VOCAL BEHAVIOR OF THE GREAT-TAILED GRACKLE (*QUISCALUS MEXICANUS PROSOPIDICOLA*)

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Various authors have commented on the unusually large vocal repertoire of the Great-tailed Grackle (*Quiscalus mexicanus*). Pearson (1921:521), for example, remarked that grackles possess "an astonishing repertoire of whistles, calls, and guttural sounds," while Townsend (1927:553) "was struck with the great variety of its clear and at times musical notes and songs mixed with others that were not so pleasing." Selander and Giller (1961) described five vocalizations of both *Q. mexicanus* and the closely related Boat-tailed Grackle (*Q. major*), but mentioned that these birds also possess additional notes. In the present study, vocalizations of the Great-tailed Grackle (*Q. mexicanus prosopidicola*) are described, with the aid of spectrograms, and interpreted in terms of causation and function. The latter aspect is considered to include both the effect on the behavior of associates and the adaptiveness in relation to the habitat and habit of the species concerned.

Field studies were conducted, 1968–1970, in the Austin area, Travis County, south-central Texas. A summary of the recording localities and other details is given in table 1. All vocalizations were recorded, but not analyzed, with a Nagra 3B portable recorder at a tape speed of 7½ ips, using an Altec 633A microphone mounted on a 24-inch parabolic mirror. Audiospectrograms were made on a Kay Electric Company Sonograph Model 661A, using the wide-band and "high-shape" filter settings.

By analyzing the situations in which a particular vocalization occurred and by observing the responses of other birds, it proved to be quite easy to assign functions to some sounds because they are used repeatedly in situations which are essentially similar. In the case of others, however, there frequently is no detectable response on the part of other birds hearing the vocalization, and it is extremely difficult to detect any particular pattern from the variety of circumstances in which the sound may be used. In order to obtain some understanding of such vocalizations, I used a technique similar to that described by Tinbergen (1959) which involved recording the sounds immediately preceding and following a certain vocalization. Given a sufficient number of observations, whenever the occurrence of an unfamiliar sound is highly correlated with another vocalization of known function, the former can be said to function in a similar context, or as the result of a similar motivation.

VOCALIZATIONS

SONG

As has been accurately described by Selander and Giller (1961), full song consists of four distinctive phrases (fig. 1A–D). Most comments by earlier workers pertain to the introductory phrase of the song, which has variously been described as resembling the "scrapings of a cornstalk fiddle" (Bendire 1895:504), "breaking of sticks" (Bailey 1902:303), "sharpening of a saw," "drawing a stick sharply across the quills of a dried goose-wing," "tearing the dry husk from an ear of corn" (Baird et al. 1905: 226–227), "crackling of twigs" (Friedmann 1925:550), and "brush-breaking" (Simmons 1925:186). Although the number of low, guttural notes in the introductory phrase varies from one to six, three occur most commonly. In the second phrase, an undulatory *chewe* may be repeated 1–12 times, with a corresponding change in duration as measured on spectrograms. Normally this phrase makes up the greater proportion of the full song, while the third phrase, consisting of a brief repetition of the harsh sound of the introductory phrase, invariably occupies the smallest proportion. The song ends with a series of 1–11 loud *cha-we* notes. Measurements of 90 spectrograms gave an average song length of 5.7 sec and a dominant frequency of the song ranging between 2 and 8 kHz.

Song is much used by males in proclaiming territory. In the breeding season when a male is on his territory, vigorous and oft-repeated song is often sufficient, without any other form of aggressive display, to discourage and put to flight intruding males. In competing bouts between rival males, song serves as an important strategy to intimidate and repel the opponent. The fact that the average number of notes in

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TABLE 1. Summary of recordings made of Great-tailed Grackles.

		No. of birds			No. of vocalizations	
Date	Locality[a]	♂♂	♀♀	Juv.	recorded	spectrographed
1968						
Mar. 8	Zilker Park	4			118 (17)[b]	10
13	Zilker Park	5			186 (83)	14
Apr. 29	Zilker Park	2	1	1	280 (7)	11
29	U. T. campus	2			243 (0)	9
30	Municipal airport	3	1		333 (10)	15
May 2	Municipal airport	1			99 (4)	12
5	Parks & rec. dept.	2			89 (16)	3
6	Parks & rec. dept.	1	1	1	149 (12)	7
9	Parks & rec. dept.	2		1	130 (15)	14
June 15	U. T. campus	2			170 (6)	17
20	Assumption Cemetery	3	2		320 (0)	9
22	U. T. campus			3	92 (0)	4
30	U. T. campus	1			7 (0)	3
July 1	U. T. campus	2			112 (5)	15
3	U. T. campus	2	1		103 (16)	24
4	Zilker Park	4			139 (6)	22
Nov. 22	Zilker Park	5			55 (25)	6
29	Zilker Park	4			76 (3)	3
1969						
Apr. 2	Municipal auditorium	5	2		248 (17)	7
4	Municipal auditorium	2	1		123 (5)	6
5	Municipal auditorium	3			53 (6)	3
7	Municipal auditorium	3	1		53 (5)	2
9	Parks & rec. dept.	1			79 (30)	2
10	Parks & rec. dept.	5	2		298 (48)	7
15	Parks & rec. dept.	3	1		83 (32)	19
16	Municipal auditorium	1			92 (0)	3
17	Parks & rec. dept.	1	1		110 (6)	13
18	Parks & rec. dept.	3	1		117 (4)	12
18	U. T. campus	1			17 (2)	1
19	Municipal auditorium	2			124 (25)	16
22	Evergreen Cemetery	2			55 (1)	1
23	Evergreen Cemetery	1	2		75 (12)	17
24	Evergreen Cemetery	1			57 (9)	4
May 1	Evergreen Cemetery	3	1	2	128 (17)	10
17	Evergreen Cemetery	1			81 (11)	7
19	Evergreen Cemetery	2			55 (8)	1
27	Evergreen Cemetery	3			112 (11)	5
June 26	Zilker Park	1	1	1	39 (0)	1
July 2	Parks & rec. dept.	1	1		30 (0)	1

[a] All localities are in Austin area, Texas.
[b] Numbers in parentheses indicate number of full songs recorded.

the introductory and terminal phrases is higher in song directed to males (2.23 and 1.68, respectively) than to females (2.11 and 1.17) shows that the song is given with greater vigor whenever it is directed to males. In contrast to the effect of full song on other males, females are attracted to the singing male in the breeding season and remain at the breeding colony, quickly returning when chased.

Most frequently song is delivered from a conspicuous position in the tops of trees, but it is also given from the ground or in flight. A short forward step, possibly functioning to attract attention due to the movement or reflection of light from the bill and glossy plumage, sometimes precedes the vocalization. From an acoustical point of view, the complex song seems to be well suited for its dual function of advertisement and defense, since it carries far (especially the *cha-we*) and gives plenty of clues for location (cf. Marler 1955, 1957, 1959).

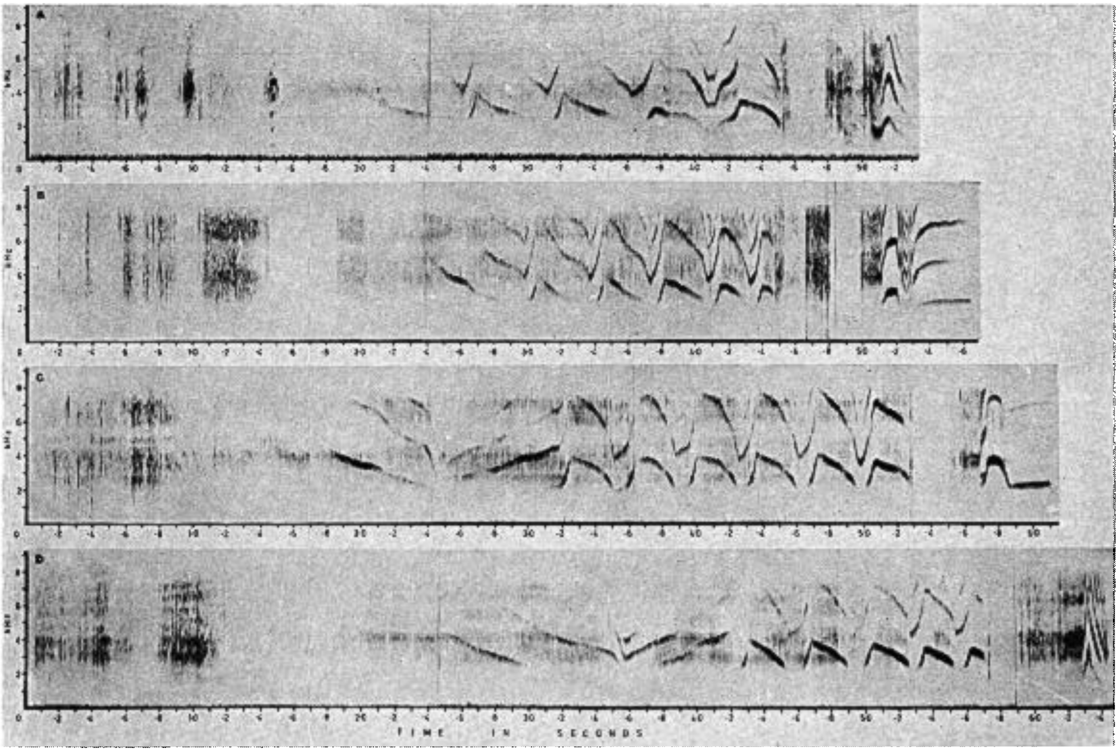

FIGURE 1. Audiospectrograms of vocalizations of *Q. mexicanus*. A–D, full song of four adult males.

Full song, accompanied by display, is given with regularity only in the breeding season and in the period of fall recrudescence of the gonads. Outside the breeding season, it is largely restricted to periods when the birds are leaving the roost in the morning, when briefly revisiting old colonies during the day, and when returning to the roost in the evening. Song is all but absent during the time of molt in August. Incomplete songs, consisting of any of the four phrases separately or in any combination thereof, can be heard throughout the year. The loud terminal phrase of the song given alone is especially common.

According to Selander and Giller (1961), first-year males frequently give atypical versions of the terminal phrase, in which the notes ascend rather than descend in pitch. This, however, is not a characteristic of first-year males alone, since adults often give a series of *cha-we* notes, of which some are ascending and some descending in pitch (fig. 2A). Two banded adult males who were breeding in both the 1968 and 1969 seasons are also known to have used the ascending terminal phrase regularly in song. The possibility is therefore suggested that the two song types represent slight differences in motivation, as was found in the case of the American Redstart, *Setophaga ruticilla* (Ficken 1962), the Yellow-headed Blackbird, *Xanthocephalus xanthocephalus* (Nero 1964), the Yellow Warbler, *Dendroica petechia* (Morse 1966), and the Blackburnian and Black-throated Green Warblers, *D. fusca* and *D. virens*, respectively (Morse 1967). As the nesting cycle progresses, seasonal variation in the performance of these two song types, involving an increase in the relative number of ascending phrases, is apparent (table 2). Taken together with the fact that the ascending *cha-we* is often uttered rather quietly, it can be argued that the "atypical"

TABLE 2. Seasonal variation in proportion of ascending and descending terminal phrases of full song of *Q. mexicanus*.

	Song with single terminal phrase		
Month	ascending	descending	Ratio
Jan.	4	31	1:7.8
Feb.	60	462	1:7.7
Mar.	182	1161	1:6.4
Apr.	327	884	1:2.7
May	462	417	1:0.9
June	161	53	1:0.3
July	276	103	1:0.4
Aug.			
Sept.			
Oct.	358	50	1:0.1
Nov.	142	131	1:0.9
Dec.	9	38	1:4.2

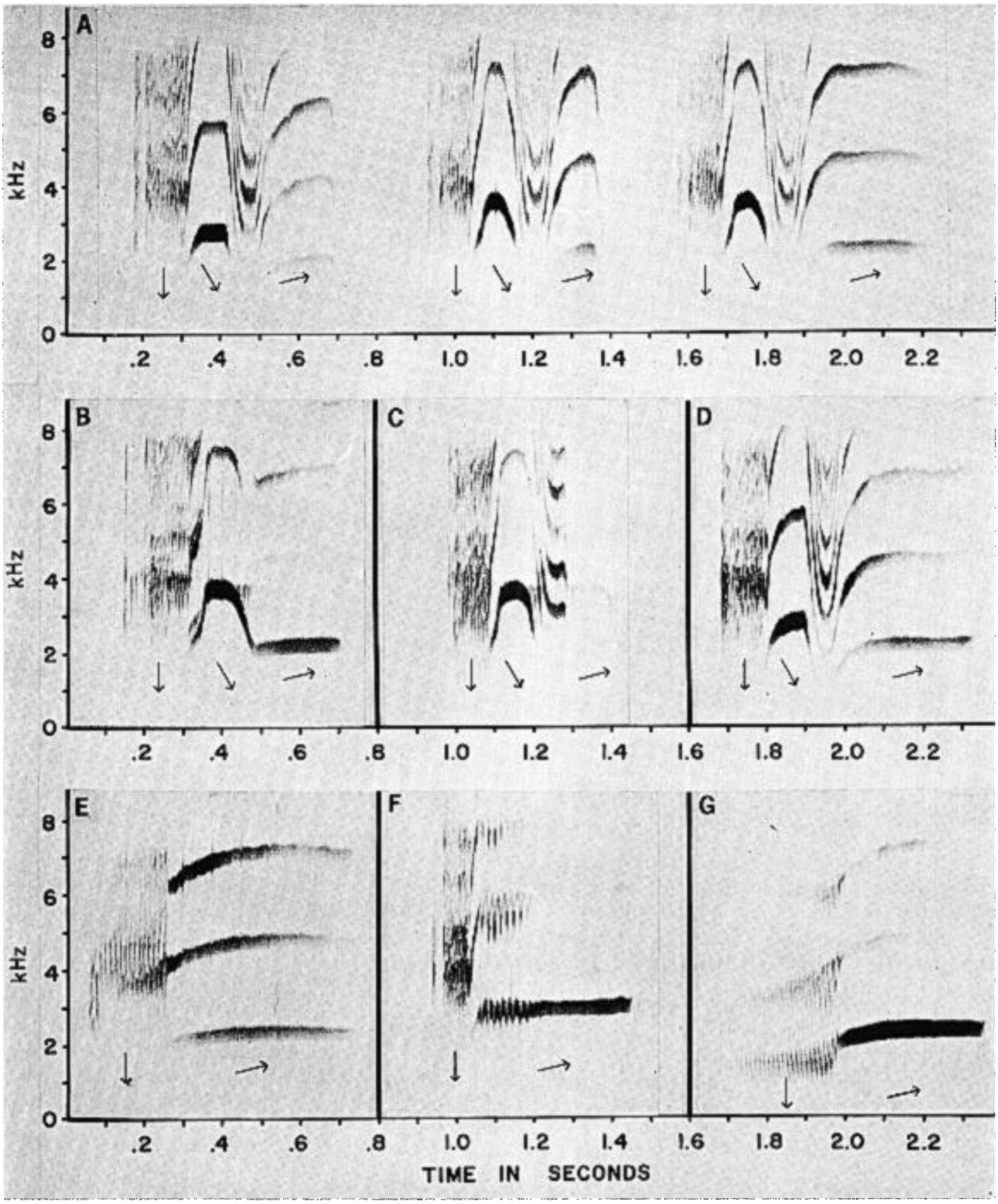

FIGURE 2. Audiospectrograms of vocalizations of *Q. mexicanus* males. A, three successive descending terminal phrases of song; B–D, descending terminal phrases of songs; E–G, ascending terminal phrases of songs. Corresponding parts of the terminal phrases are indicated by arrows.

song represents a low-intensity version expressing a weaker motivational state. An interesting finding in connection with the ascending terminal phrase was made at a sympatric breeding colony of *Q. major* and *Q. mexicanus* near Sabine in eastern Texas. There, all *Q. mexicanus* males used the ascending note exclusively (fig. 2E–G). An element of learning is probably involved in this case because the first part of the phrase resembles the *tireet* notes of the *Q. major* song (fig. 8A–B) to some extent.

Song in *Q. mexicanus* is limited to the males. This is not unusual since song in female birds is relatively uncommon (cf. Nice 1943), especially in species where there is a striking sexual dimorphism. Even under sustained treatment

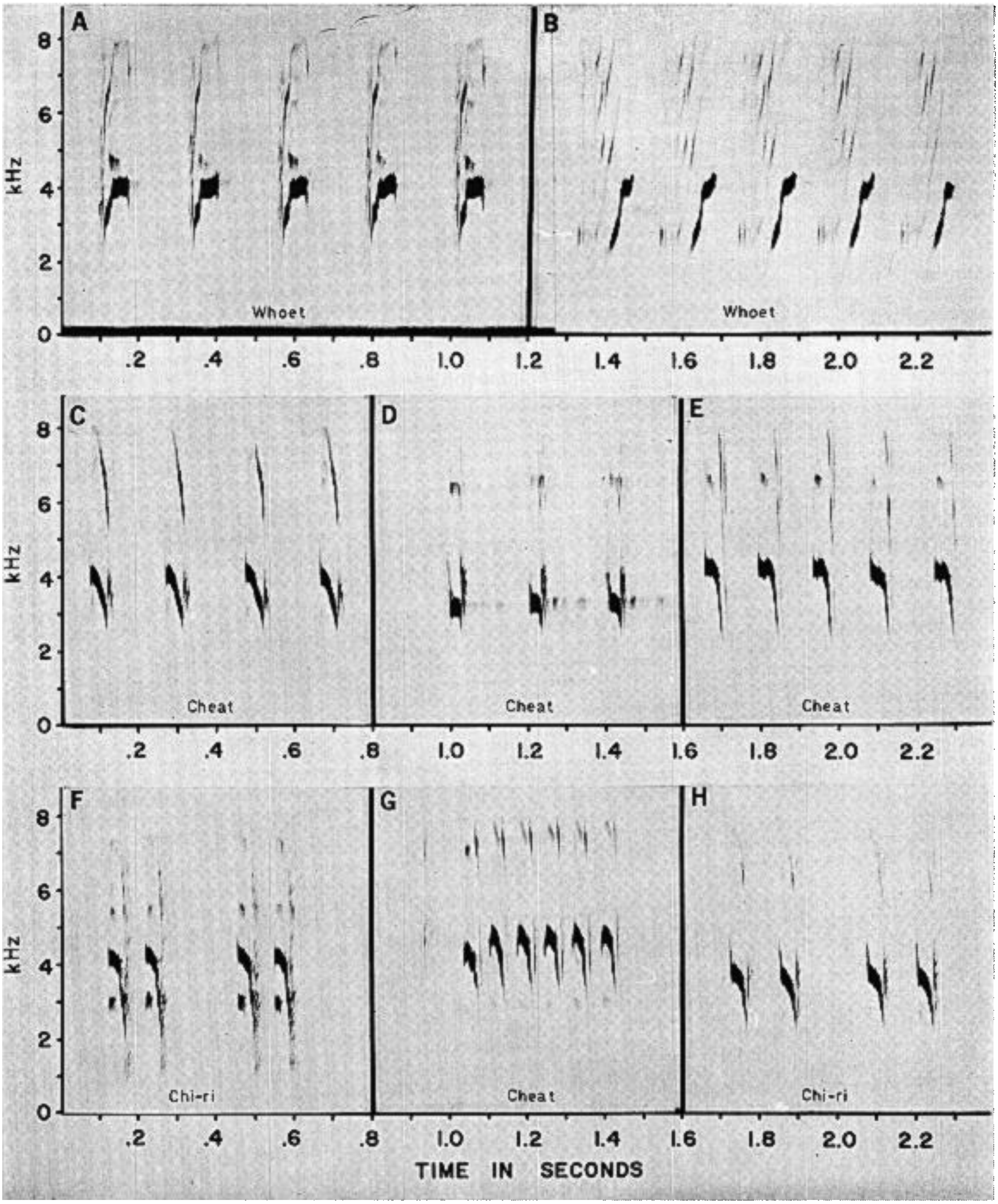

FIGURE 3. Audiospectrograms of vocalizations of *Q. mexicanus* males. A–B, *whoet* notes; C–E, solicitation *cheat* notes; F, *chi-ri* or double-note version of *cheat* call; G, rapid series of solicitation *cheat* notes; H, *chi-ri* or double-note version of *cheat* call.

with testosterone, females do not produce the male song, although they are induced to perform other characteristically masculine behavior (Selander and Giller 1961). During the course of this study, however, females were observed on a few occasions to utter sounds which somewhat suggested the first part of the male song. As was found in the case of Song Sparrows, *Melospiza melodia* (Nice, loc. cit.), all instances occurred in the early spring before the start of nest building when the birds are highly aggressive. Occasional female song accompanied by plumage display has also been reported for various other icterids. Saunders (1929:17) suggested that singing females are "unusual individuals, that possess some trace of masculine characteristics," but it is more likely that such vocalizations have a threat function, the importance of which depends on the particular dominance relationship existing between the sexes (Selander, as quoted in Nero 1964).

SOLICITATION CALLS

The vocalization most frequently heard in the breeding season is the male's solicitation call (fig. 3C–E), which indicates his interest and readiness to mate. These calls consist of a varying number of clear, medium-pitched *cheat* notes. As many as 37 notes, delivered at a rate of about 6/sec, have been recorded on spectrograms in a single series. Occasionally males rapidly repeat the *cheat* notes at more than twice the normal speed (fig. 3G). *Chi-ri*, or double-note versions of the call, in which one *cheat* rapidly follows another with a longer interval before the next note, also occur (fig. 3F and H). The *chi-ri*, as is often the case with solicitation calls, is most frequently preceded by the introductory phrase of the song. Such vocal combinations probably indicate an aggressive tendency on the part of the male whenever a female is approached. Of the 988 solicitation calls, 90 per cent were elicited by females, especially those carrying nesting material or food. The rest of the calls, mostly those series consisting of fewer than four *cheat* (or *che*) notes, were directed to males and even to individuals of other species. Males use the call not only throughout the breeding season, but also during the rest of the year, though with much less vigor. From March to June, unlike other times of the year, solicitation calls are often among the first sounds to be heard when the males arrive at breeding colonies early in the mornings. It may be given in flight, from perches, and on the ground while running and half-circling a female.

At high levels of intensity, when the solicitation calls are almost always accompanied by the solicitation posture, the *cheat* notes are replaced by a series of high-pitched *che* notes (fig. 4C–E and G). Through various intermediate forms, depending on the level of excitation, the strained quality of the peeping notes is eventually obtained (fig. 4B). Females have a similar note (fig. 4A), called the "pleading peeps" by Skutch (1954), but it is softer and has a more refined quality. Accompanied by the solicitation display, this vocalization is given to males as an invitation to copulate. A given female uses the note only for about one week after the nest has been constructed.

An extreme form of the solicitation call of males is represented by the *teet* note, which is of longish duration, falling slightly in pitch, and is uttered with a deliberate firmness (fig. 4H). The fact that this vocalization is normally delivered from a conspicuous position in the territory, that it is often immediately followed by a head-up display, and that it is relatively often associated with the whistle, incomplete song, and solicitation calls (fig. 5), indicate that it may share some of the functions of territorial advertising with full song.

The *kli-teet* of males may not be really distinct from the *teet* call. However, it differs from the latter in being preceded by a short, high-pitched note (fig. 4F). The *teet* part is also more accentuated and of slightly longer duration than the regular *teet* note mentioned above. Apparently the call serves a function similar to that of the *teet* note, but a higher degree of aggressiveness is involved. That is apparent from the fact that the *kli-teet* is sometimes used in competing bouts, accompanied by a simultaneous forward step in the direction of a rival male. Figure 5 also indicates a relatively greater association with full song, as compared with that of the *teet* call.

ALARM CALLS

A low, single-syllable *chut* with a wide frequency range is used by both sexes throughout the year in low intensity excitement (fig. 6A–B). Those of females have a higher pitch and are softer, but on occasion they do grade into a louder, harsh sound. At higher intensities of excitement, females usually repeat the *chut* notes at a faster rate than males. In 20 separate cases during which the observer stood quietly near a nest for a period of at least 10 min, the different females were clocked, giving a maximum of 183 notes/min as compared with the 150 of the opposite sex. Each *chut* is generally accompanied by a simultaneous flick of the tail, moving rapidly upward and slowly downward with lateral spreading at the bottom of each stroke, which signifies unrest and a tendency to fly. The *chut* is used in situations of mild disturbance, such as humans walking at a distance, squirrels near the nesting trees, and sudden noises. It is also common after strong disturbances have died away. Often the call is interspersed with preening, when it appears to represent such a low level of arousal that no response on the part of other birds has been observed.

Grackle males possess a loud, low *clack* which possibly originated as a double-note version of the *chut* (fig. 6C–E). A comparable call in females is lacking. Outside the breeding season, when the calls are not so common,

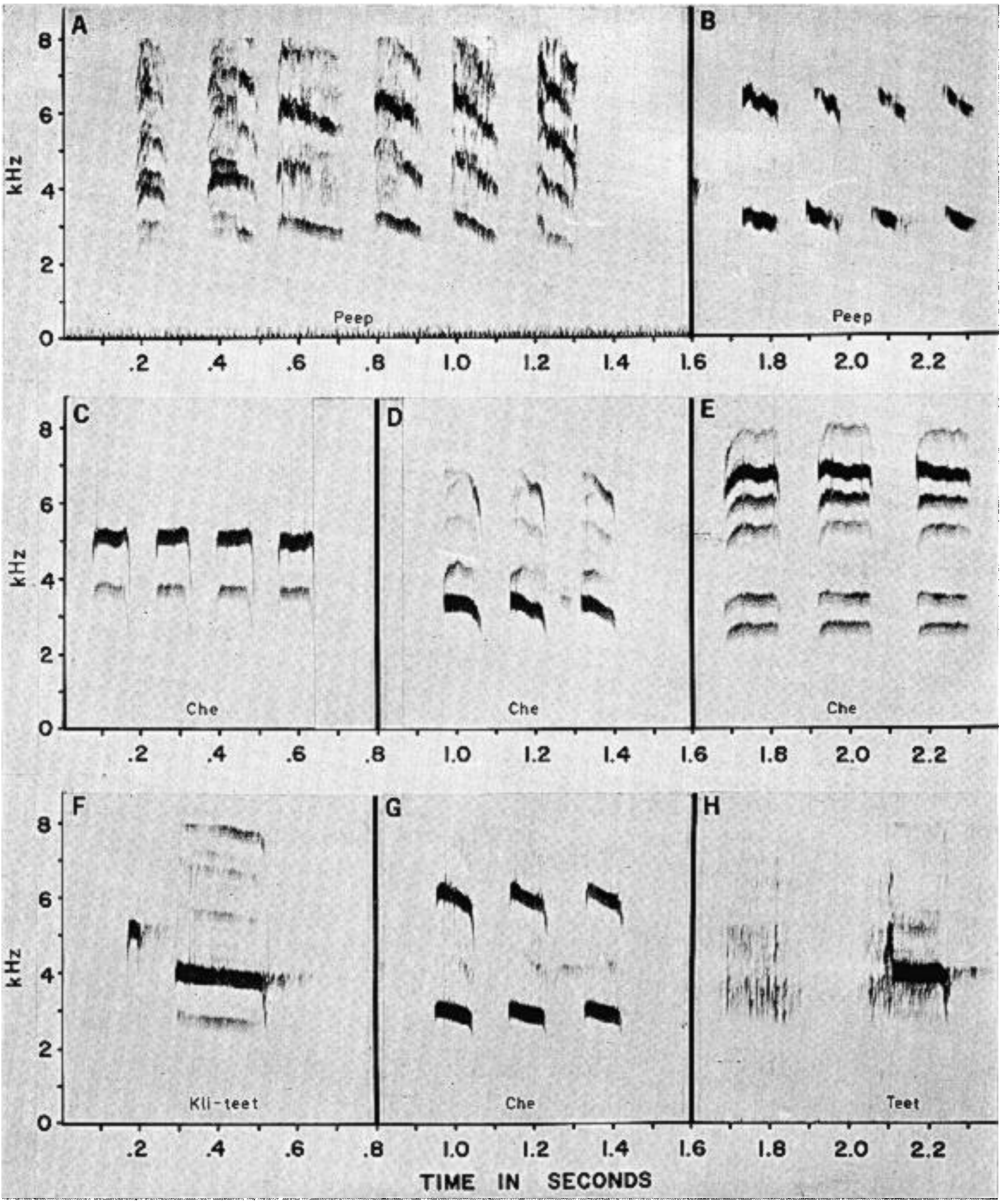

FIGURE 4. Audiospectrograms of vocalizations of *Q. mexicanus*. A, high peeping notes of female; B, high peeping notes of male; C–E, solicitation *che* notes of male; F, *kli-teet* call of male; G, solicitation *che* notes of male; H, single *teet* of male introduced by first part of song.

1–15 notes may be given in quick succession. But in the breeding season it is mostly used as single, separate notes which may be repeated up to 47 times per minute in times of extreme danger. The *clack* is given in response to strong disturbances at the nesting colonies and roosts. It is usually elicited by the approach of humans and other potential predators, and is also used during panics and when mobbing. Frequently the call is given in flight as the bird flees from a source of danger.

Another warning note, limited to males, is a harsh, slightly ascending squack. Usually it occurs as a single note during the breeding season, but in exceptional cases as many as eight squacks in rapid succession have been

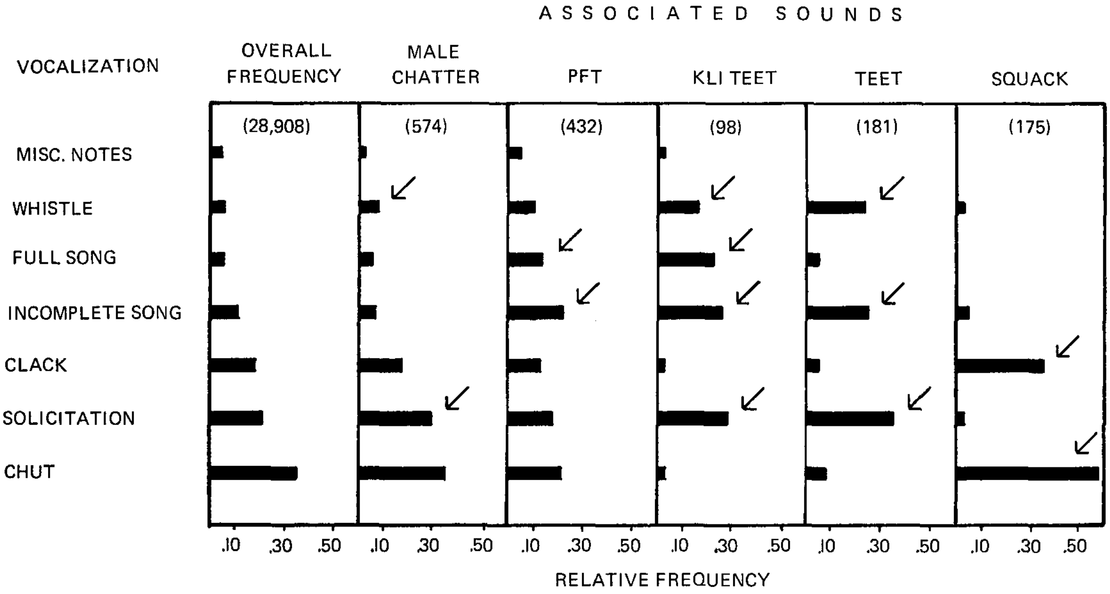

FIGURE 5. Histogram showing association of *Q. mexicanus* vocalizations with various rare sounds. Number in parentheses indicates number of observations in each case. Arrows point to major increases in frequencies as compared with those of the "overall frequency."

recorded. It occurs as a moderately strong response in situations which also elicit the *chut* and *clack* warning notes (fig. 5).

MISCELLANEOUS NOTES

Whistle. One of the most pleasing sounds in the vocal repertoire of grackles is the finely-tuned whistle given by males alone (fig. 7A). According to Skutch (1954:325), this is the most characteristic vocalization of *Q. mexicanus*, and he describes it as "a single, long-drawn utterance, something between a squeak and a whistle, which rises through the musical scale." He also refers to the note as resembling "the slow swinging of a gate with rusty hinges." Although the whistle normally rises in pitch, it may sometimes be inverted, being delivered with a descending pitch (fig. 7D). Its significance, if any, is unknown. Most commonly two whistles are given in quick succession, but series consisting of 3–5 notes, and especially single whistles, are not infrequently heard. The whistle probably has a strong threat function, since it is often followed immediately by bill-tilting (head-up), a short-range hostile display. Almost 70 per cent of the 828 calls were directed at approaching males in order to repel and scare them off from intruding on established territories. Airplanes, flying members of other species, and females also elicit the call. Sometimes, when a male is initially startled by the sudden appearance of a female from the dense cover of the trees, he may start uttering a whistle, only to break off abruptly and follow it by solicitation notes the moment he "realizes" his "mistake" (fig. 7B). Since the whistle is mainly given in response to flying individuals, it is initiated as soon as the birds start moving from the roost, and is commonly heard early in the mornings when the flocks disperse for the day, or late in the afternoons when the birds are again making their way to their sleeping quarters. Various males sometimes precede the whistle by a number of notes resembling the *chut*, but with a sweeter, more open, sucking or "kissing" quality (fig. 7A). In other cases whistles, or portions thereof, are regularly incorporated into the second phrase of the song (fig. 1C). Although the whistle is limited to males, according to Skutch (1954), females sometimes attempt to deliver a weak and squeaky imitation thereof.

Chatter. The chattering call, probably corresponding to the *tlick-a-lick* of Skutch (1954), is characterized by the rapid repetition of notes with a short duration and a wide frequency range of 2–8 kHz (fig. 6H). Females give the call only from late March until early July, when nest building is initiated and territories established. It is used mostly during aggressive encounters between females as they move to and from their territories, and when leaving the nesting site while building, incubating, or feeding. At times it is also given at the close approach of first-year and adult males near the nest. There is usually an increase in chat-

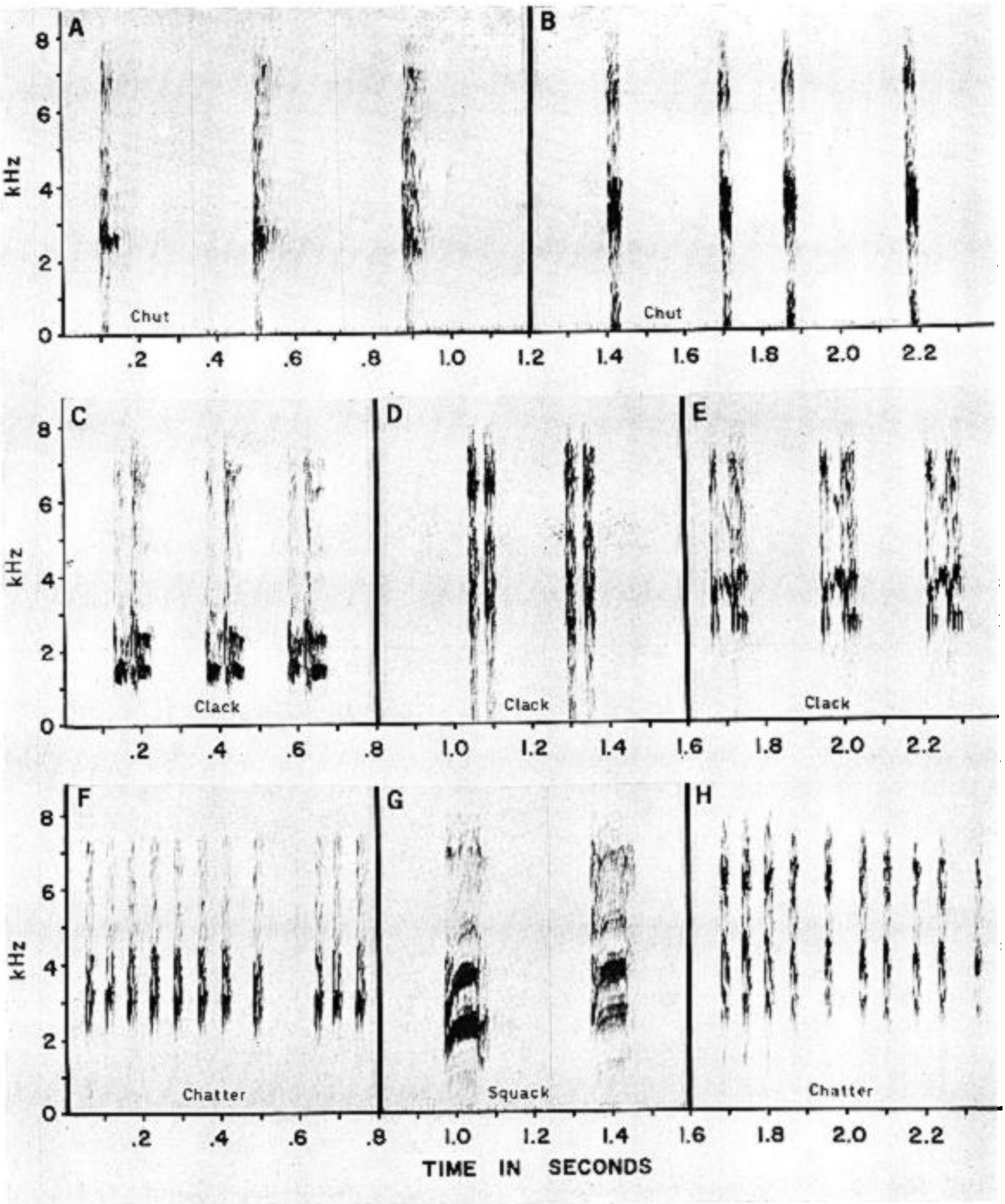

FIGURE 6. Audiospectrograms of vocalizations of *Q. mexicanus*. A, *chut* of three males; B, *chut* of female; C–E, *clack* of three males; F, male chatter; G, squack of two males; H, female chatter.

tering calls just before nightfall when the females settle down at the breeding colonies where they are incubating or brooding. Selander and Giller (1961) believed the chatter to be restricted to females, as is the case in Redwinged Blackbirds, *Agelaius phoeniceus* (Orians and Christman 1968). However, as was found in the case of Brewer's Blackbird, *Euphagus cyanocephalus* (Williams 1952), and Yellow-headed Blackbirds, *Xanthocephalus xanthocephalus* (Nero 1964), males also give the sound, and recordings have been obtained from two males that used the call frequently. As shown in figure 6F, most of the energy of the male chatter lies between 2.5 and 4.5 kHz. Since 82 per cent of the 132 male chattering calls were immediately preceded or followed by a few solicitation notes as part of the vocal-

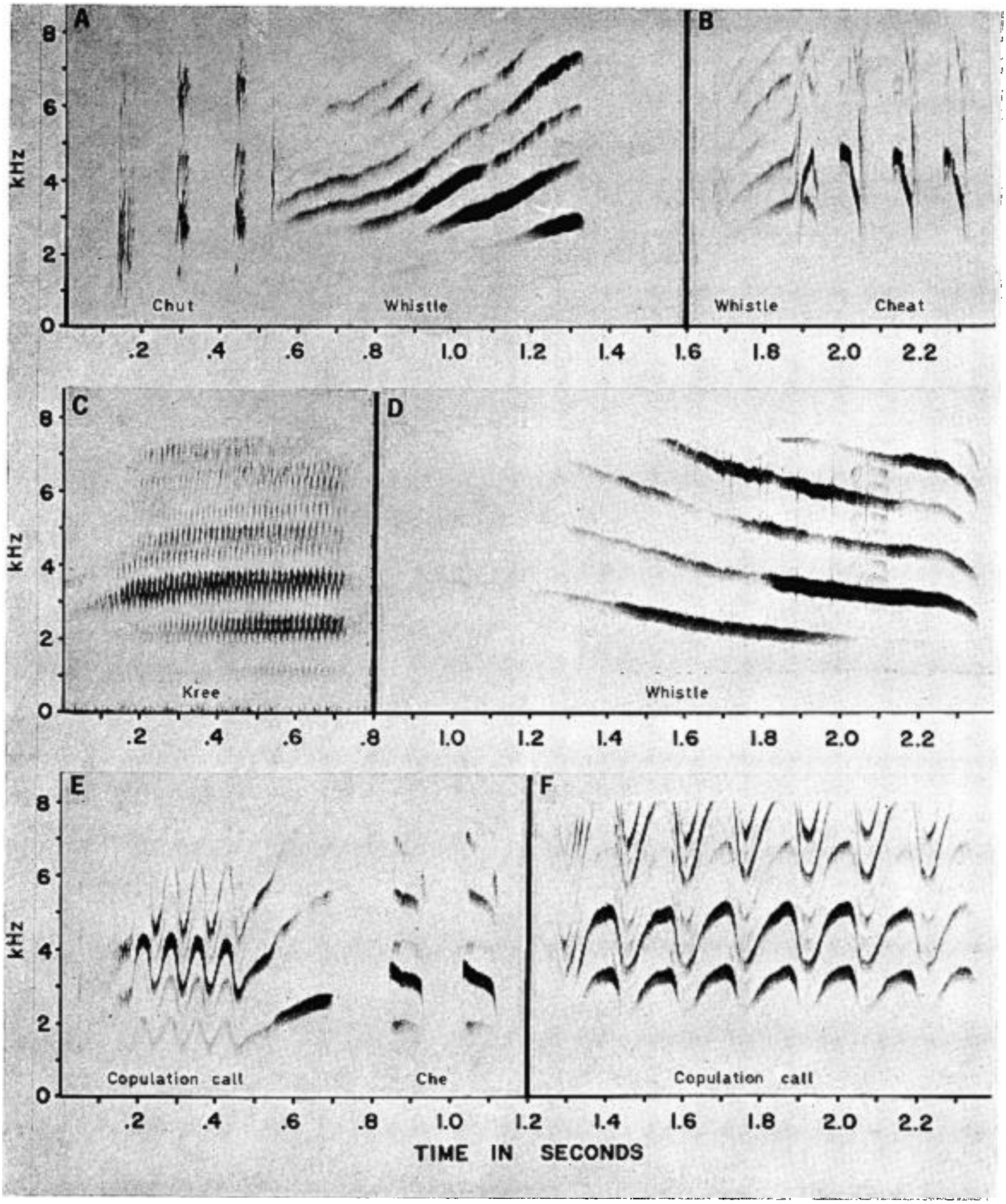

FIGURE 7. Audiospectrograms of vocalizations of *Q. mexicanus* males. A, ascending whistle introduced by three "kissing" *chut* notes; B, sharply broken off whistle, followed by three solicitation *cheat* notes; C, scratchy *kree*; D, descending whistle; E, copulation call, followed by two solicitation *che* notes; F, copulation call.

ization, the male chatter could be used in the same circumstances as the solicitation call. The call probably has a slight aggressive motivation, since it is not only relatively often associated with solicitation notes, but also with the whistle (fig. 5). An inference from the female chatter would suggest the same.

Pft. Members of both sexes occasionally utter a series of "puffing" notes that sound like a short, sudden expulsion of air (fig. 8D). These notes are the softest sounds in the vocal repertoire. They have poor carrying power, being inaudible at distances greater than 10 yards. For this reason, *pft* notes are probably heard more often in the breeding season, when observations can be made at close range, than

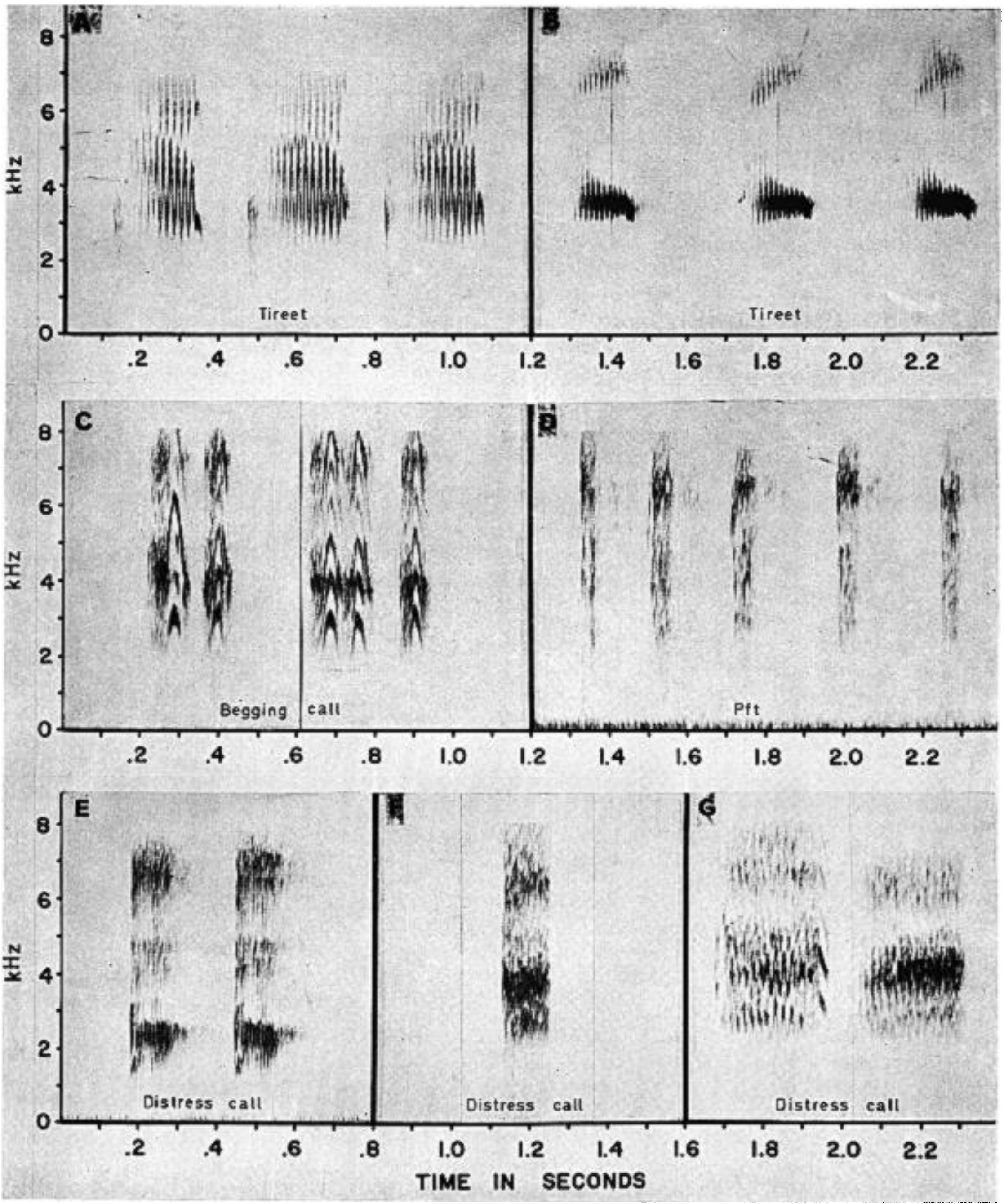

FIGURE 8. Audiospectrograms of vocalizations of *Q. major* and *Q. mexicanus*. A–B, first part (*tireet*) of songs of adult *Q. major* males; C, begging call of *Q. mexicanus* fledgling; D, *pft* notes of *Q. mexicanus* male; E, distress call of *Q. mexicanus* male; F, distress call of *Q. mexicanus* female; G, distress calls of *Q. mexicanus* fledglings, respectively.

during the rest of the year when the birds are relatively wary. Low amplitude flicks of the tail and wings usually accompany the sound, which is delivered with a wide open bill. Little is known about the communicative function of the *pft* notes, except that they are given near nests, on the ground while foraging, and in the presence of males and females as well as humans. As suggested by the movements of the tail and wings, a bird giving this vocalization appears to be restless and uneasy. But, due to a moderate degree of aggressiveness at the same time, indicated by the relatively frequent association of *pft* notes with full and incomplete song (fig. 5), the bird is probably slightly reluctant to fly. Nice (1943) mentioned a similar note, described as *puh*, which is used by Song Sparrows (*Melospiza melodia*) in aggression towards a person endangering the young.

Distress call. A distress call, given by males and females, both adults and fledglings (fig. 8E–G), has a rather loud, harsh, squealing quality, with most of its energy between 3 and 5 kHz. In cases of extreme anxiety, as when a bird is handled by humans, the call is readily elicited from fledglings. At other times it is given by adults when chasing potential predators. This call strongly attracts other members of the same species, which fly directly to the spot and begin uttering alarm calls such as *chut* and *clack.*

Copulation call. At the height of the breeding season, when males are actively seeking matings, they emit a rapid series of vibratory notes in the presence of females (fig. 7E–F). Spectrographically, the note bears a resemblance to the second, undulatory phrase of the song, which normally is quite variable in length and number of rhythmic segments, but it differs in that (1) it is not accompanied by a hissing sound, (2) it is delivered at approximately twice the speed, and (3) more emphasis is placed on the initial rise in pitch of each segment.

Whoet. On the campus of the University of Texas a few males were heard to give a call not unlike that of a Mockingbird (*Mimus polyglottos*) or Cardinal (*Richmondena cardinalis*). Although vocal mimics are mainly ground-frequenting species or birds that feed on or near the ground (Armstrong 1963), this is the first case of mimicry among ground-feeding members of the Icteridae. The only other icterid previously reported to mimic is the Yellow Troupial, *Icterus icterus* (Wallace 1896). Spectrographically the vocalization seems to be a mirror image of the solicitation *cheat* notes, with ascending rather than descending pitch (fig. 3A–B). The vocalization has a somewhat lower frequency range, and the successive notes, ranging from 1 to 13 with an average of 5 notes in a series, are delivered at a slightly slower rate. Almost 90 per cent of the 188 calls were preceded by the introductory phrase of the song. The vocalization is mostly directed at other males, and presumably serves the same function as the whistle.

Kree. Q. mexicanus males occasionally emit a peculiar sound designated as *kree.* It is a scratchy, long-drawn call which bows up slightly at the start and then continues on the same pitch, unlike the whistle (fig. 7C). Associated behavior and the responses of other birds are unknown, but the call appears to have an aggressive connotation similar to the whistle.

Begging call. Nestlings utter a faint, high-pitched peeping sound whenever the parent bird returns to the nest with food. The peeping is also elicited by any slight jarring or tapping of the nest. Older nestlings and fledglings utter a number of hoarse, scraping notes, quite different from the peeping sound, with a frequency of 5–8 kHz (fig. 8C). These calls are given periodically by fledglings perched alone, and presumably serve as a guide to the returning female. When the parent is in view, the young bird begs vigorously and persistently, with the wings quivering and the head and neck stretched forward.

INDIVIDUAL RECOGNITION

Sexual and individual recognition play a major role in the relationships and social interactions among members of a colony. Undoubtedly recognition among birds is accomplished mainly by means of auditory and/or visual cues. A considerable amount of observational evidence dealing with individual recognition among birds by means of vocal characteristics has been recorded in the literature (Weeden and Falls 1959; Tinbergen 1961; Ficken 1963; Buckley and Buckley 1970). That peculiarities of the *clack* may at least occasionally be effective in individual distinction among grackles is suggested by an instance in which a number of foraging females paid no attention to the clacking of a certain male, but immediately took flight when the same sound was delivered by another individual. Both birds seemed to be hidden from the females' view on that particular occasion. The first-mentioned male, however, was known to be an easily disturbed individual who often uttered the *clack* repeatedly, even for the slightest danger.

For vocal recognition to occur individually, there must be a certain amount of variation upon which discrimination can be based. The greater this variation with respect to a particular feature, the greater is the likelihood of detecting differences. Following Hutchison et al. (1968), I calculated a discrimination ratio (SD/mean) as an indicator of the extent to which a parameter can presumably be used as the basis for discrimination (table 3). On the basis of this and other considerations, full song is the vocalization most likely to assist in inter-individual identification. Because of conspicuous and regular differences in the appearance of spectrograms, songs of different males can easily be identified, especially with respect to the shape of the terminal and undulatory

TABLE 3. Discrimination ratios for vocalizations of 30 male *Q. mexicanus*.

Measure	Range	$\bar{x}$	SD	Ratio[a]
Duration, full song	3.7– 8.1	5.7	1.6	0.29
Duration, third phrase	0.2– 0.8	0.5	0.1	0.28
No. peaks, second phrase	2.5–11.5	6.8	1.8	0.27
Duration, terminal phrase	0.3– 0.9	0.6	0.1	0.25
Duration, second phrase	2.3– 6.0	3.9	0.9	0.23
Duration, introductory phrase	0.8– 1.7	1.2	0.2	0.22
Max. frequency of fundamental of terminal phrase	2.0– 4.0	3.3	0.6	0.19
Duration, whistle	2.3– 4.9	3.9	0.6	0.17
Duration, *clack*	0.6– 1.1	0.8	0.1	0.17

[a] Standard deviation/mean.

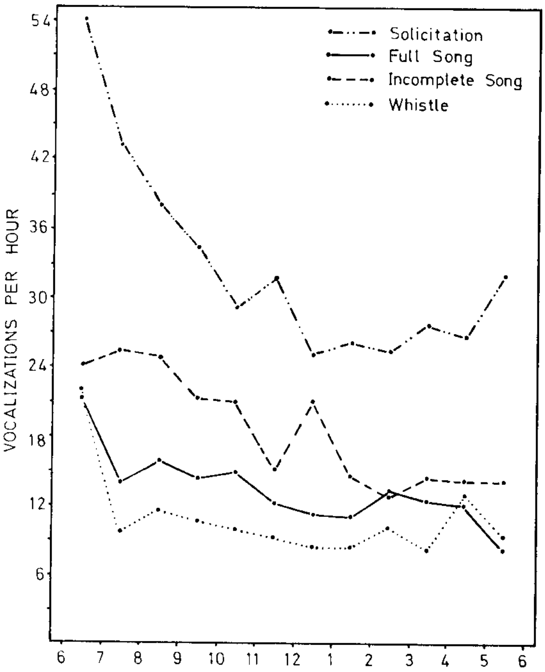

FIGURE 9. Average vocal output per hour of 10 *Q. mexicanus* males, each observed continuously for a period of 12 hr in April 1969.

phrases (fig. 1A–D and 2A–G). In the field it is mainly the last part of the song, perhaps partly because of its intensity, that contributes to the tracing of particular birds. The regular incorporation of additional notes in the song, such as the one shown between the first and second phrases in figure 1A, may also be helpful, as are peculiarities in other vocalizations.

It was established that the duration of songs from two specific males did not change significantly when recorded 7 and 26 days later in April and May ($t = 0.22$, $df = 14$; and $t = 0.59$, $df = 13$, respectively). Though conclusive evidence is lacking, this is probably also true for longer periods of time. Owing to the fact that songs of individual birds not only remain constant, but also differ in detail of fine structure and in the overall relationship of the component parts, it is indeed very plausible that grackles themselves recognize the sounds as distinctive.

DIURNAL CYCLE

Although the frequency of singing is affected by such factors as the stage of the breeding cycle, proximity of territories, territorial conflicts, and weather conditions, *Q. mexicanus* males vocalize vigorously throughout most of the day in the breeding season. Like virtually all diurnal species, they display a vivid outburst of vocalizations in the early morning hours (fig. 9). Since non-territorial males are more likely to be in search of unoccupied territories (maximum flying activity), and unmated females are more likely to be seeking mates at that time (56 per cent of all copulations observed took place before 10:00), large vocal outputs at dawn are adaptive. Such prolonged singing in the first few active hours of the day is largely dependent upon stored energy not consumed during the night (Verner 1965), and following warm rather than cold nights, it continues for longer periods without interruption to forage. A second peak, never as high as that in the morning, is reached in the late afternoon, when the opportunity for attracting females or repelling males is increased due to the presence of birds which are slowly returning to the communal roost.

Characterizing the diurnal variation in singing time, the U-shaped configuration of the four major vocalizations combined (excluding warning notes such as the *clack* and *chut* whose utterance is triggered by unusual stimuli) decreases from 120 to 66, indicating an average of 75 vocalizations per hour during the course of the day. The mid-day decrease in vocalization is probably due to the corresponding increase in foraging, when grackles are usually silent, giving only an occasional *chut* or other sound. It can also be argued that much of the time in the mid-afternoon is spent resting, a view supported by the low flying activity of males at that time, which is possibly associated with the heat and other environmental factors. With the exception of days with abnormally bad weather conditions, the amount of singing is usually not reduced on inclement days, suggesting that above a certain threshold of stimulation, vocalizations

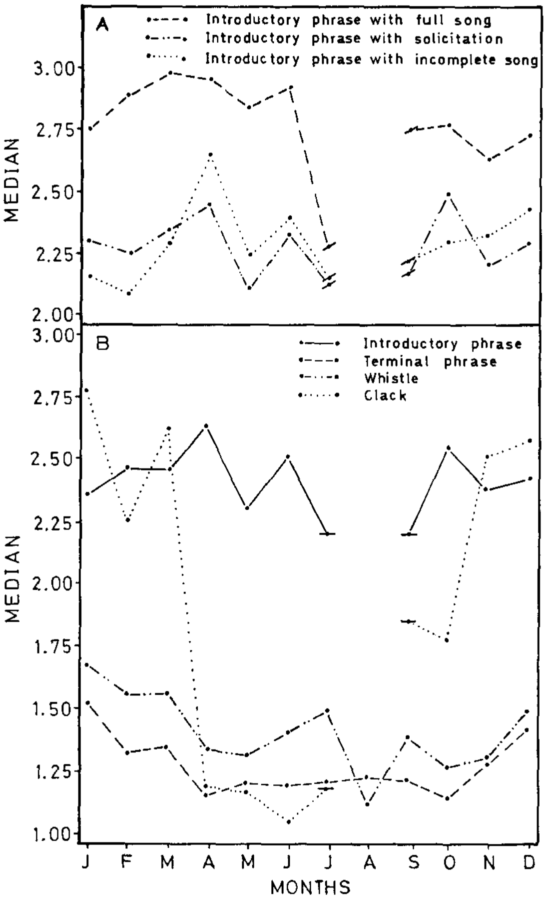

FIGURE 10. Seasonal variation in monthly median frequency of occurrence of major vocalizations of *Q. mexicanus* males.

are not inhibited by unfavorable weather. In the winter months, however, weather conditions dramatically affect male vocalizations concerned with courtship and territoriality. A similar effect has been noted by Selander and Hauser (1965).

SEASONAL CYCLE

It has long been known that the onset of territorial behavior in spring, including the establishment of territories, aggressiveness towards other males of the same species, interest in nest-sites, and sexual responsiveness, coincides with the seasonal growth of the gonads. In grackles, evidence of the correlation between the gonadal cycle and seasonal variation in behavior was presented by Selander and Hauser (1965). From figure 10A–B it is also apparent that there is a close relationship between frequency of the major vocalizations of males and events in the testis cycle. This is especially clearly illustrated by the graph of the combined introductory phrases in figure 10B where the three main peaks of the median correspond to the high level of testicular activity in the breeding season and in October. During periods of lower median values following the breeding season and in the winter, the testes are relatively inactive (Selander and Hauser, loc. cit.). In May, midway in the breeding season, the pronounced decrease in the median frequency reflects the partial regression of the testes of adult males, which produces a similar bimodal form in the cycles of testis volume, histologic stage, and relative interstitial cell numbers (Selander and Hauser, loc. cit.). The almost complete disappearance of the introductory phrase (and *clack*) in late summer correlates with both gonadal regression and the postnuptial molt (Selander 1958), which severely drains the energy resources of the individual. With the breakdown of the introductory phrases into three categories associated with full song, incomplete song, and solicitation, respectively, it is of interest to note that the median values of full song are consistently higher than those of either the incomplete song or solicitation (fig. 10A), probably indicating a higher degree of aggressiveness. This view is further strengthened by the fact that the maximum value occurs in May, when male competition in establishing territories is most intense.

Although the amount of vocalization is positively correlated with the testicular activity, the median value of notes given in quick succession at a time, both with respect to the *clack* and the combined terminal phrases associated with full song and incomplete song, show an inverse relationship with the male gonadal cycle (fig. 10B). The large number of single, independent though oft-repeated utterances in the breeding season can, however, be explained in terms of the lowered threshold associated with the higher levels of excitement. No well-marked trend is discernible from the seasonal frequency of the median values of the whistle, but there is a suggestion of a similar inverse relationship (fig. 10B). The rather steep decline of the median in August reflects the tendency of the birds to frequent foraging areas in fields surrounding Austin, so that the opportunity of repelling approaching males from former breeding sites, most of which are located in the city, is reduced to a minimum. From the foregoing account it is apparent how intimately the different vocalizations are connected with the breeding cycle, and consequently with the seasonal recrudescence and regression of the gonadal cycle.

DISCUSSION

Various vocalizations have been described, but the distinction between some of the sounds is not always very obvious. Low intensity solicitation notes may, for instance, grade into the high-pitched *che* and peeping notes, while the *kli-teet* is linked to the solicitation *che* via the *teet*. Judging from their physical structures, a graded series of notes, encompassing the chatter and the different alarm calls, can be arranged in the following way:

—— *clack* —— squack
chatter —— *chut*
—— *pft* —— distress call

All these vocalizations show affinities to the same basic pattern, probably represented by the chatter or *chut*, which also occurs in many other species of the Icteridae. It is perhaps of significance that the latter series is mainly composed of warning notes, the items of information most immediately relevant to survival.

Nevertheless, adult males are considered to possess a total of 16 different patterns of sound, while adult females have only five. This relatively large sexual difference in the number of vocalizations can be related to the type of mating system, in which intense and prolonged interaction between males should favor the evolution of more complex displays and vocalizations (Orians and Christman 1968). The fact that the maximum number of distinctive sound signals in birds is about 20 (Armstrong 1963), and that the total number of vocalizations of many other well-studied passerine birds is very nearly the same, prompted Thorpe (1961) to suggest that there is some common factor working in all these species which limits to approximately 15 the number of main items of information conveyable by this means.

As shown by Crook (1964), Orians and Christman (1968), and Williams (1969), the vocalizations of birds evolved under the selective pressure of the environment. Marler (1955, 1957, 1959) found that the physical characteristics of the different sounds are closely attuned to the information that they convey. With respect to grackle vocalizations, five general categories, based upon their spectrographical structures, can be recognized and, to some extent, correlated with functional categories.

The first group includes sounds of short duration with a wide frequency range (*chut*, fig. 6A–B; *clack*, fig. 6C–E; chatter, fig. 6F and H; squack, fig. 6G; *pft*, fig. 8D; and distress calls, fig. 8E–G). All these are used in situations of some kind of alarm (or aggression, as with the chatter), and, with the exception of the male *clack* and squack, are given by both sexes. Calls of this nature are easily located as to the source (Marler, loc. cit.), and are effective in attracting other birds for mobbing purposes or in drawing attention to potential predators.

The second category also consists of calls with broad frequency ranges, but with extended duration (whistle, fig. 7A–B and D; and *kree*, fig. 7C). The calls are given by males only, and apparently have a threat function. Since most of the energy of these sounds is confined to the lower frequencies, differences of phase at the two ears can give information about the direction of the sound, but the use of time differences is eliminated by the gradual start and end of the sound without any sudden discontinuities or breaks (Marler, loc. cit.). Vocalizations of this type are therefore capable of repelling rival males without revealing the position of the calling bird too readily, thereby restricting possibly dysgenic fighting.

Call notes with a restricted frequency range, brief duration, and frequent repetition are grouped together in the third category, which includes the *cheat* (fig. 3C–H), *whoet* (fig. 3A–B), and begging call (fig. 8C). These probably serve to attract or repel individuals from a distance, so that the calling bird must announce its location, but not indicate it too readily to possible predators. A compromise, reflected in the form of the call, is therefore reached between various selective pressures which make precise localization difficult but allow for distant orientation.

The *teet* (fig. 4H), *kli-teet* (fig. 4F), peeping (fig. 4A–B), and solicitation *che* notes (fig. 4C–E and G) are included in the fourth category. Characteristically, they have a difficult-to-locate horizontal configuration (Marler, loc. cit.), being of restricted frequency range, of extended duration, and often beginning and ending rather imperceptibly. Since the vocalizations function at close quarters, either in aggressive encounters (*teet* and *kli-teet*) or when vigorously soliciting a copulation (*che* and peeping), there is no need for precise location of the sounds, because the birds are in full view of each other. At the same time, potential predators are not attracted to the site at a time when the attention of the birds is distracted and they are more vulnerable to attack.

Full song (fig. 1A–D), the copulation call (fig. 7E–F), and the different vocal combinations regarded as incomplete song constitute the fifth and final category. These vocalizations have complex physical structures which provide ample clues for accurate localization.

They are given exclusively by males, and may serve various functions as discussed previously.

SUMMARY

Vocalizations of the Great-tailed Grackle (*Quiscalus mexicanus prosopidicola*) are described, with the aid of spectrograms, and interpreted in terms of causation and function. The importance of vocal sounds in individual recognition, as well as the diurnal and seasonal cycles of vocalizations, are discussed.

ACKNOWLEDGMENTS

This study represents a portion of the dissertation presented to the Faculty of the Graduate School of The University of Texas at Austin in partial fulfilment of the requirements for the Ph.D. degree. The valuable advice and criticism of R. K. Selander, under whose supervision the study was carried out, are gratefully acknowledged.

LITERATURE CITED

Armstrong, E. A. 1963. A study of bird song. Oxford Univ. Press, London.

Bailey, F. M. 1902. Handbook of birds of the western United States. Houghton, Mifflin and Co., Boston and New York.

Baird, S. F., T. M. Brewer, and R. Ridgway. 1905. A history of North American birds. Vol. 2. Little, Brown and Co., Boston.

Bendire, C. 1895. Life histories of North American birds, from the parrots to the grackles. Smithsonian Contr. Knowledge 32:1–518.

Buckley, P. A., and F. G. Buckley. 1970. Color variation in the soft parts and down of Royal Tern chicks. Auk 87:1–13.

Crook, J. H. 1964. The evolution of social organisation and visual communication in the weaver birds (Ploceinae). Behav. Suppl. 10:1–178.

Ficken, M. S. 1962. Maintenance activities of the American Redstart. Wilson Bull. 74:153–165.

Ficken, R. W. 1963. Courtship and agonistic behavior of the Common Grackle, *Quiscalus quiscula*. Auk 80:52–72.

Friedmann, H. 1925. Notes on the birds observed in the lower Rio Grande Valley of Texas during May, 1924. Auk 42:537–554.

Hutchison, R. E., J. G. Stevenson, and W. H. Thorpe. 1968. The basis for individual recognition by voice in the Sandwich Tern (*Sterna sandvicensis*). Behaviour 32:150–157.

Marler, P. 1955. Characteristics of some animal calls. Nature 176:6–8.

Marler, P. 1957. Specific distinctiveness in the communication signals of birds. Behaviour 11: 13–39.

Marler, P. 1959. Developments in the study of animal communication. *In* P. R. Bell [ed.] Darwin's biological work. Wiley, New York.

Morse, D. H. 1966. The context of songs in the Yellow Warbler. Wilson Bull. 77:444–455.

Morse, D. H. 1967. The contexts of songs in Black-throated Green and Blackburnian Warblers. Wilson Bull. 79:64–74.

Nero, R. W. 1964. Comparative behavior of the Yellow-headed Blackbird, Redwinged Blackbird, and other icterids. Wilson Bull. 75:376–413.

Nice, M. M. 1943. Studies in the life history of the Song Sparrow. II. Vol. 6. Trans. Linnaean Soc. New York.

Orians, G. H., and G. M. Christman. 1968. A comparative study of the behavior of Redwinged, Tricolored, and Yellow-headed Blackbirds. Univ. California Publ. Zool. 84.

Pearson, T. G. 1921. Notes on the bird-life of southeastern Texas. Auk 38:513–523.

Saunders, A. A. 1929. Bird song. New York St. Mus. Handbook 7. Albany, New York.

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

Selander, R. K., and D. R. Giller. 1961. Analysis of sympatry of Great-tailed and Boat-tailed Grackles. Condor 63:29–86.

Selander, R. K., and R. J. Hauser. 1965. Gonadal and behavioral cycles in the Great-tailed Grackle. Condor 67:157–182.

Simmons, G. F. 1925. Birds of the Austin region. Univ. Texas Press, Austin.

Skutch, A. F. 1954. Life histories of Central American birds. Pacific Coast Avifauna, No. 31.

Thorpe, W. H. 1961. Bird-song. Cambridge Univ. Press, London.

Tinbergen, N. 1959. Comparative studies of the behaviour of gulls (Laridae): a progress report. Behaviour 15:1–70.

Tinbergen, N. 1961. The Herring Gull's world. A study of the social behaviour of birds. Revised ed. Basic Books, New York.

Townsend, C. W. 1927. Notes on the courtship of the Lesser Scaup, Everglade Kite, Crow, and Boat-tailed and Great-tailed Grackles. Auk 44: 549–554.

Verner, J. 1965. Time budget of the male Long-billed Marsh Wren during the breeding season. Condor 67:125–139.

Wallace, A. R. 1896. A narrative of travels on the Amazon and Rio Negro. Reeve, London.

Weeden, J. S., and J. B. Falls. 1959. Differential responses of male Ovenbirds to recorded songs of neighboring and more distant individuals. Auk 76:343–351.

Williams, H. W. 1969. Vocal behavior of adult California Quail. Auk 86:631–659.

Williams, L. 1952. Breeding behavior of the Brewer Blackbird. Condor 54:3–47.

Accepted for publication 24 February 1971.