Factors that must be accounted for in the evaluation of colonial status are the general social structure of groups of birds which involves possibly contagious behavior, and nest dispersion in time as well as in space. Consideration must be given to the background noise variables, age of nesting birds in the group, and the effect of nest-site availability on nest dispersion.

A census was taken of the grackle population in a 3.5 square mile area around the Michigan State University campus to identify changes that may have occurred in the population since the 1952 census by Eyer (1954). A study was also made of nestlings to determine criteria for sexing birds of known age, to complement and evaluate an earlier scheme by Willson et al. (1971).

STUDY AREAS

This study was carried out in the months of March to July in the years 1968, 1970, and 1971 in three locations in Ingham, Kent, and Shiawassee counties, Michigan.

In 1968, I censused the breeding birds in a 1.3 acre buttonbush swamp called Manhattan Marsh. (T.6N., R.11W., 1/4 mile from Reed's Lake, 42°50'N, 85°30'W, East Grand Rapids, Kent County, Michigan) The swamp was bordered by landfill areas to the north and east, an old field to the south, and a road to the west. Water depth in the swamp varied but was never more than 1.5 meters. Two pools in the northwest and southwest sections were deeper than the eastern edge and an east-west strip between the pools. The dominant plants are buttonbush (Cephalanthus occidentalis) which occur chiefly in areas where the water is 0.5 meters or more deep, cattails (Typha latifolia) in areas where the water depth is 0.5 meters or less, and several large black willows (Salix nigra) which are located along the southern and northwest edges of the swamp. All 30 active grackle nests were placed in buttonbushes.

In 1970, a breeding bird census was conducted in a wet second-growth forest at the Rose Lake Wildlife Research Station. (T.5N., R.1E., 42°40'N, 84°20'W, Section 21, Shiawassee County, Michigan) The dominant plants in the 20-acre area are quaking aspen (Populus tremuloides) which covers approximately the southwest quarter with a very dense 15 to 30 foot tall forest, willows (Salix spp.) which form a dense, shrubby cover in the southeast and northeast sections and along the banks of a stream on the northern edge of the area, and spruce (Picea spp.) and red pine (Pinus resinosa) planted in rows in the center. The area is bordered to the east and north by roads, to the south by a controlled wetland, and to the west by an old field. The 30 grackle nests in this area were all located in conifers. A similar breeding census was conducted in 1971 in the same Rose Lake area but more emphasis was placed on a detailed study of the grackles and less on other species. The 16 grackle nests were placed in the conifers.

Also in 1971, a count was made of the breeding grackles on the Michigan State University campus. This is part of the area previously censused by Eyer (1954). Due to limitations in time and the abundance of the grackles, the area censused in 1971 was decreased from 12 to 3.5 square miles which mainly includes the central university campus and some surrounding farmland. (T.4N., R.2W., 42°40'N, 84°20'W, East Lansing, Ingham County, Michigan) The campus now is primarily landscaped and extensively planted with ornamental shrub and tree species from temperate areas throughout the world. Shrubby swampland no longer exists in the area although a small cattail swamp still remains north of the railroad tracks. Figure 1 shows the area and both 1952 and 1971 colony sites. Most of the 151 grackle nests in the censused area were built in conifers; the rest were located in man-made structures.

METHODS AND MATERIALS

From the middle of March until the second week in April, 1971, during the pair formation and early nest-building period, data were collected concerning the relationship of group size and the intensity of breeding activities. Group size and the number and type of vocalizations occurring within five minute observation periods were recorded. All observations were made before 10:00 EST. Vocalizations were broken down into two categories based upon the presence or absence of responses from other birds. The display vocalizations used as major components in this breakdown were the Ruff-out Squeak (ROS) of the male, and the Ruff-out Chuga (ROC) of the

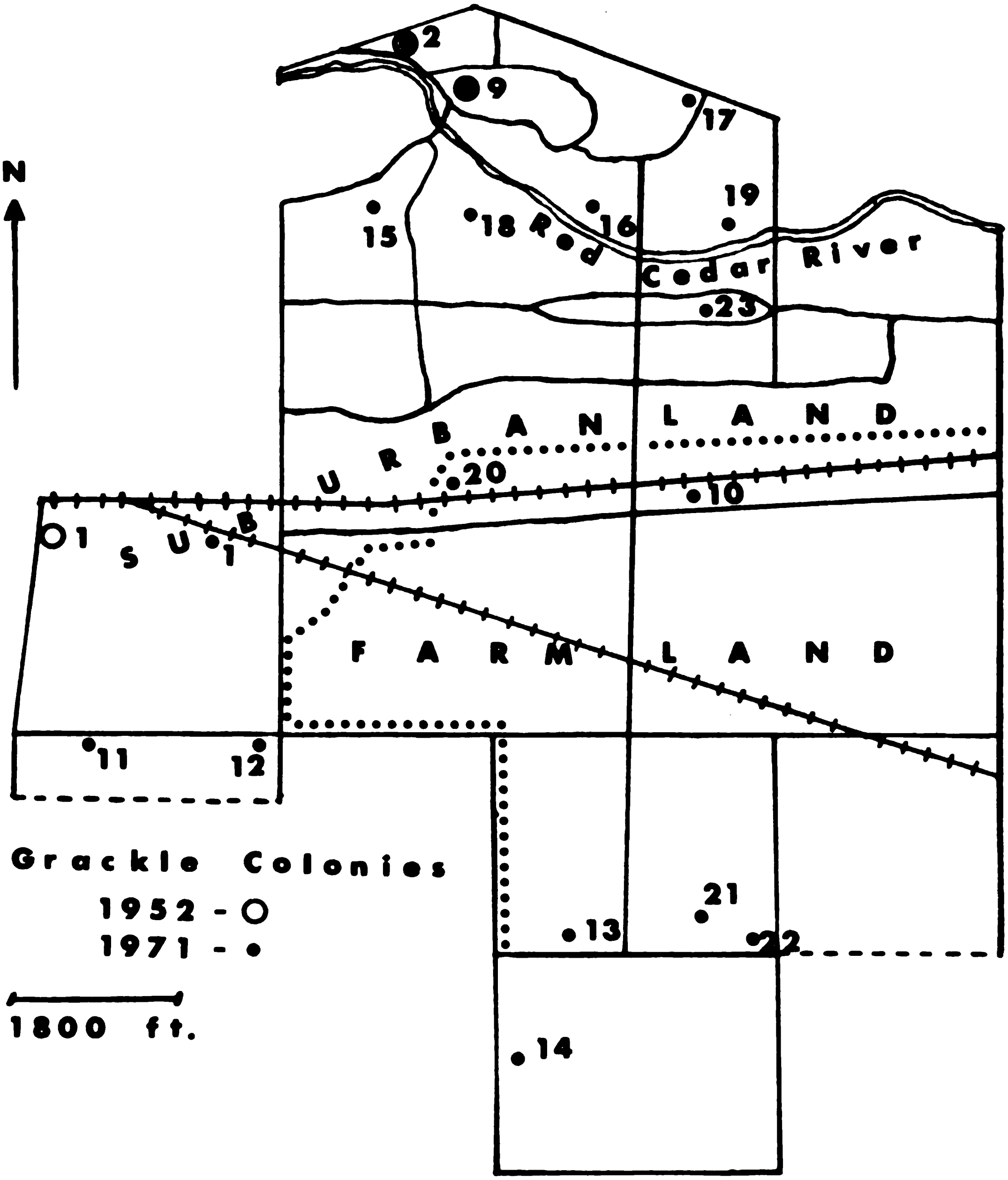

Figure 1. Locations of nesting colonies of Common Grackles, East Lansing, Michigan. None of the 12 solitary nests is shown.

female (Ficken, 1963). The categories paired the ROS or ROC with two possible response alternatives, a situation in which a response was given by another bird and a situation where no bird responded to a particular vocalization. The recording technique necessitated that many ROS's or ROC's be recorded twice, once as a stimulus and once as a response, if the vocalization was part of more than one sequence. Regression analysis (Sokal and Rohlf, 1969, pp. 420 ff.) is the appropriate technique for testing the relationship between these variables. A colony was defined as more than one pair of grackles. Distance between nests was usually less than 50 feet, but at times was as great as 220 feet. Nests in the Manhattan Marsh and Rose Lake areas were visited daily in 1971, and two or three times weekly in 1968 and 1970. Nests in the censused area in East Lansing were visited at most two or three times during the 1971 nesting season and often only once. As is the case with Eyer's (1954) census, I attempted to census only breeding birds, not the entire population, so any non-breeding surplus escaped notice.

Nests located during the building stages were followed especially closely. Table 1 gives the length of time required by a female to build a nest, lay her eggs, incubate them, and rear the young to fledging. Data from Eyer (1954), Peterson and Young (1950), Bent (1958), and Schaller and Emlen (1961) were used in addition to my own in compiling this table. From available information about a particular nest, I used this table to estimate the date when that nest was started. Names

Table 1
Time Table of Common Grackle Reproduction

Stage of Cycle	Length of Stage			Cumulative Days
Platform	1[a]	3.1[b]	3[c]	1
Outside Cup	2.5			4
Mud Cup	2	3	2	6
Lining	3	2.4	2.1	8-9
Wait	2.8	3.6	2.1	12
Egg Laying	4-5	4-5	4-5	16-17
Incubation	12.7	----	12.9	30
Hatch to Peeping	0-3	----	----	33
Peeping[e]	4-8	----	----	34-38
Crouching to Visual Stimuli	8-12[d],13	----	----	38-42,43
Screeching or Squawking[e]	9-12,13	----	----	39-42,43
Fledging to Leave Area	----	2-3	----	45,46

Data from: a - Eyer (1954); b - Peterson and Young (1950); c - this study; d - Schaller and Emlen (1961).

e - These references to sounds made by the nestlings include only sounds audible for distances of 30 to 50 feet or more. "Screeching or Squawking" is the same as the "location call" of various authors.

of nest-building stages are those of Eyer (1954), but not the parallel ones of Peterson and Young (1950), or Holcomb and Twiest (1968), which have been adjusted for presentation in the table. In many cases a nest was determined to have been started between two dates, as much as two weeks apart in cases where only one observation was made during the incubation period. In all cases the nest was assumed to have equal probability of being started on any day during the interval. Mean starting dates for each colony and the population as a whole were computed from these data with days during the nesting season numbered consecutively (April 1 = 1, May 1 = 31, etc.). A variance of nesting dates was computed for the entire population and for each colony based only upon those nests for which the starting date was known with ± 1 day. Mean colony nesting dates and variances were tested against the total population estimates to determine the extent of any significant deviations, using Student's t-test and the F-test respectively.

This procedure differs from that of Horn (1970) in that the statistical variance is used as a measure of the temporal closeness of nestings in a colony, and all nests in a colony area are included as part of that colony. By excluding late nesting individuals a large number of the younger birds would be eliminated from consideration as members of a colony to which they really belong. The difference in the methodology is based primarily on the use of dates of beginning nest-building for the data set in this study as opposed to the dates of beginning egg-laying in Horn's study (1970). Horn believes that invalid results may be obtained by using the variance of nesting date within a colony as the measure of synchrony unless a population variance canbe used for comparison. Part of the purpose of conducting the 1971 census was to provide a population against which the synchrony of a certain colony could be tested. If the variance within a colony is significantly less than the variance of the population as a whole, the evidence favors social interactions synchronizing nest-building behavior. If the colony variance is not significantly different from that of the population, it is an accurate predictor of population variance. Thus colony members are not having a synchronizing effect on each other because they are no more synchronized than the entire population.

Following the same reasoning, there will be occasions when the mean nesting date for a colony is significantly earlier or later than that of the population of which the colony is a part. In these situations, a cautious statement can be made about the age structure of the colony. If the colony nests earlier than the population, it is composed primarily of older birds, and if it nests later, it is composed of younger birds. Selander and Hauser (1965) found that in the related Great-tailed Grackle (Quiscalus mexicanus) first year females breed later than older adults. Gonadal maturation of first year males also occurred later than that of the adults, although they do not breed. Common Grackles of both sexes breed in their first year. Assuming the same situation is true for Q. quiscula, an earlier nesting colony will be composed primarily of older birds, and a later nesting colony will consist mainly of first year birds.

The nest site itself was catalogued for each nest as to location and type of site, i.e. mainly genus, but in some cases species of plant, or man-made structure. For each colony, an estimate of the number of potentially available nest sites was also determined, based on a one tree : one nest theorem. Since more than one nest may be placed in a single tree, these estimates are conservative ones. Unfortunately, a light meter was not available to measure the threshold density of vegetation necessary before a tree might be used as a site.

The relationship between available sites and sites selected, noted by tree genus or species, was tested using Fisher's Exact Test or a G-test for independence in R x C contingency tables (Sokal and Rohlf, 1969, pp. 59 ff.). These very easily performed tests involving the functions $Y = \log f!$ and $Y = f \ln f$ respectively are superior to χ^2 tests especially for my purposes. Only colonies where more than one site was available were tested.

Eggs were marked with nail polish in the Rose Lake colony in 1971. Young birds were individually marked on the foot or tarsus, using a black felt-tip marker during their early nest life. The felt-tip marker is preferable to nail polish for marking the young because it is easier to apply, lasts just as long, and dries much more quickly, which prevents the young bird from rubbing the marker all over itself. Birds were ringed with U. S. Fish and Wildlife Service aluminum bands after the eighth or ninth day in the nest, and color-banded with plastic leg bands on the 11th or 12th day of nest life. On each visit to the nest the young were weighed in grams, and on most visits the wing, tail, tarsus, culmen, and the innermost primary (No. 1) on the right wing were measured in millimeters. The wing measurement was taken from the bend of the wrist to the tip of the manus in young birds, and to the tip of the longest primary in older nestlings, the tail from its base on the pygostyle to the tip of the longest central rectrix, the tarsus from the center of the tibiotarsal joint to the last undivided tarsal scute, the culmen from the tip to the posterior end of the cornified area, the innermost primary from its projection through the skin to the tip. In addition, the per cent of this primary length taken up by the erupted feather was recorded. Weights were taken with a Pesola 100 gm. x 1 gm. division scale obtained from Bleitz Wildlife Foundation, Hollywood, California.

Seventy nestlings collected for sex determination contributed significantly to a near 100% mortality at the Rose Lake colony in 1970. The birds were taken in either the 9th, 10th, 11th, or 12th day of nest life. Sex was determined by internal examination of the gonads and the same measurements were taken on these specimens as on the living nestlings. Most of the specimens were deposited in the Michigan State

University Museum as spirit or skeletal material. The remainder were given to the Grand Rapids, Michigan Public Museum as skeletal material.

RESULTS AND DISCUSSION

Changes in the East Lansing Population

Eyer's (1954) census of the East Lansing population was taken in May, 1952. He found 74 nesting paris, 72 in nine colonies and two solitary, in a 12 square mile area. (Because his paper will be referred to often for comparison with the present census, it will not cited every time.) My 1971 census was limited to a 3.5 square mile area in the center of Eyer's census tract (Figure 1). I found 151 nesting pairs, 139 in 17 colonies and 12 solitary pairs. The 1952 grackle population in the 1971 census area was 24 pairs in three colonies and no solitary pairs. Both of these censuses are conservative estimates of the actual population, since nonbreeding pairs may have been missed in the 1952 census, and some early nesters had already finished before the 1971 census was complete. Most nests, both colonial and solitary, were located in coniferous trees of nine or more different species. These included several different species of spruce (*Picea*), red or Norway pine (*Pinus resinosa*), white pine (*P. strobus*), Austrian pine (*P. nigra*), several species of fir (*Abies*), Scot's pine (*Pinus sylvestris*), juniper (*Juniperus* spp.), Arborvitae (*Thuja occidentalis* and some ornamental *Juniperus*), Japanese red pine (*Pinus densiflora*), and Ponderosa pine (*P. ponderosa*). Of these potential sites the Austrian pine appears to be the most favored kind of tree, with the others selected about equally as nesting places if *P. nigra* was absent. Certain ornamental *Juniperus* species are very similar in color and texture to the *Thuja occidentalis*. In the analysis that follows these are included as "Arborvitae" rather than as "Juniper". Numbers in the following discussion indicate the number of the colony in Figure 1 and Tables 2, 4, 5, and 6. Table 2 presents a comparison of the two censuses.

Three of the 17 colonies discovered in 1971 were used in 1952 as well. Two of them, colonies No. 2 with 23 nests and No. 9 with 11 nests, are essentially the same now as they were before except that the trees used for nesting are larger. Each contained nearly twice as many nests as in the previous study. The third colony, No. 1, where Eyer carried out much of his detailed work, was a marsh in 1952, but has since been filled along the eastern edge and a superhighway occupies the central and western portions of it. This colony, which has switched from a marsh to a suburban nesting habitat, is the same size as during the earlier study.

Colony No. 14 was composed of ten nests, all in the same Austrian pine. It is the only potential grackle nesting site in a quarter-square-mile area. The closest potential site was an occupied pine, the only nest in a pine at Colony No. 13. This coincidence may indicate that the tree was saturated, as discussed in greater detail later.

Table 2

Common Grackle Breeding Population in East Lansing, Michigan

Colony	Breeding Pairs	
	1952[a]	1971
1	6	6
2	12	23
9	6	11
10	NE[b]	14
11	NE	3
12	NE	10
13	NE	10
14	NE	10
15	NE	6
16	NE	11
17	NE	11
18	NE	3
19	NE	4
20	NE	2
21	NE	7
22	NE	5
23	NE	3
Loners - no.	0	12
" - %[c]	0	8.1
Total - colonies	3	17
" - pairs[d]	24+5	151+10
Mean colony size - pairs[c]	8.0	8.5
Density - Birds/mi^2	13.7	87

a - data from Eyer (1954)
b - Nonexistent
c - differences not significant ($p>0.05$); other pairs of items not tested
d - includes estimate of suspected error

The nine pairs at Colony No. 16 and three pairs at Colony No. 23 were the only grackles in the census area not nesting in coniferous trees. The nests were placed in open-air concrete parking ramps. These colonies provided the only examples of the minimum internest distance tolerated by female grackles. As with many other colonial Icteridae (Chapman, 1928; Skutch, 1954; Schafer, 1957; Orians, 1961b; Selander, 1965) the female defends an area around the nest. Once, at each ramp, a female started building a nest too close to an already active nest and was unable to finish building in one case (internest distance 10 feet, Colony No. 23), or to lay any eggs in the other case (internest distance three feet, Colony No. 16). These colonies also provide the only cases I know about where an entire nestful of young starved in spite of both parents being present. This was true of both active nests at Colony No. 23 where no young fledged from the colony. All the young of one nest at Colony No. 16 also starved, perhaps because of predation on the parents although that seems unlikely. The young at Colony No. 23 were emaciated, weak, and small for their age. A possible cause of death in a high-use parking ramp is carbon monoxide poisoning, but as many nests in Colony No. 16 fledged young successfully, I discount this as a mortality factor.

Twelve pairs of grackles (8.1%) nested solitarily in 1971, an increase of 5.4% over Eyer's figure. This increase is not significant and thus gives little insight into the mechanism maintaining or retarding the occurrence of solitary nesting. This feature of grackle biology deserves further study. All isolated nests were located in coniferous trees, about equally divided between sites potentially available in 1952 and those that were unavailable at that time. Not all sites were isolated either, as nests were located in extensive borders of pines planted around parking lots as well as in single trees.

The supporting vegetation for five of the 17 colonies occupied in 1971 was present in 1952. These areas account for 85 of the 151 nesting pairs (56% of the current population) which is an increase of 61 pairs (253%) over the earlier figure for the same area. An increase in the number of available nest sites has probably been a factor in the increase of the population. This involves more sites within single trees as they grow, and new sites made available with the construction of suitable buildings and new plantings of trees. A further factor in the increase of the grackle population may be the severe reduction in the Robin (Turdus migratorius) population on the Michigan State University campus following pesticide applications for Dutch elm disease control in the mid-1950's and later (G. J. Wallace, pers. comm.). As Robins and Common Grackles compete for nest sites at times (Hamel, MS) a reduction in the Robin population would make additional nest sites available to the grackles. Conifer plantings made between the two censuses allowed 66 pairs, 269% of the original population, to breed in 1971. An increase in the nest sites available for a population creates a potential for increased production of young (Haartman, 1956) which must be taken into consideration when trying to pinpoint regulating mechanisms for a bird population. The evidence presented here indicates that nest sites were in excess of number needed at the time both censuses were made of the grackle population in East Lansing. The site is thus normally a minor factor in controlling population size in grackles in suburban areas, although the case in swamps is not yet settled. The existence of an excess of nest sites must be verified before other potential regulating mechanisms can be tested. When sites are limiting, as probably occurred in 1971 at Colony No. 14, the effects of other factors will be obscured.

Social Stimulation of Breeding and Nest-Site Selection

The group has been considered as having a stimulatory effect on individual members of bird aggregations, both behaviorally and physiologically (Lehrman, 1959; Crook, 1961; Orians, 1961b; Selander, 1965; Selander and Hauser, 1965). Austin (1951) has documented group tenacity in breeding Common Terns (*Sterna hirundo*) and Horn (1970) has diagramed social interactions among Brewer's Blackbirds. Darling (1938) claimed that group interactions produced early mean nesting dates and nesting synchrony in gull colonies. Coulson and White (1956, 1960) have since discounted Darling's findings by showing that in the kittiwake (*Rissa tridactyla*) age of breeding birds is the variable responsible for the observed effect. As is the case with the kittiwakes, young Great-tailed Grackles breed later than the adults (Selander and Hauser, 1965). Circumstantial evidence indicates that this is the case in the Common Grackle as well. In testing whether the behavior of a group of birds is stimulating individuals to synchronize some aspect of their breeding biology, it is necessary to examine the null hypothesis that there is no synchronization at the point in the breeding cycle when the contagious behaviors are most apt to be effective. That part of the cycle most appropriate for this test will vary from one species to another. In the Brewer's Blackbird, it is contagious precopulatory display by the females (Horn, 1970), and in the Common Grackle group song-display behavior is the synchronizing feature, as a short review of the phenology of the species' reproductive activities shows.

Grackles arrive on the breeding grounds in the central Michigan area in early or mid-March but do not begin nest building until the first or second week in April (Eyer, 1954; Bent, 1958). In the intervening weeks, members of a group or colony spend much of the day as a single large group or as several smaller ones in the area where the colony will be located. Pair formation occurs mainly during the earlier part of this period. Females are chased by males in the leader flights described by Ficken (1963), and the level of aggression, especially on the part of the males, is very high. Supplanting often occurs during these flights, one male aggressively taking the position directly behind the female. Head-Held-Ups (Ficken, 1963), or bill pointing (Eyer, 1954), as the display has been variously called, are very common when birds meet each other on perches, especially among the males. This display of sleeking the feathers and pointing the bill vertically upward is the generalized aggressive display of this species and perhaps serves that function among other icterids as well. As the pair formation period progresses and more birds become paired, the group begins examining various trees and shrubs in the area for their acceptability as nest sites. Commonly, the male(s) will station himself at the top of a tree and the female(s) will disappear into the foliage of the conifer or branches of the shrub where a nest might be placed. After a period of a few seconds or minutes, the pair or pairs will move to another tree and repeat the process. This activity serves to acquaint the members of a colony with the suitable sites where the females will build and the suitable points available to the males as lookout posts (Eyer, 1954). Similar kinds of exploratory activities have been noted in female American Redstarts (*Setophaga ruticilla*) as they seek out nest sites (Ficken, 1964). At times the males grackles themselves become involved in nest site evaluation, building "dummy" nests in various places (this study; Eyer, 1954; Peterson and Young, 1950). The dummy nest usually consists of a handful of dead blades of grass entwined around the twigs at the site, and is easily differentiated from actual nests in the "platform" stage. Females do not use the flimsy materials for the base of their nests that the males use in constructing the dummy nests. Data concerning the influence of a male's dummy nest on his mate's choice of nesting site are nonexistent. The nest is not always built atop a dummy nest because dummy nests are found that have not been used as bases for actual nests. The extent to which males participate in dummy nest building is not known. If many such nests are used as bases for actual nests, an observer would be unable to gauge the occurrence of the practice by simply counting dummy nests after nest-building. This study does not demonstrate a direct role for the male grackle in nest-site choice.

During the pair formation and nest-building periods, the birds are very often singing. The male's song-display is the Ruff-out Squeak (ROS) and the female's is the Ruff-out Chuga (ROC). The members of a pair keep in contact with each other by duetting, the male giving an ROS and the female responding with an ROC (Ficken, 1963). Group size tends to be larger in the pair formation period than during the nest-building period. Table 3 demonstrates this. The difference in frequency of occurrence of the group size N = 4 is enough to explain the significant interaction between group size and period of the nesting season. This is understandable since the female spends more of her time building the nest then and has less time available for the group. Because the females spend less time with the group after nest-building has begun, they have less contact with the potentially contagious behavior of the group. Thus, the place to look for any

Table 3

Frequency of Group Size *vs* Stage of Nesting Cycle

Stage of Cycle	Group Size								
	1	2	3	4[b]	5	6	7	>7	Total
Pair Formation	180	192	113	172	43	13	9	25	747
Nest-Building	112	171	61	40	21	13	4	7	429
Totals[a]	292	363	174	212	64	26	13	32	1176

a - the probability of this distribution occurring by chance <0.005.
b - this column contributes the major portion of the deviation.

synchronizing stimulation is in the group before nest-building begins, and the effects of stimulation, if it occurs, should be seen in the phenomena associated with nest-building. Further synchronization may occur at later times in the cycle, but in order to demonstrate that the colony is a dynamic grouping, a synchronization need only be shown at one point in the cycle.

The intensity of singing behavior, as measured by the number of ROS's or ROC's eliciting responses in a group of known size during a five-minute period, is the potentially contagious behavior most easily quantified in groups of the Common Grackle. As both the ROS and ROC consist of a display posture as well as a vocalization (Ficken, 1963), they can be stimulating both visually and auditorily. A bird that cannot see the other displaying in the group can nonetheless hear it and respond on the basis of the auditory stimulus. Grackles may respond to an auditory stimulus only as well as to the audio-visual stimulus of a display. A female building her nest in a tree apparently will respond just as quickly to her mate's song when he is on the ground and she cannot see him as she does when both are sitting close together in a tree. The display behavior may be contagious as indicated by the observation that when one of four or five birds sitting together in a tree displays, the others follow suit, one after the other. The appropriate test of the hypothesis that display behavior is contagious is a regression of vocalization pairs against group size. If the relationship is linear, the inference is that each bird contributes a certain amount of display irrespective of group size. In such a case, the behavior is not contagious. If the relationship between group size and vocalization pairs is non-linear, i.e. quadratic or higher order, then the inference is that the individual bird is stimulated to contribute a greater amount to the interactions of the group as the group increases in size. Figure 2 shows the regression of the square root of the vocalization pairs against group size. This regression explains more than 99.9% of the variation in the data, indicating that the relationship between vocalizations and group size is non-linear, and that the display behavior within colony groups of grackles is definitely contagious.

The hypothesis that social stimulation will have a synchronizing effect on some aspect of breeding biology readily follows upon a determination of contagious behavior patterns in the group. In the Common Grackle the nesting behavior is the first breeding event following the pair formation period of group activity. This is the test behavior for examining whether or not synchronization occurs in this species. Table 4 presents a breakdown by colony of means and variances of nesting dates. Of the four colonies on campus where a variance could be computed, three of them were significantly more synchronized than the total population. Each of these colonies had a mean nesting date earlier than the total population, significantly so in the case of Colony No. 12. The

Figure 2. Regression of the square root of number of vocalization pairs on group size. $Y = 2.568 + 0.2304X$, $p < 0.001$.

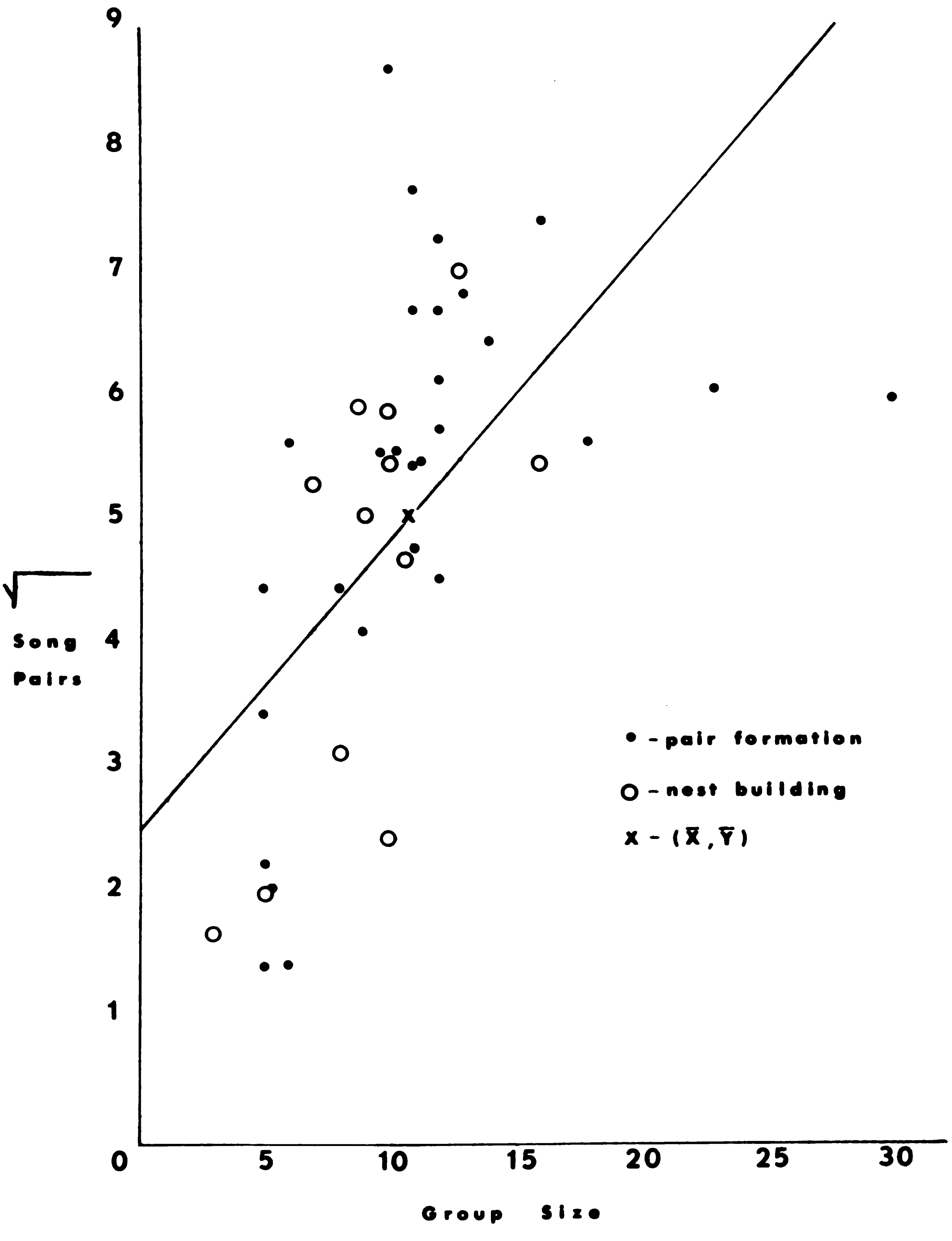
9
8
7
6
5
4
3
2
1
0
√ Song Pairs
5
10
15
20
25
30
Group Size
• - pair formation
O - nest building
X - ($\bar{X}$, $\bar{Y}$)

Figure 2.

Table 4
Colony Development in Common Grackles in Central Michigan, 1971

Colony	n	nesting date	df	s^2
1	6	26.33	--	--
2	23	8.40	--	--
9	11	20.35	--	--
10	14	9.0	6	44.62[a]
11	3	12.0	2	6.00[a]
12	10	10.62[c]	4	9.18[a]
13	10	21.14	6	600.25
14	10	--	--	--
15	6	13.75	--	--
16	11	23.80	--	--
17	11	22.0	--	--
18	3	10.33	--	--
19	4	18.12	--	--
20	2	8.5	--	--
21	7	5.14	--	--
22	5	20.25	--	--
23	3	23.75	--	--
24	12	19.12	--	--
Rose Lake, 1970	30	15.57	26	551.41[b]
Rose Lake, 1971	16	15.73	13	235.00[b]
Total, East Lansing	151	15.53	23	1568.16

a - These variance figures are significantly ($p<0.01$) different than the total population variance; b - these variances are not significantly different at $p=0.05$; c - this mean colony nesting date is significantly different than the population mean, $p<0.05$.

one colony where there was no significant synchronization had a mean nesting date later than the population mean. The fact that within-colony variances are less than the population variance demonstrates that the birds are synchronizing each other's nesting behavior. There is no reason to believe that environmental conditions over the area of the census were different enough to warrant consideration of this factor as the proximate one triggering within-colony nesting. The mean nesting date at the Rose Lake colony ten miles away from all the campus colonies was the same for two consecutive years even though 1970 was a normal year and 1971 was a dry year. Both mean dates were the same as the mean date for the East Lansing grackles. In addition, the colony means are not distributed along a discernible geographic gradient in the census area itself. The mean nesting date and colony variance data suggest that the late-nesting birds which I assume to be young birds (cf. Selander and Hauser, 1965) may be less efficient at achieving synchronized breeding than the adults. The techniques discussed in this paper provide the necessary tools for determining whether or not such an hypothesis is accurate.

The unique parklike atmosphere of the Michigan State University campus provides appropriate conditions to test the effects of this contagious behavior in yet another independent way regarding nesting. In several places where there was a nesting colony of grackles, there were several species of trees which offered a diversity of potential nest sites.

The literature concerning phenomena associated with choice of nest sites by the Common Grackle is an abundant and interesting one. Published records of nest sites include a great variety of locations, such as swamp shrubs, cavities in trees, deciduous and coniferous trees, Osprey (_Pandion haliaetus_) nests, beaver lodges, bird houses, and man-made structures (Attwater, 1892; Stockard, 1905; Cameron, 1907; Cahn, 1920; Youngworth, 1932; Lloyd, 1943; Axtell, 1955; Bent, 1958). However, one important point about nest-site choice is that the birds in a single area or colony are generally noted as all nesting in a single type of site (e.g. Golsan and Holt, 1914; Peterson and Young, 1950). Certain observers have noted that a colony may switch nest sites from one year to the next without changing colony location (Tracy, 1896; Peterson and Young, 1950). This switching phenomenon has also been noted in the Brewer's Blackbird (Dawson, 1923, p. 86).

Table 5 shows the sites available to and used by different colonies. In 13 of the 14 colonies recorded in the table, the modal nest site for that colony was the same as the site first chosen. In seven of these cases the modal nest site was not the same as the most abundant site. Due to the small number of nests in any given colony, it is difficult to perform G-tests for independence of site availability and site choice. Because of this factor and because of elimination from the testing of colonies containing trees with more than one nest, only six colonies could be tested for the

Table 5
Nest Site Choice in Central Michigan Grackles

Colony[a]	Nest Sites[c]								
	Spruce	Red Pine	White Pine	Austrian Pine	Arbor-vitae	Scot's Pine	Juniper	Button-bush	Rare Sites[d]
Manhattan Marsh, 1968								*many:30	8:0
Rose Lake[b], 1970	*180:29	200:1							
Rose Lake[b], 1971	*180:15	200:1							
1			40:0	3:1		*120:4			6:1
2	≥15:1	5-10:0	3:2	*6:20					
9	24:0	4:0	*11:8		1:0				5:3
10[b]	18:3	2:0			4:2	2:0	*12:9		many :0
12					10:2	*30:8			
13	80:9	*4:1							
15		*500:5	56:1			30:0			
17	52:2	19:1	4:1	*23:6			5:0		25:1
19	*5:3		1:1						
21	1:0	4:1					*8:6		
22	*8:5		14:0						

* - site where first nest in colony was placed; a - only colonies with more than one site available are included; b - significant interaction ($p<0.01$) between available sites and sites chosen; c - figures expressed as "available sites : sites chosen"; d - Fir, Black Willow, Tamarack, Hemlock, Ponderosa Pine, Japanese Red Pine, and unidentified shrubs fall into this category.

relationship of choice and availability of nest site. The results were mixed. Three of the colonies, Rose Lake in both years and Colony No. 10, show very significant interaction indicating that the birds are choosing the sites, i. e. that the nests are being placed in trees in some other fashion than as a function of the abundance of that tree. The other three colonies, Nos. 1, 12, and 13 do not show significant interaction. These results can rightly be questioned in the cases of colonies Nos. 1 and 13 because of a limited number of nests in Colony No. 1, and a very limited number of one of the nest sites at Colony No. 13, factors which interfere with the operation of the tests. Colony No. 12 yielded a valid test and the nests were indeed placed in that colony in proportion to their availability. There are two possible explanations of this result. Nest sites may not have been selected in that colony in any other manner than at random, or, the peculiar conditions of site availability masked out any choice behavior on the part of the birds. Despite this potentially negative result, the modal nest site, except for the aberrant case discussed below, invariably occurs in the site where the first nest was placed regardless of the relative availability of that site. This indicates that the contagion of display behavior carries over into a socially facilitated nest-site selection. Measurements of the spread of nests within colonies were taken for eight of the colonies (Table 6). In only Colony No. 13 was the first nest at a distance much greater than the average

Table 6

Placement of First Nest in Relation to Centroid of Colony

	< mean distance to centroid	Placement at mean distance to centroid	> mean distance to centroid
Colony	Rose Lake, 1970	14	13
	Rose Lake, 1971	16	
	2	23	
	21		

distance to the centroid, or numerical center of gravity, of the colony. Thus, not only was the first nest the trigger for site choice by members of the colony, but also this nest is close to the center of the colony as well with other nests being built around it rather than away from it.

Balancing the gregarious tendency of the females to build near to the first begun nest is the increased aggression built up by nesting close together, since the females defend their nest sites. Figure 3 presents the measurements of distance to nearest neighbor for the following seven colonies: Rose Lake, 1971, and colonies Nos. 13, 1, 14, 23, 16, and 21. As the internest distance is in most cases a function of the spacing of the sites the largest internest distances do not provide as much information as the minimum distances. It is in the latter case where the aggressive behavior of the birds becomes a factor in determining the spacing of nests. Eighty-six per cent of the nests sampled lay within 60 feet of their nearest neighbor, well within the range of potential visual and auditory stimulation by other birds. Three nests in the East Lansing population were unsuccessful because they were built too close to already active nests. Both of those built within five feet of an already active nest failed, and one of 13 built between five and ten feet of the nearest nest also failed. From these data a rough estimate of five to ten feet can be made as the minimum distance defended around a nest site.

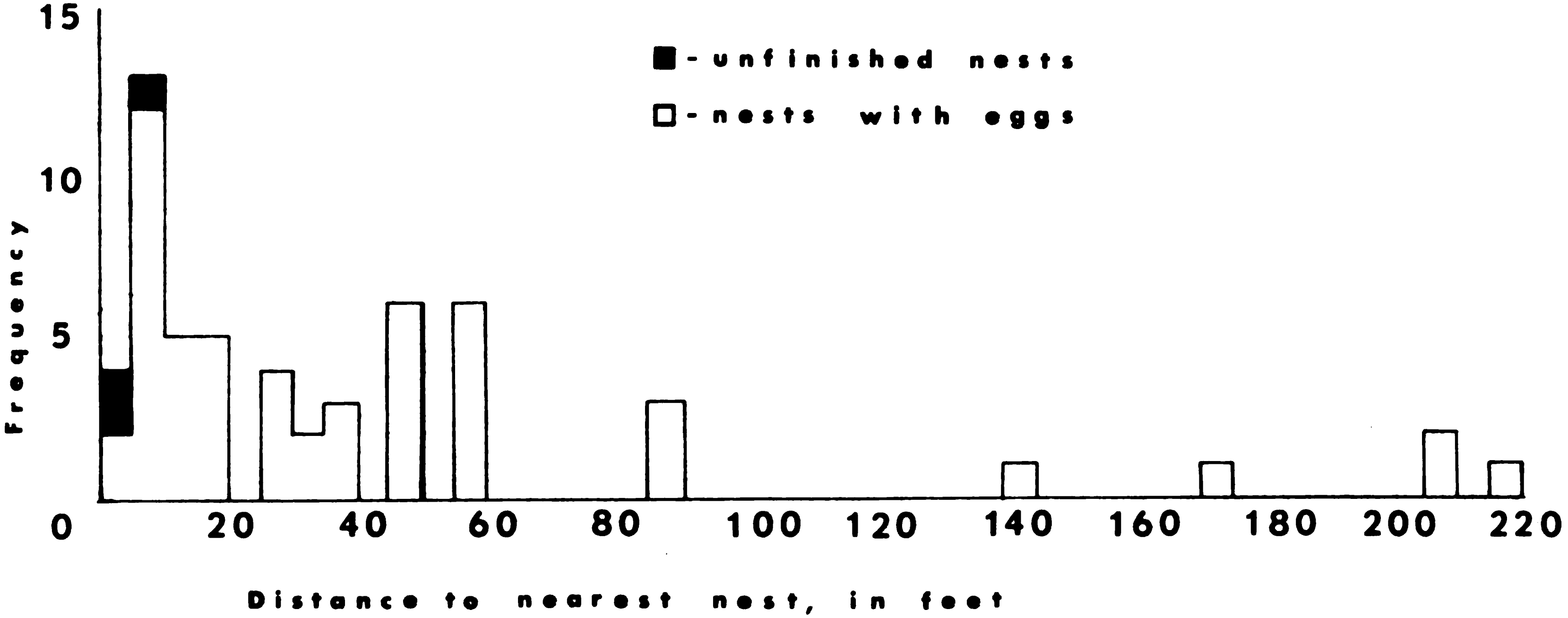

Figure 3. Internest distances in grackle colonies.

The existence of many potential but unused nest sites in the colonies in Table 5 indicates that nest sites are not normally a limiting factor for the grackle population. This is not always the case. For example, Colony No. 14 consisted of ten nests all within the same medium-sized Austrian pine, the only potential nesting location within a circle of a quarter-mile radius. As it was discovered too late to observe the number of pairs that may have tried to nest there, it is uncertain whether ten was the maximum number in that colony site or not. One nest in Colony No. 13 was perhaps the oddest nest of all studied. While located in one colony, it was begun a week earlier than the other nests in that colony and was placed in a different site than all the others. The adults of this nest foraged toward the south while the other birds were doing their primary foraging to the north. This circumstantial evidence suggests that that nest may not have belonged to the colony. Since it was placed in the site nearest to Colony No. 14 approximately two-tenths of a mile to the south, it may have been a member of the latter colony, indicating that the Austrian pine occupied by that colony was saturated. Had Colony No. 13 not developed the potential relationship of the aberrant nest there to Colony No. 14 would not have been recognized. It would have been considered simply as a solitary nest. The function of solitary nests in the population is still unexplained, but a promising lead is that some of the nests are the efforts of pairs unable to find sites in established colonies. In such a situation, solitary nests may serve as guides for the subsequent adoption of new colony sites.

Sex of Nestlings

In the absence of cloacal protuberance or incubation patch information adult grackles may be sexed by wing and tail measurements (Wood, 1969). There is some evidence that culmen, tarsus and weight measurements can also be used to sex the birds (Snyder, 1937). In all of these measurements the males are somewhat larger than the females although there is some overlap in values. A scheme for sexing nestling Red-winged Blackbirds has been developed by Nero (1960) based upon the weight of known-age birds. A preliminary study of young grackles carried out at Manhattan Marsh in 1968 indicated that marked size differences existed among nestlings late in nest life, and further that a color phase phenomenon might be associated with this size difference. In 1970, 70 nestlings were collected from the Rose Lake colony. The sex ratio of this sample was not significantly different than 1:1. After all the young were sexed and measured, I tried to relate differences in measurements and color phase with sex, and since the birds were collected at known ages, the relationship with age was also tested. No significant difference between the respective male and female means was noted for any measurement at any age. The variation of the wing length, first primary length, tail length, and weight of the specimens was so high that these variables were eliminated from any other consideration, leaving culmen and tarsus measurements as the most reliable characters to use for sexing the young. The variations in even these two characters were very large among nine- and ten-day old birds so only culmen and tarsus data for 11- and 12-day old nestlings were used for the following analysis, a sample of 28 nestlings. Figure 4 presents the data on these 28 nestlings. The ages are pooled because essentially no difference existed between the two subsamples for these criteria. Because of the small sample size no attempts were made to test this distribution. In dealing with criteria for determining sex of animals externally, measures of central tendency of the distribution of a criterion are not as important as the overlap between the two groups. Each individual, representing one point in a distribution, cannot be assigned to either class which overlaps its measurement, even though the classes have significantly different means. Criteria were determined as follows: the lower limit of the male distribution for both tarsus and culmen was set above the measurement of the largest female, and the upper limit of the female distribution was set below the measurement of the smallest male. The results of the application of these techniques are shown in Table 7.

Tarsus and culmen measurements were available for 18 young 11- or 12-days old from fieldwork in 1971. Application of the sexing criteria to these birds allowed identification of 13 of them (72%) into known sex categories, nine females and four males; five of the young were intermediate. The proportion of unidentifiable young in the 1970 and 1971

Figure 4. Tarsus and Culmen measurements and color phase of nestling grackles. One individual, an "Intermediate" female, Tarsus = 25 mm, Culmen = 12 mm, has been omitted from the graph to conserve space.

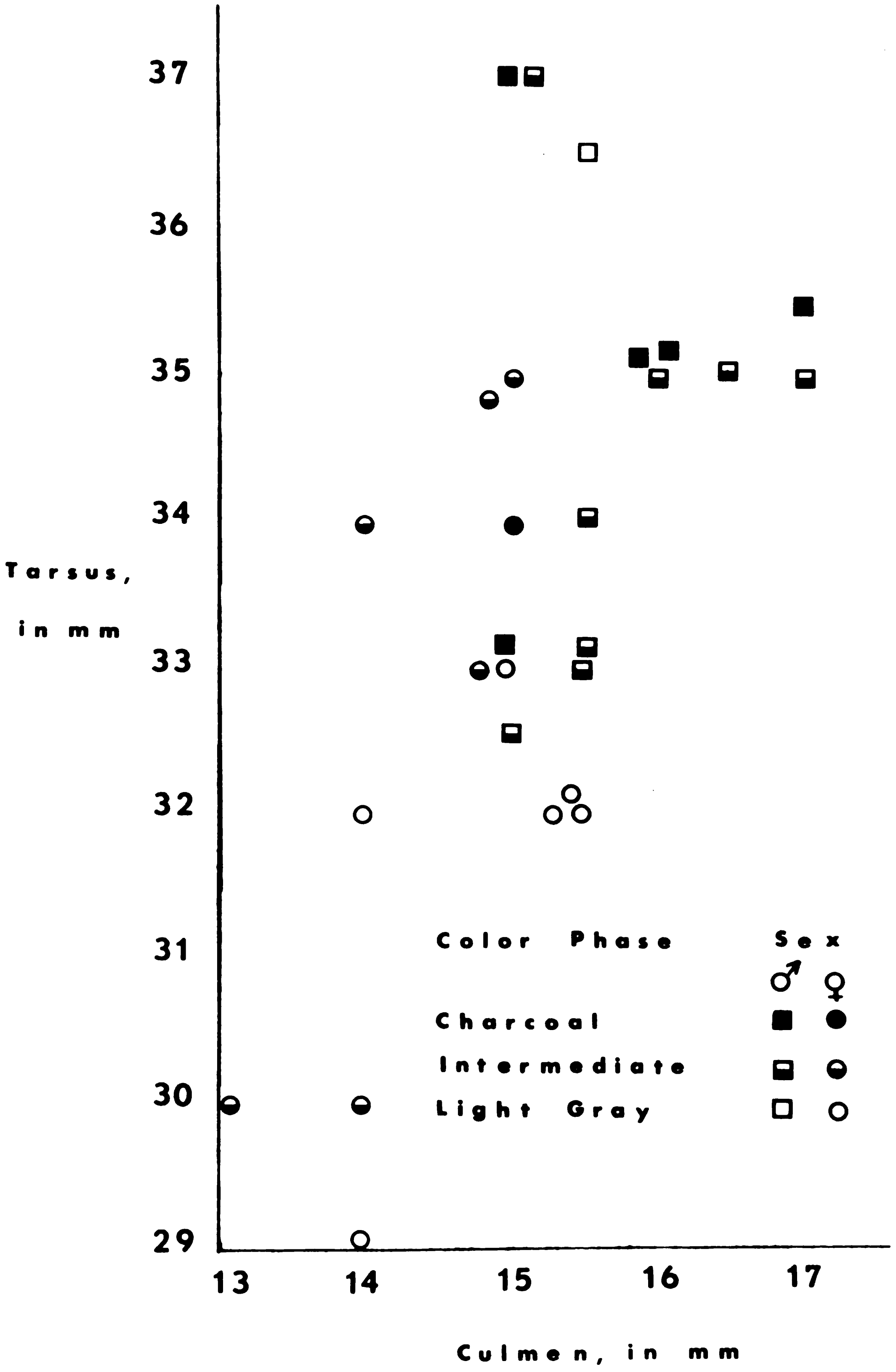
Tarsus, in mm
37
36
35
34
33
32
31
30
29
13
14
15
16
17
Culmen, in mm
Color Phase
Sex
♂
♀
Charcoal
Intermediate
Light Gray

Figure 4.

Table 7

Criteria for Sexing Nestling Grackles 11 and 12 days Old

Criterion	Component Classes	Sample Differentiated
1. Tarsus[a] measurement alone	> 35 = M[b]	4 M
	$32 < x \leq 35$ = U	10 M, 6 F
	≤ 32 = F	8 F
	identified	12 - 43%
	unknown	16 - 57%
2. Culmen measurement alone	≥ 16 = M	6 M
	$15 \leq x < 16$ = U	8 M, 8 F
	< 15 = F	6 F
	identified	12 - 43%
	unknown	16 - 57%
3. Combination of Tarsus and Culmen measurements		
Tarsus > 35 and/or Culmen ≥ 16 = M		9 M
Tarsus intermediate AND Culmen intermediate = U		5 M, 5 F
Tarsus ≤ 32 and/or Culmen < 15 = F		9 F
	identified	18 - 64%
	unknown	10 - 36%
4. Tarsus length Illinois (Willson et al., 1971)	≥ 33 = M	13 M, 6 F
	$31 \leq x < 33$ = U	1 M, 4 F
	< 31 = F	4 F
	identified	17 - 61%
	unknown	5 - 18%
	MISIDENTIFIED	6 - 21%

a - all measurements expressed in millimeters
b - M = male; F = female; U = unknown sex

samples is approximately one-third of the total number, not a very high amount considering that about 20% of the adults are intermediate (Wood, 1969). More females than males are represented in the 1971 sample because some nestlings had fledged from the nests before the measurements were taken. As males are generally larger than females it is not unlikely that the early nest leaving group is biased in favor of males. The broad overlap of the measurements of the two sexes necessitated that these criteria have a wider range of intermediacy than Willson et al. (1971) allowed, based upon data from Illinois birds.

Data from this study only permit comparison of length of tarsus criteria used in the two sexing schemes. The tarsus criterion of Willson et al. (1971) is included in Table 7. The sample of nestlings used was the sample collected at Rose Lake in 1970. Because these birds were younger than the 13-day olds for which the criteria were designed it might be expected that slowly maturing males would be identified as females. However, the scheme incorrectly identifies six females as males, more than are correctly identified as females, and no males are misidentified. It is not clear how the sex of the Illinois nestlings was determined. The Common Grackle in Illinois is the same subspecies, Q. q. versicolor Vieillot, as that in Michigan (A.O.U., 1957), and as this subspecies is very constant throughout its large range (cf. Chapman, 1892) it seems unlikely that differences in measurements at locations within several hundred miles of each other should exist. Therefore, extreme caution should be exercized in applying the criteria of Willson et al. (1971) in sexing young grackles.

Contingency analysis based upon sex and color phase of nestlings using the G-test is shown in Table 8. The three color phases refer to the pinfeathers of the crown and upper breast viewed in good light. They are regions along a color continuum rather than discrete sets. "Charcoal" birds are very dark, almost black in coloration and appear rather glossy. "Light gray" birds are much paler, gray or tan gray, and appear dull rather than glossy. Two of the 70 nestlings had blurred vertical breast streaks in addition to being "light gray." Two of 34 nestlings handled in 1968 at Manhattan Marsh were also light gray with streaks. "Intermediate" birds are an intermediate gray color and not glossy. Color phase does not appear to have any direct relation to size (Figure 4), but it is significantly related to sex (Table 8). The probability of obtaining at random the distribution in Table 8 is less than 0.05. This character is not an accurate one for sexing the young since all three phases occur in both sexes. It is not known if this color phasing is related to the iridescence of the adult plumage but the possibility seems worthy of further study.

These criteria for sexing nestling grackles are not statistically significant and they are based upon limited sample sizes. They must therefore be used with a great deal of caution. They are presented here as is because collecting large samples of young would seriously hinder my continuing

Table 8

Color Phase Distribution in Nestling Grackles

Sex	Color Phase			
	Charcoal	Intermediate	Light Gray[a]	Total
Male	6 (5)[b]	19 (8)	3 (1)	28 (14)
Female	3 (1)	15 (7)	11 (6)	29 (14)
Total[c,d]	9 (6)	34 (15)	14 (7)	57 (28)

a - with pronounced streaking of the breast in two of 61 individuals
b - numbers in parentheses indicate 11- and 12-day old nestlings
c - data from Rose Lake, 1970; $p<0.005$ of obtaining the total distribution at random
d - $p<0.05$ of obtaining the distribution of 11- and 12-day old nestlings at random

studies of grackle population structure and recruitment in central Michigan. I will greatly appreciate any feedback from others who attempt to use these criteria.

SUMMARY

Social behavior of Common Grackles was studied in three locations in central Michigan with the purpose of evaluating whether or not this bird is nest-site limited, whether or not breeding aggregations of the birds are formed because the birds are actively colonial or simply distributed as a function of available nest sites, and to determine changes in a population censused 20 years previously. In addition, a study was conducted to determine criteria for sexing nestlings of known age.

Breeding Common Grackles are actively colonial rather than passively distributed as a function of available nest sites. Breeding display between males and females in colony groups is highly contagious. It stimulates synchronized initiation of nest building by the females in terms of nesting date and nest-site choice as well. A brief discussion of the potential effect of age on breeding time is made.

A census of the breeding population in East Lansing, Michigan indicated that nest sites are not now limiting grackle populations as a whole, and that the population in the area has increased six-fold in the past 20 years.

Tentative criteria are presented for sexing 11- and 12-day old nestlings on the basis of tarsus and culmen measurements. The potential significance of a previously unrecorded

color phase series among the nestlings is discussed.

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