VOCALIZATIONS OF THE MALLARD (*ANAS PLATYRHYNCHOS*)

RICHARD L. ABRAHAM

Department of Ecology and Behavioral Biology
University of Minnesota
St. Paul, Minnesota 55101

Qualitative descriptive information on both vocal and visual displays of waterfowl is abundant (e.g., Heinroth 1910, 1911; Lorenz 1953; Weidmann 1956; Johnsgard 1965; McKinney 1965a, 1969, 1970), and quantitative data are available for visual displays of a few species of ducks (e.g., Weidmann 1958; Weidmann and Daily 1971; Simmons and Weidmann 1973; Johnsgard 1960; McKinney 1961, 1965b; Dane et al. 1959; Dane and van der Kloot 1964; Field 1970). But quantitative data on vocal displays of adult waterfowl are conspicuously absent. Sonographic illustrations are available for selected vocalizations of several species of adult ducks (Frith 1967; Johnsgard 1971), but to my knowledge, no one has attempted to record and analyze the full vocal repertoire of a single species.

Since the Mallard (*Anas platyrhynchos*) is one of the most studied waterfowl, a quantitative description of the vocal repertoire of this species is a logical place to start. My objectives were to review and extend the qualitative descriptions of the vocal displays of the Mallard already available (primarily, Lorenz 1953; Weidmann 1956), to provide quantitative information on daily and seasonal variations in frequency of selected vocalizations in individuals and groups, and to measure the variability of specific vocalizations, both within and between individuals. This information is intended to provide a basis for experimental and comparative investigations of the functions and evolution of Anatid vocalizations.

MATERIALS AND METHODS

In September 1967, 40 wild juvenile Mallards (20 males, 20 females) were captured at the Roseau River Refuge in northern Minnesota and transferred to flight pens at the University of Minnesota's Cedar Creek Natural History Area. Observations on these birds were conducted from December 1967 through May 1970.

During the three winters, the birds were held in a wintering house which had four individual compartments, each having an indoor concrete swimming pond and an attached outside pen to which the birds had access in good weather. Five birds of each sex were placed in each compartment.

During the second week of April 1968 and 1969, the birds were transferred to four 32 ft × 16 ft holding pens at Cedar Creek. Several days later, two pairs with strong pair-bonds were selected from each of the four compartments. One pair from each compartment was then placed into a 90 ft × 90 ft × 12 ft flight pen. Thus, each of the two observation pens had a group of four pairs that had been visually separated for 5 months.

Birds were individually marked with colored nasal discs similar to those described by Bartonek and Dane (1964). A food dish was placed in the corner of each pen and a 2-ft wide strip of long grass for nesting cover was left around the edge. Observations were made from a blind overlooking both pens. McKinney (1967) described these pens in greater detail.

During the first year, observations were made at irregular intervals during daylight hours. It was apparent, however, that there were marked seasonal and diurnal variations in the frequency of certain vocalizations, particularly during spring and fall. In an attempt to quantify them, observations in the second year were standardized as much as possible.

During April, May, and June 1969, all vocalizations were systematically recorded every other day during the second and third hours after sunrise. These 2-hr observation periods were divided into twelve 10-min segments in which presence or absence of the different vocalizations was recorded for each individual bird. Thus, each bird has 12 "opportunities" to be recorded for each vocalization during each observation period.

In addition to the 2-hr morning periods, observations were also made at irregular daytime hours, especially around dusk. Several sunrise to sunset watches and two all-night watches were also conducted.

Tape recordings were made of vocalizations of the captives whenever possible. Vocalizations were recorded with a Uher 4000 R-L tape recorder and number 514 microphone. When birds were out of microphone range, a 20-inch plastic, parabolic reflector was used. Tape speed was generally 3¾ ips, but a speed of 1⅞ ips was used when it was necessary to run the recorder continuously for long periods. Spectrograms were made using a Kay Electric Co. Sona-graph, model 7029 A, at H-S and wide band settings.

RESULTS

TERMINOLOGY

Although the *raehb* and *quack* are the basic Mallard sounds, each sex has a diversified vocabulary. It is difficult to characterize these calls using our alphabet, and previous investigators often used different onomatopoeic renditions to describe the same call, some in English and some in German. Some of these call names will continue to be used, but in a few cases new renditions have been composed.

The Condor 76:401–420, 1974

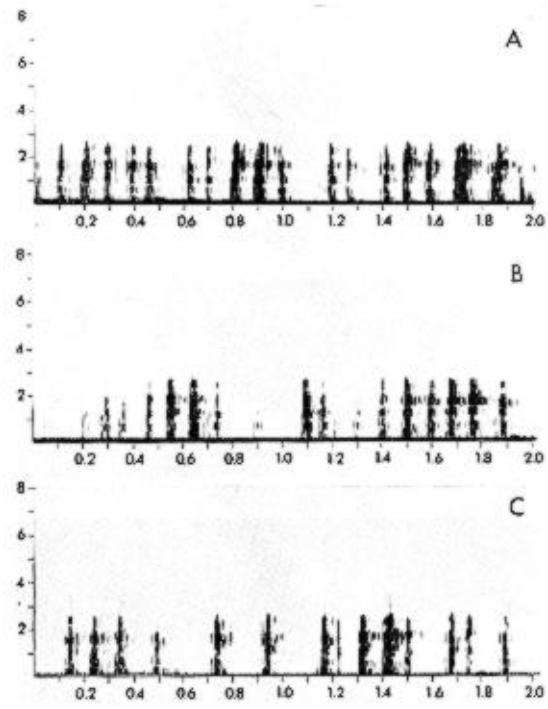

FIGURE 1. Audiospectrograms of Inciting calls of three different females. The vertical time scale is in kilocycles per second (from 0 to 8 kHz); the horizontal time scale represents seconds.

In addition to providing an onomatopoeic rendition of the various sounds, calls are also characterized here according to their physical dimensions as determined from spectrograms.

Giving titles to vocalizations is an ethological convention, but I have found it impossible to arrive at a uniform system of classification. Some titles such as Persistent Quacking and Decrescendo are descriptive, while others such as Inciting and Repulsion carry implications about motivation or function. However, these terms will continue to be used since they are already well established in the literature.

The terms "vocalization" and "call" are used interchangeably to refer to total behavior patterns (e.g., Decrescendo, Repulsion, Slow *Raehb*, etc.). "Note" will be used to characterize a tone of a single, definite pitch and duration. Some vocalizations may consist of only one note, while in others two or more notes are given in characteristic patterns. For instance, males give double-noted *Rabrab* calls in aggressive situations. Each note can be uttered alone, but most often they occur in pairs given in series. The term "phrase" will be used to denote the period of time from start of one note to end of last note. Finally, the word "whistle" will characterize a pure tone which is virtually free of harmonic content.

FEMALE VOCALIZATIONS

Inciting call. This important call is part of the Inciting display given by a paired female or by a female which is in the "mood" to pair. The vocalization (fig. 1) has been described by Lorenz (1953) as a loud, tremulous *queg geg geg geg*.

Females utter the sounds before, during, and after making sideward head movements. Apparently, the function of the ritualized threatening movement is to show preference for one male and rejection of another. According to Lorenz (1953), Inciting is phylogenetically derived from threatening of the enemy combined with swimming toward the preferred male. Because of the high degree of ritualization of the behavior, it is not always clear toward which male the female is directing her head movements (Lorenz 1958). The title of the call is somewhat misleading since in most instances the behavior does not cause the chosen male to fight or chase the other male.

The range of duration of the individual notes in the Inciting call was 30–150 msec (table 1). Although the total range is relatively small, successive notes can be on minimum or maximum ends of the range. The same is true for frequency, amplitude, and duration of intervals between notes. In general, the longer notes tend to have more sound energy per unit of time. The notes have more abrupt beginnings than those of most other female vocalizations.

The distance between the female and the approaching strange male when she gives Inciting varies greatly. In the earlier phases of pair formation, females give Inciting only when strange drakes are within a few feet. In spring, when territories were well established in the breeding pens, females sometimes gave Inciting when there was no other male, except her mate, within 60 ft.

During the early phases of pair formation, the male gives no obvious call or movement in response to the female's Inciting, but as the pair bond grows stronger he begins threatening an approaching drake with a series of rapid *rabrab* notes. In some instances, the male may turn to his Inciting mate and utter *Rabrab* calls with his bill pointed upward at a 30° angle.

Inciting was observed most frequently during the first 2 weeks after the birds were released into flight pens, and it gradually disappeared once females began incubating (table 2). In part, this decline in frequency of Inciting (and also male *Rabrab* calls) can be attributed to the greater amount of time that females spend on their nests during egg-

TABLE 1. Physical characteristics of Mallard vocalizations (time in msec, frequency in kHz). Samples were selected on the basis of good quality recordings and spectrograms, and therefore are not random.

Vocalization	Range	Mode	Average frequency[a]	No. analyzed	No. of individuals sampled	Other characteristics (see text for use of terms)
Female Inciting					3	Frequency, amplitude, note duration, and interval duration are all variable within a relatively small range compared to other female vocalizations. Notes have abrupt beginnings with faint endings.
Note duration	30–150	50		98		
Interval	10–400	100		86		
Frequency	0.10–4.00		1.40	98		
Female Decrescendo					7	Most energy falls in the 0.10–4.0 kHz range, but there is usually energy in first few notes of a Decrescendo which ranges to or past 8.00 kHz; amplitude becomes progressively less; last notes are sometimes less than one-third of amplitude and frequency range of the first notes; interval is greater between later notes; note duration and phrase duration vary greatly between individuals.
Note duration	50–600	250		417		
Interval	10–250	0		347		
Frequency	0.10–8.00		1.85	417		
Duration of phrase	1000–3900	1600		69		
Female Quacks					6	Amplitude is greatest in first part of note and is relatively consistent from one note to the next; most energy falls in the 0.10–4.00 kHz; frequency range is greatest in first part of note; interval duration is variable except during spring Persistent Quacking when interval is very constant.
Note duration	200–450	350		33		
Interval	100–450	150				
Frequency	0.10–8.00		1.85	23		
Repulsion Call of Female					1	Abrupt start and stop to notes; most energy falls in the 0.10–4.00 kHz range; sometimes a note will have 2 or 3 harmonics; second and third notes usually loudest, fourth note quietest.
Note duration	70–110	90		11		
Interval	100–150	120		8		
Frequency	0.10–8.00		2.00	11		
Nesting Female					2	The bill-closed *Kn* sounds may have as many as four harmonics, each approximately 0.50 kHz wide at 0.75–1.25, 1.75–2.25, 3.00–3.50, and 4.00–4.50; the fundamental is the one in the lower frequency range; often a 10–30 msec bill-open *quai* will precede the 50 msec *Kn* by 15–25 msec.
Note (*Kn*) duration	30–70	50		35		
Note (*quai*) duration	10–100	40		15		
Interval	100–250	150		34		
Frequency (*Kn*)	0.75–4.50		1.00	35		
Frequency (*quai*)	0.10–2.50		1.25	15		
Female Preflight					3	Females utter two types of Preflight notes, one with bill closed (*Kn*), the other with bill open (*gack*); the *Kn* often leads into a series of *gacks*; amplitude and duration increase with successive notes; notes have very abrupt beginnings; sound interval duration often decreases in later notes.
Note (*gack*) duration	50–250	150		38		
Note (*Kn*) duration	50–90	50		15		
Interval	100–300	200		45		
Frequency (*Kn*)	0.75–1.75		1.00	15		
Frequency (*gack*)	0.10–3.50		1.75	38		
Female Alarm					1	The most striking feature is that sound energy is spread throughout the frequency span and duration more evenly than in a normal *quack*.
Note duration	300–400	400		3		
Interval	470–550			2		
Frequency	0.10–4.00		1.85			
Male Slow *Raehb*					5	Frequency span fairly constant throughout note, occasionally range is lower toward end of note; intensity greater in first part of note; total amplitude is considerably less when compared to female's *quack*.
Note duration	270–450	350		28		
Interval	250–indef.	350		17		
Frequency	1.00–4.00		1.85	28		
Male *Rab*					3	Intensity is constant throughout single note, but total sound energy is less than in a *raehb*; intensity is usually greater on second notes of *rabrab* phrase.
Note duration	50–130	100		44		
Interval	70–320	140		37		
Frequency	1.00–3.00		1.65	44		
Duration of *rabrab* phrase	270–500	350		11		
Male Postcopulatory Whistle					1	Pure tone with slight downward inflection.
Note duration	150	150		1		
Frequency	2.00–2.60		2.30	1		

[a] Average frequencies were determined subjectively by estimation of the frequency on either side of which lies half of the sound energy (Oring 1968).

TABLE 1. *Continued.*

Vocalization	Range	Mode	Average frequency[a]	No. analyzed	No. of individuals sampled	Other characteristics (see text for use of terms)
Grunt-whistle by Male					3	The Grunt-whistle vocalization is a pure tone whistle followed by an extremely low frequency grunting sound.
Whistle duration	90–200	150		7		
Frequency	2.50–3.70		3.00	7		
Interval	40–60	50		7		
Grunt duration	200–270	230		7		
Frequency	0.10–0.60		0.35	7		
Phrase duration	350–520	400		7		

[a] Average frequencies were determined subjectively by estimation of the frequency on either side of which lies half of the sound energy (Oring 1968).

laying and start of incubation. Nevertheless, few Inciting calls were recorded from females which came off the nest during late incubation or after hatching and were "available" to give Inciting. After the female begins to incubate, less and less time is spent with the male. There are fewer aggressive interactions between pairs until finally all aggression disappears, and there is no "need" to perform Inciting. The display was not observed in the captive birds from mid-July through mid-September.

The Inciting display is given by females on land or in the water. Dzubin (1957) and Lebret (1958) reported that the Inciting call occurred quite commonly during aerial chases in spring, and Lebret stated that this was the most common call of the flying female Mallard. Flying captive females were heard giving the call on only a few occasions, always in early spring. Perhaps, captive females must spend so much of their time avoiding the wire of the pen walls during short aerial chases that they are rarely in appropriate aerial position relative to other birds to give Inciting.

Decrescendo. The Decrescendo (Lorenz 1953) is one of the most familiar vocalizations of the Mallard: *qua Quack quack quack quack quack.* Hochbaum (1955) has labeled the vocalization the "hail call" and indicates that hunters often imitate the sound to attract passing birds to decoys. The strongest accent is usually on the first or second syllable and the remaining notes decrease in amplitude. Decrescendos from four different birds are depicted in figure 2. The distinctive characteristics of the call are: (1) the decreasing amplitude of successive notes; (2) smaller frequency range in the later notes; (3) shorter duration of the last few notes; and (4) increase in interval duration between successive notes.

It is generally agreed that the average number of notes is six (Lorenz 1953; Weidmann 1956; Johnsgard 1965). In order to check this statement, special efforts were made throughout the study to record as many Decrescendos as possible from marked females. Birds which were not used in the flight pens were grouped together and allowed to pair. Mates of these pairs were separated and the calling which resulted was monitored by tape recorders during the evenings. Each bird was individually marked, and when a bird called, it was identified and a note was made of the corresponding tape footage. In this way, tapes were collected from which individual variation could be determined. It appeared that each female gave calls ranging quite closely around a certain mode (table 3). For example, female 114, recently separated from her mate, was recorded uttering 42 Decrescendos in one evening, and of this total, 34 had only two syllables. Some females tended to call more frequently than others in response to separation from their mates. This appeared to hold true from one year to the next.

The observed range in the number of notes

TABLE 2. Frequency of four vocalizations in eight captive females during three sunrise to sunset watches. Numbers represent 15-min time periods in which each call was recorded.

Date	Spring persistent quacking	Preflight calling	Repulsion calling	Inciting	Total hr observed
23 April 1969 (Before laying or early laying)	11	48	0	159	14.0
2 May 1969 (Late laying or early incubation)	0	2	22	120	14.25
21 May 1969 (Late incubation)	0	0	41	20	15.0

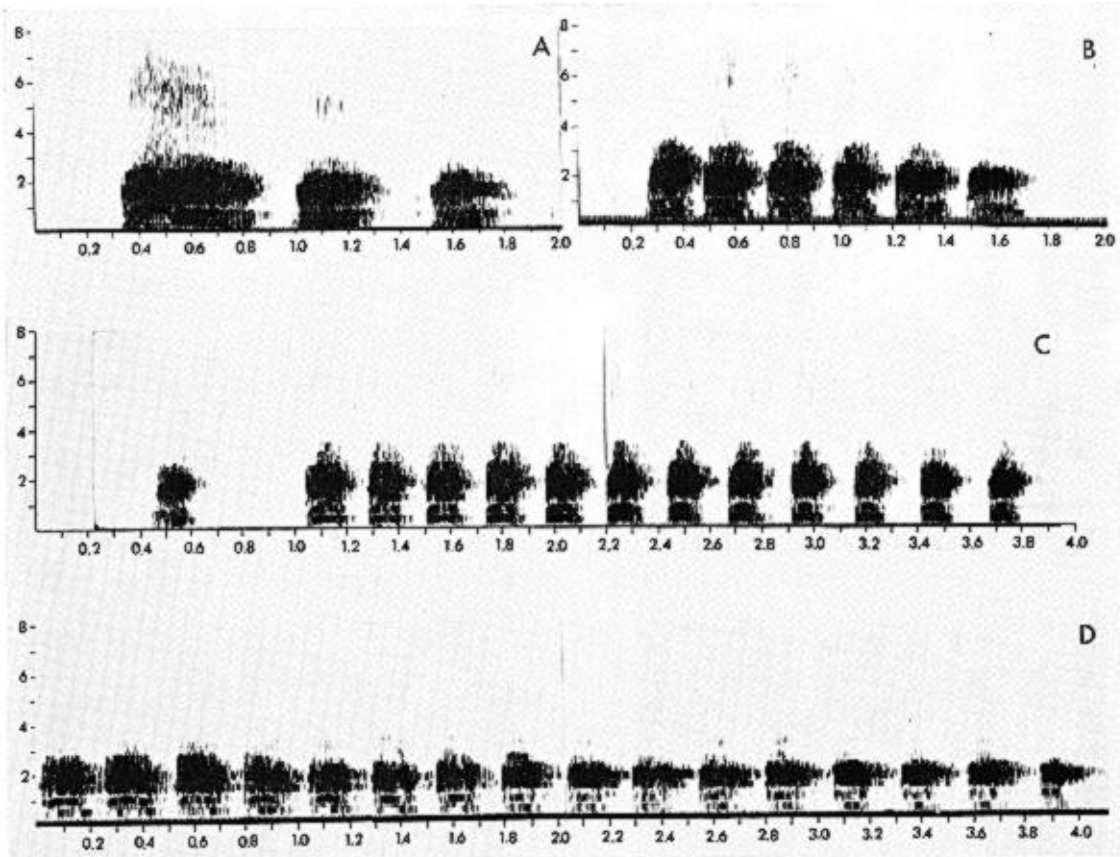

FIGURE 2. Audiospectrograms of Decrescendos of four different females: A, female 116; B, female 131; C, female 117; and D, female 127.

of 687 recorded Decrescendos from the captive females was 1–17. Johnsgard (1965) reported a range of 1–20. One-note Decrescendos were probably more frequent than my records suggest (table 3). They were difficult to identify with confidence when many birds were calling and some were probably missed.

Occasionally, there is a "starter" note which precedes a normal Decrescendo phrase by 300–500 msec (e.g., female 117, fig. 2). This note usually is lower in amplitude than the second note.

Decrescendos given by the same individual have similar physical characteristics (compare figs. 3 and 4). The parameters which make each individual's call distinct are not necessarily the same. Number of notes, duration of notes, notes per unit of time, spacing of interval between notes, and amplitude of notes can all vary to different degrees in individuals.

TABLE 3. Range of variation in number of notes of female Decrescendos recorded during two field seasons.

Female no.	No. of notes																	
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	Total
114	4	47	8	4														63
116	1	6	132	16	2	1	1											159
123			2	7	3													12
129			7	119	39	5												170
131					41	18	5											64
128					9	5	2											16
115					2	0	11	21	23	2								59
111						5	2	0	1									8
118						2	6	0	3	3	2	2	2					20
127							4	7	39	31	9	7	5	3	6	1	1	113
117													2			1		3
Total	5	53	149	146	96	36	31	28	66	36	11	9	9	3	6	2	1	687

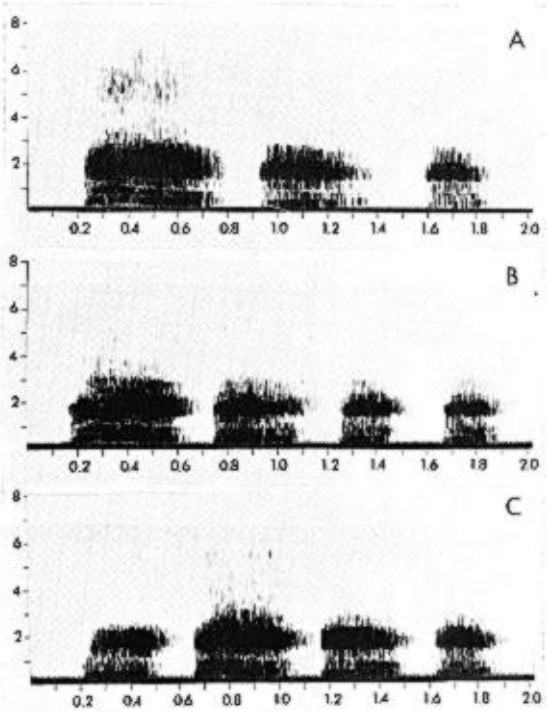

FIGURE 3. Audiospectrograms of different Decrescendos from female 116.

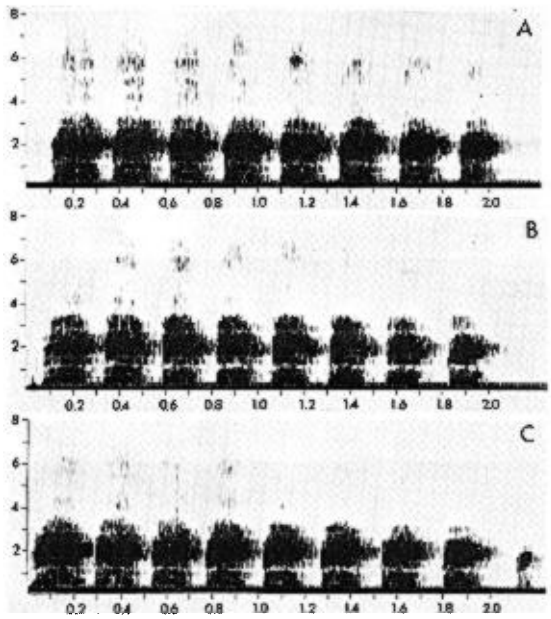

FIGURE 4. Audiospectrograms of different Decrescendos from female 115.

According to Heinroth (1910), the Decrescendo functioned to attract the mate or passing conspecifics. Lorenz (1953) and Weidmann (1956) believed that the call was uttered mainly by unmated ducks or by fast-paired ones, especially when a male has flown by. On several occasions, females, which have been silent for an hour or more, have been heard suddenly responding to a pair or single duck flying over the pens by giving a burst of Decrescendos.

Decrescendos were seldom heard from paired females that had established territories in the breeding pens, probably because the pair-bonds were very strong and the individuals were seldom separated. In 2 years, only six Decrescendos were heard at this season, and all of these were from one individual.

A female usually utters the Decrescendo when she is separated somewhat from the males around her. A sitting or swimming female will give the call during or after stretching her neck upward. The stimulus initiating the first call in a group of birds is difficult to detect. In many instances, females will call in response to their mate's Slow *Raehb* (Lockner and Phillips 1969 and table 4). In addition, however, they will also respond to another female uttering a Decrescendo. The call is very contagious and can easily be elicited from a group of unmated females or females separated from their mates by playing a tape-recorded Decrescendo to the group.

A 44-day laboratory experiment was conducted during January–March 1970 to determine: (1) what experimental situation would provide maximum and minimum number of Decrescendo calls in response to visual but not auditory separation of females from their mates; (2) the relationship between female Decrescendos and male Slow *Raehb* calls; and (3) if the response showed waning after repeated testing of the same individuals. The results are given in table 4.

Three pair of wild Mallards that had been captive for 2 years were used in the experiments. The experimental design was similar to that used by Lockner and Phillips (1969) in which they showed that female game farm Mallards would respond with a Decrescendo call to visual but not auditory separation from their mates. The Decrescendo calls of the females and the Slow *Raehb* calls of the males were recorded for an hour before and after sunrise and sunset while the birds were held in two 20-ft pens separated from each other by another pen. The sides of the pens had 12-inch strips of plywood along the lower edges so that the birds could hear but could not see each other.

There were eight experimental testing situations: three females grouped with their three mates in the same pen (A); three females

TABLE 4. Number of female Decrescendos and male Slow *Raehbs* recorded from mates in response to visual but not auditory separation during 4-hr recording sessions conducted for eight different experimental situations. The situations were: A1 and A2, three females and three mates together; B, three females separated from their mates; C1, C2, C3, each female separated individually from her mate alone; D1, D2, D3, three females separated from one of the female's mates.

Situation			No. of Decrescendos					Total Decrescendos recorded	No. of Decrescendos that had Slow *Raehb* 1–5 sec preceding call	No. of Decrescendos that had Slow *Raehb* 6–60 sec preceding call	No. of Decrescendos that had no Slow *Raehb* Within 1 min preceding call
			Series I	Series II	Series III	Series IV	Series V				
♀♀♀	A_1		0	0	0	0	0	0	0	0	0
♀♀♀	A_2		0	0	0	1	0	1	0	0	1
♀♀♀	B	♂♂♂	85	16	5	0	0	106	82	17	7
1 ♀	C_1	1 ♂	13	1	0	0	0	14	11	0	3
2 ♀	C_2	2 ♂	4	3	2	2	0	11	6	2	3
3 ♀	C_3	3 ♂	7	39	23	13	30	112	7	4	101
♀♀♀	D_1	1 ♂	4	6	0	0	0	10	9	1	0
♀♀♀	D_2	2 ♂	25	12	9	0	0	46	14	10	22
♀♀♀	D_3	3 ♂	76	–[a]	1	0	7	84	33	18	33
			214	77	40	16	37	384	162	52	170

[a] Malfunction of recorder for this recording session.

separated from their three mates (B); a single female separated from her mate (C1, C2, C3); three females separated from a single mate of one of the females (D1, D2, D3). The testing was done in the following order: A1, B, C1, C2, C3, A2 (*A* was repeated to reinforce the pair bonds), D1, D2, D3. The conditions were changed in sequence (A1, B, C2, C3, C1, A2, D2, D3, D1 . . . A1, B, C3, C1, C2, D3, D1, D2) after each series. Each series was repeated five times.

The experiments showed that: (1) conditions B (three females separated from three mates), C (one female separated individually from her mate), and D (three females separated from one of the female's mates) all resulted in significantly more calling ($P \leq 0.05$ one sample runs test; Siegel 1956) than condition A (three females grouped together with their three mates); (2) neither situation B, C, or D proved to be more effective than the other in producing Decrescendo calling; (3) except in a few instances the frequency of calling was less in later replications of the same situation; (4) since there were over three times as many total calls in a 5-sec period as there were in a 55-sec period (162 versus 52), it appears that Decrescendos are many times "triggered" by the mate's Slow *Raehb*; and (5) the Decrescendos recorded in situation D (three females separated from one of the female's mates) were given most often by the mate of the male from which they were separated. When the experiment was first started, females were selected on the basis that each female could be identified from the other two by voice alone. After the experiment was underway, it became obvious that two of the females sounded somewhat similar in some instances. Only the calls of the mate of male 1 were positively identifiable. Of the 10 Decrescendos recorded in situation D1, 9 were from his mate. The same appeared to be true for D2 and D3, except that it was difficult to document with accurate counts.

Decrescendo calls can be heard from wild birds at any time of day, but were heard most frequently shortly before and after sunrise and sunset from the captive birds. Decrescendos were seldom heard during the mid-afternoon from any of the captive birds, even if the females were separated from their mates. The calling usually began about one-half hour before sunset (table 5). These data are from nonbreeding females which had preferred males and responded with Decrescendos when separated from them. Weather seemed to have some influence on the rate of calling. If the days were warm and sunny, calling often did not start until after sunset. On overcast or rainy days, calling seemed to be spread out more evenly during my 2–4-hr watches. Occasionally, calling was also heard throughout the evening, especially on moonlit nights.

Of all Mallard vocalizations, the Decrescendo is the one which has the most obvious diurnal periodicity, but other vocalizations also tend to be heard more frequently during morning and evening hours. During the rest of the day, including the evening, Mallards tend to be polyphasic in their vocal activity. The birds are active for 30–45 min and then inactive from 20 min to 2 or 3 hr.

TABLE 5. Frequency of Decrescendo calling by 12 females separated from their mates in relation to time of sunset during April, May, and June 1969 and 1970.

Time span observed	Total hr observed	Decrescendos recorded	Rate/hr
2½–1½ hr before sunset	11	23	2.1
1½–½ hr before sunset	12	67	5.6
½ hr before sunset–½ hr after sunset	12	266	22.2
½–1½ hr after sunset	3.5	106	30.0

Spring Persistent Quacking. Females give single *quacks* or a group of *quacks* in irregular or regular patterns. One of the patterns I understand best is a behavior associated with the beginning of the breeding period labeled as "Persistent Quacking" by Hochbaum (1944), Dzubin (1957), and Hori (1963). The calling consists of a series of single evenly spaced *quacks*, given at a rate of about 1 or 2/sec, the calling rate varying with the individual. The monotony of the calling is the most striking characteristic of Persistent Quacking. Spectrograms of portions of bouts of Persistent Quacking from different females (fig. 5) illustrate how little variation there is in the duration of notes, duration between notes, amplitude, and frequency of each note.

According to Dzubin (1957), Persistent Quacking was characteristic of paired females about to begin laying. The female gave these notes both in morning and evening twilight periods. Hori (1963) stated that the primary period was early morning, mainly shortly before and after dawn. This was also the case in my penned birds.

Females called with or without their mates, but in either case they appeared very "nervous." Wild birds were observed flying around a marsh about a half-mile wide, calling all the way around. While calling, their heads were moving from side to side. Persistent Quacking was most frequent in the captive birds during the weeks before they began laying (tables 2 and 6). Three birds were observed calling on 6, 7, and 8 consecutive days. One bird was heard giving 185 *quacks* in a 10-min period. While doing this calling, the birds would stretch their necks upward, often while performing preflight head-jerking. The calling which occurred in this situation should not be confused with the Preflight call which will be discussed in the next section.

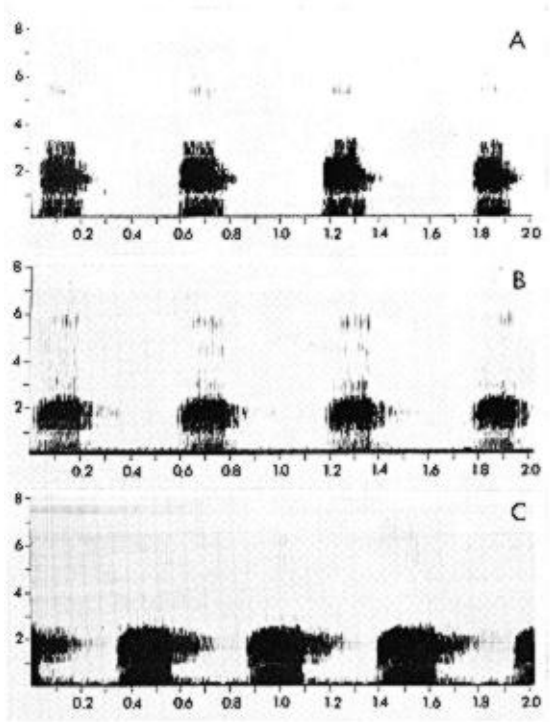

FIGURE 5. Audiospectrograms of portions of bouts of Spring Persistent Quacking by three different females: A, female 117; B, female 20; and C, female 118.

The number of flights around the pen were

TABLE 6. Occurrence of Spring Persistent Quacking, Preflight calls, and Repulsion calling by females in 1968 and 1969 flight pen seasons. (Number above the line indicates the quantity of birds in which calling was observed; number below the line indicates quantity of birds under observation). Records are based on observations conducted every day from 1–4 hr after sunrise.

	Days before first egg was laid											Days after first egg was laid									
Vocalization	10	9	8	7	6	5	4	3	2	1	0	1	2	3	4	5	6	7	8	9	10
Persistent Quacking	0/5	0/5	0/5	1/8	4/9	3/10	5/10	6/10	7/12	4/12	6/12	1/12	1/12	0/12	1/12	0/12	0/12	0/12	0/12	0/12	0/12
Preflight Calls	1/3	–	1/3	–	4/6	–	5/7	–	4/8	–	2/8	–	0/8	–	0/8	–	0/8	–	0/8	–	0/8
Repulsion Calling	0/8	–	0/8	–	0/8	–	0/8	–	0/8	–	7/8	–	3/8	–	5/8	–	6/8	–	5/8	–	5/8

counted by a fellow observer, Julie Barrett. She indicated (1973) that their frequency increased at the same time as the birds started these periods of Persistent Quacking. McKinney (1967) in his pen study of captive Shovelers (*Anas clypeata*) also found that the number of flights was greatest before eggs were laid.

Two of the four females which laid eggs in 1968 and seven of the eight captive birds which laid eggs in 1969 were observed Persistent Quacking. Three females laid eggs both years. Two were observed calling during both years, the other, only during the second year. Persistent Quacking first was observed 30 days before the first egg was laid. The last bout of Persistent Quacking was heard 4 days after the first egg was laid. The frequency of calling dropped off markedly after the first egg was laid. During the 10 days preceding the first egg, calling was observed on 35% of bird days; whereas, during the 10 days after the first egg was laid, calling was observed on only 2% of bird days.

It seems that this type of calling might be maladaptive in that it must make the presence of a pair conspicuous to predators. However, perhaps there is an advantage in being conspicuous to other Mallards. Persistent Quacking may play a role in advertising the presence of a breeding pair and this behavior may be important in pair-spacing on the breeding grounds.

Preflight call. The Preflight sounds of a female are a series of short, sharp notes. The sounds can vary greatly in intensity, from a whimpering sound given when the bill is closed to a harsh *gack* given with the bill open (fig. 6). As the moment of take-off approaches, the short sounds become louder. It is probable that these predeparture sounds provide mutual stimulation promoting a simultaneous take-off of the group. At the same time as the sounds are being produced, the bird is repeatedly jerking the forepart of her body upward. These calls and associated movements are particularly characteristic of birds preparing to take wing "of their own will" and for some reason are delaying take off. It is relatively easy to predict fairly accurately when the bird will leave the ground, even though it may be out of sight. Figure 6 B and C are illustrations of a call given by a female which eventually took wing. The sound given after the bird jumps into the air is similar to the call a female gives when she is alarmed. Lorenz (1953) has labeled the Preflight sounds as the "Going-away" call.

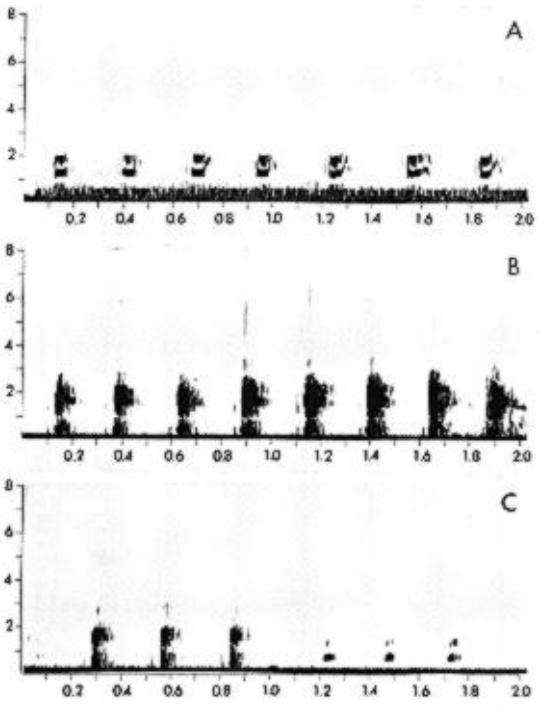

FIGURE 6. Audiospectrograms of a series of female Preflight calls: A, given with bill closed; B, given with bill open; and C, given with bill open and bill closed.

Preflight vocal behavior is especially characteristic of females during the days when they are searching for a nest site (tables 2 and 6). The captive females, while walking around looking for a nest site, often make short vertical flights, rising 1–3 ft above the ground. I got the impression that, if the birds were not enclosed by wire, these flights would have developed into nest-searching flights. In addition to the flights, these birds repeatedly gave Preflight head-jerking. These flights, head-jerking movements, and related calls are probably all indicators of restlessness associated with the prelaying period.

Repulsion call. Repulsion behavior (Lorenz 1953) is characteristic of females which are incubating or caring for young. Repulsion is given by a female as she is pursued by a strange drake intent on "raping" her. It occurs often when a strange male approaches an incubating female on her nest. He chases her off and as she flies or walks off, she tucks her head back "into her shoulders" (Lorenz 1953), with her neck and head stretched back. At the same time her bill is opened with the upper mandible very conspicuously raised. The tail feathers are fanned and back feathers are ruffled. Accompanying the strange posture

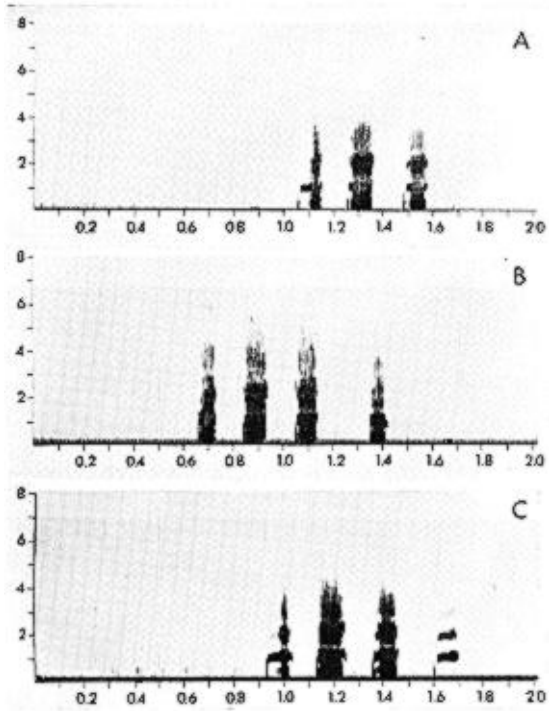

FIGURE 7. Audiospectrograms of different Repulsion calls of female 127.

is a series of harsh notes rendered as *gaeck* by Lorenz (1953).

Repulsion behavior was not observed until shortly before or after the females had begun incubation (tables 2 and 6). As soon as clutches were near completion the Repulsion posture and call became very frequent. The call is a series of loud harsh *gaeck* sounds uttered in regular patterns. The notes have abrupt starting and stopping points. Very often the call is a series of three or four notes, the second louder than the first and the third not as loud as the second but louder than the first (fig. 7). If the chase develops into an aerial pursuit, the female continues giving the call. The behavior does not appear to intimidate the pursuing males. In fact, sometimes it seems to attract males.

It appears that Repulsion behavior is definitely indicative of an incubating female, female with a brood, or a female which has lost her clutch. Birds off the nest with or without their mates will utter the call when approached by a hostile stranger. In the earlier phases of incubation, the mate may chase off the attacker, but toward the end of incubation the female receives no aid from her mate. In a few instances, females that were being harassed while their mates were nearby gave a mixture of the Inciting sound and Repulsion call. The sideways head movement characteristic of "pure" Inciting was not very evident in these instances.

On many occasions, birds which were giving Repulsion calls attracted other males. It is difficult to distinguish what part the call plays in the attraction because the female trying to escape often splashes, this also is very obvious to nearby birds. On one occasion it became apparent that the call itself had a powerful attracting effect on nearby males. While observing two males loafing on a small open water area within a cattail region on the edge of a larger lake, a female, which had been incubating, swam through some cattails into the area occupied by some males. Immediately, one of the males began harassing her and attempted to copulate with her. The other male, which apparently was her mate, tried to beat off the mounted male. While she was being harassed, she gave sharp *gaeck* calls. Upon hearing the call, two males, both loafing about 150 yards away from the female and out of sight of her, came flying in a straight line and attempted to join the "rape" attempts. The group broke up when the males began fighting among themselves and the female was able to fly away.

Sowls (1955) noted that the female Pintail (*Anas acuta*) also exhibits Repulsion behavior, and he proposed that a similar behavior functions in attracting males for renesting. Phillips and van Tienhoven (1962) came to a similar conclusion and suggested that the same is true for the Mallard. Phillips (pers. comm.) reported that females which had lost their nests exhibited behaviors much like Repulsion, except in the instances he observed the females made no apparent attempt to chase off attracted drakes.

McKinney (1969) reported that behavior similar to Repulsion can be observed in incubating, tame female Mallards when approached by man. He mentioned that the posture was similar but that the call was lacking. On several instances in which wild, incubating hens were disturbed, I have observed behaviors similar to the one which is a response to an attacking drake, except that the posture was not as rigid. In some cases a wing-thrashing behavior was also present and was interpreted as part of a "Distraction Display." The call accompanying this distracting behavior is somewhat like a Repulsion call except that the notes are shorter and not so hoarse in quality. It will be described in more detail under the Alarmed call heading.

Only a few Repulsion calls were heard from females with broods. Three females whose clutches were destroyed before hatching still

gave Repulsion calls a week after the clutch was destroyed. Smith (1968) reported that broody behavior was observed in the Pintail for as long as 2 weeks following nest destruction. Perhaps behaviors like these may be what Sowls (1955) has termed "teasing" behavior. It seems probable that the "Teasing" call and Repulsion notes are the same. Since the call does not seem to intimidate males, its suggested original function of repelling (Lorenz 1953) probably has been at least partially lost. Now it appears primarily to be a means of attracting males to females requiring fertilization for renest clutches.

Repulsion calls have been heard at other times of the year, but only from females which had been in the laboratory and subjected to abnormal photoperiod. Experimental studies are needed to determine the function of this most interesting call.

Calls of the broody female. Except for an occasional Repulsion call in response to an intruding male and an Alarmed call in response to a sudden disturbance, female Mallards were silent after incubation started. Females often gave Preflight calls during the period when they were searching for a nesting area, but after incubation started, this restless type of behavior was not observed.

As the hatching date nears, the female again begins calling. The "Maternal" call consists of a series of low frequency, low amplitude notes uttered at irregular intervals. A series of these notes are depicted in figure 8. Females were heard uttering the broody notes 2 days before hatching took place. McKinney (1969) pointed out that the calls became increasingly louder and more frequent as the hatching point drew closer. Gottlieb (1965) reported that at exodus a female called at a rate of 4 notes/sec, and in a more recent paper (1968a) he presented a sonogram representation of such a series of notes. Bjarvall (1968) reported a mean calling rate of 8 notes/min with an observed range of 0–46 during 20-10 hr before exodus, and a mean calling rate of 40 notes/min with an observed range of 0–219 during 7.5–0 hr before exodus. There is great fluctuation in the rate of the female's calling, but it is obvious that the rate increases as the time of exodus approaches. See Hess (1972) for a more detailed analysis of the subject.

It also appears that the quality of the call changes from a bill-closed *gn gn gn gn* to more of a bill-open *quai quai quai* as the point of exodus draws closer (compare A and D in fig. 8). If the female is alarmed while she

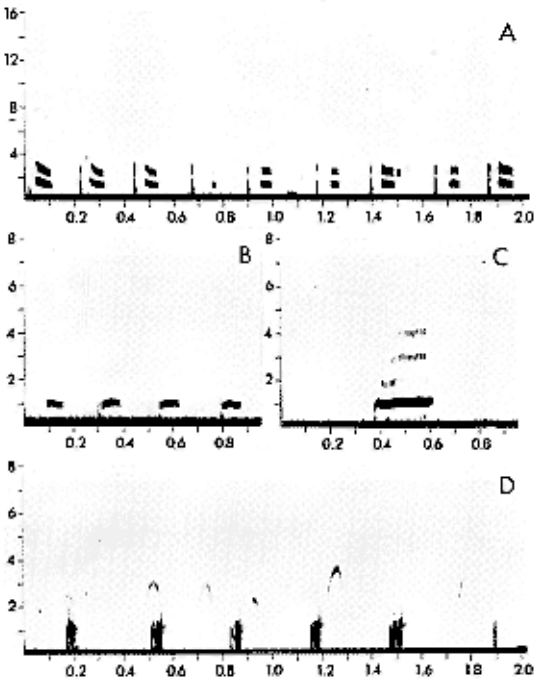

FIGURE 8. Audiospectrogram of calls of broody females: A and B, notes from different incubating females; C, alarm note of female with young; and D, female calling when young are still on the nest, the faint inflected lines above the female's notes are duckling *peeps*.

is with the brood, the amplitude and duration of the sound increases (fig. 8C).

Females of other species of ducks have also been heard to utter maternal notes during the later stages of incubation (Collias and Collias 1956; Collias 1962; McKinney 1970).

The call uttered during the late incubation stage quickly develops into a "Leadership" call (Weidmann 1956) soon after hatching. It has characteristics similar to notes given at hatching time, but there appears to be more variation in pattern and intensity. A female seems to give these notes quite frequently when she wants her brood to follow. Presumably, the soft, repetitious notes are effective at close range in communication between parents and ducklings, but they are not loud enough to betray the presence of the brood to predators. Stimuli which elicit these sounds are the sudden approach of an enemy, i.e., bird of prey, dog, or man. They are given also when a female moves from an open area of water into the marsh-edge vegetation. As the vegetation gets thicker, the mother's call gets louder and faster. The response of the ducklings is to come together into a more compact group. Weidmann (1956) suggested that notes used in such instances were a combination of the leadership sound and de-

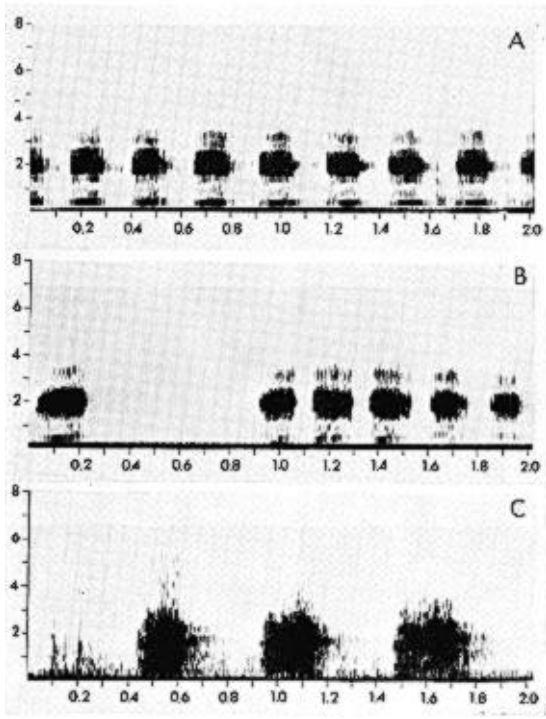

FIGURE 9. Audiospectrograms of Decrescendo-like call of female with young and Alarmed call: A and B, two different Decrescendo-like calls from female 118; C, response of same female to author looking into pen.

parture sounds. Several investigators (Collias and Collias 1956; Klopfer 1959; Weidmann 1956; Boyd and Fabricius 1965) have tried to induce the following response in ducklings by imitating the leadership sound. More extensive reviews of these experiments are given by Bateson (1966) and Sluckin (1964).

The Leadership call was heard often from wild birds but very seldom from penned ones. Perhaps situations eliciting maternal calling in captive birds did not arise since the pen had fairly short grass, allowing the female to be in constant sight of the ducklings, or possibly, the calls were so quiet that they could not be heard.

Another female call which was heard after hatching was a Decrescendo-like call. It sounded similar to the Decrescendo which was discussed previously, except it had the nasal quality of a Repulsion call (fig. 9A and B). Smith (1963) referred to a call of the broody female Pintail as a "Broody Decrescendo." In the Pintail the call is used in harassment situations. The Decrescendo-like call of the broody Mallard might be homologous to the Pintail's call except that the call of the Mallard was not observed in the same situations. The female uttered a series of descending notes which vary in number from 1–20. The stimulus for the call was not evident, and no obvious response was observed from the surrounding adults nor from the female's ducklings. At least there was no apparent movement to or away from the calling female. Two of the eight females that brought off broods were recorded giving the calls 1–2 weeks after the broods had hatched. Perhaps, these calls represented the "reappearance" of Decrescendo calling, with other components superimposed.

Alarmed call. When the female sights a large, flying predator, she sometimes utters a single *quaaack.* On hearing this call the other birds nearby, some of which may be sleeping, immediately hold their heads up and begin tilting them sideways as they scan the sky. In such situations this sound of the female was recorded much less frequently than the homologous Slow *Raehb* of the drake. Upon seeing an overhead hawk, one or several of the drakes in the pen will almost invariably call, but this was not the case with females.

A similar sounding call can be heard from a female which has been suddenly disturbed (fig. 9C). The call given in this situation is uttered by a female just before or after she jumps into the air, and sonograms of notes given in these two situations appear somewhat similar (compare fig. 9C with last few notes of fig. 6B).

Another type of Alarmed call is given by a female with a brood after she has been disturbed. The call which often accompanies the "Distraction Display" is a series of short, nasal notes uttered in an irregular pattern. The notes are not as harsh as the notes of a Repulsion call but they closely resemble it. These calls have not been analyzed by sonogram.

Stephen (1963) reported that females with eggs will give the sound of alarm much more readily than females with broods when flushed by man. He suggested that such an alarm note could be used as an indicator of whether a female had a nest or brood.

Of the several types of female calls, the Alarmed call was the only one which was heard with any regularity during the molting period. Molting females in the flight-pens could be made to vocalize only if they were cased from their grassy hiding places. Oring (1964) wrote that during a summer of study he "never" heard a call from a flightless Mallard.

Miscellaneous notes. Females give single *quacks* or a short series of *quacks* in other situations. Weidmann (1956) cited several examples of solitary females giving single

quacks until they are joined by other birds. He also mentioned that wild birds often try to get into the cages in which captive ducks are calling. He said that the caged animals called whether or not they could see the other ducks. In many cases, he could detect no escape drive, and he concluded that the ducks had a genuine "appetency" for company.

Many experienced duck hunters can remember instances in which single female Mallards have swum to within 100 or 200 yards of a set of decoys, at which point they began to give a series of *quacks*. If one uses a wooden duck call, the females seem to answer each note of the caller. Females hidden in dense cattails can also be enticed to answer imitated Mallard calls.

Occasionally, one can hear a series of eight or nine *quacks* followed by a Decrescendo. It appears that a Decrescendo and single *quack* on occasions have the same function. Probably the Decrescendo is a more specialized call-note and has a slightly higher threshold of activation.

Other quiet, quacking-like sounds which the female utters are whimpering *Kn* sounds mixed with more intense *quais*. The sounds are often uttered by a female as she gives precopulatory head-pumping. The soft whimpered notes probably indicate her readiness to copulate. Birds moving short distances while changing places on land or water can also be heard giving the quiet notes. One of the most likely situations in which to hear these sounds is from a group of feeding ducks. Hochbaum (1955) reported a female "Food" call which sounds something like *tuckata tuckata tuckata*. Frequently, females have been observed giving soft whimpering sounds intermixed with preflight sounds while moving from one ear of corn to another. Many times while feeding a female may come too close to a male and she may utter the Inciting call. Collias (1962) suggested that the *tuckata* sounds described by Hochbaum (1955) are actually the Inciting notes of the female. My observations suggest that there is a characteristic sound from a feeding flock, but the sounds appear to be made up of a conglomeration of vocalizations including Inciting, none of which seems likely to indicate presence of food to other ducks.

MALE VOCALIZATIONS

The male Mallard produces several types of sound: a flute-like whistle, a grunting sound, and a nasal *raehb*. The tone of the drake's voice is much different from that of the female; the difference probably is due to

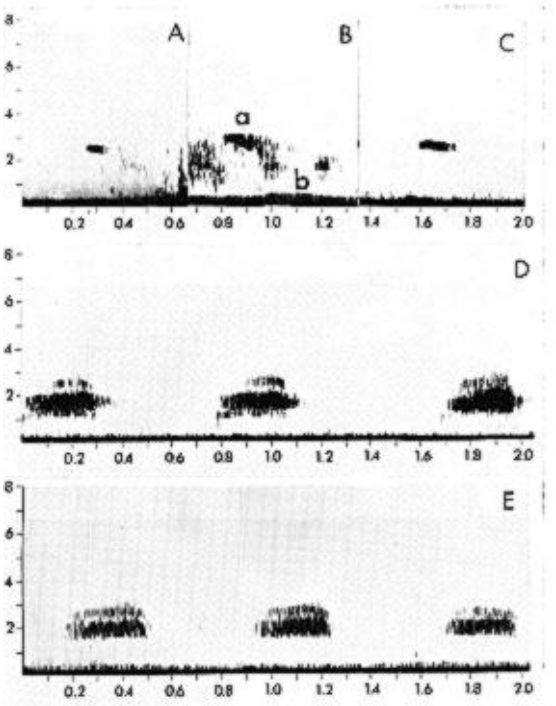

FIGURE 10. Audiospectrograms of Courtship Whistles, Postcopulatory Whistles, and Slow *Raehb* calls of male: A, whistle given in "Down-up display"; B, sounds uttered during "Grunt-whistle display" (*a* is above whistle and *b* is above grunt); C, whistle given during "Postcopulatory display"; D and E, Slow *Raehb* calls of two different males.

structural differences in the trachea and associated syrinx (Phillips 1922–26; Johnsgard 1961). Abs (1970) made measurements of resonant frequencies from isloated tracheas of male (with bulla ossea) and female Mallards and found a significant difference in the quality of the sounds produced. He concluded that the bulla ossea functions in the production of a wider band of resonant frequencies between 500 and 2000 Hz.

The nasal *raehb* is the male's most common vocalization. This rasping sound is given with a variety of intensities and rhythms, the most familiar being a slow monosyllabic, drawn-out *raehb* and a rapidly uttered double-noted *rabrab*. These are the two extremes, but there are gradations from one to the other. Physical characteristics of the male sounds are described in table 1.

Courtship whistle and grunting sound. The flute-like whistle of the male is produced on only two occasions, both of which are in the presence of a female. One situation is during social courtship when the male performs either a "Down-up" or "Grunt-whistle" display (fig. 10 A and B). During the Grunt-whistle display, the male lowers his bill to the water

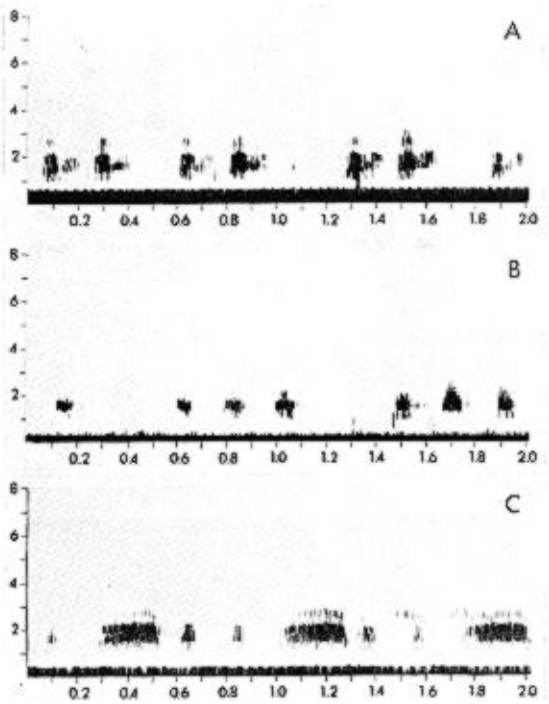

FIGURE 11. Audiospectrograms of variations of the male *Rabrab* call: A, recorded from male swimming side-by-side with another male, both of which were in the "Bill-up'" posture; B, call of male being mildly harassed by author; C, call of male whose mate was being harassed by another male.

surface and then arches his body upward, and at the peak of the arch the bill is flicked sideways, producing a fine spray of water droplets. While the head is being brought backward, a pure tone whistle near the 3.0 kHz range is emitted. A low frequency "grunt" is produced 40–60 msec after the whistle. Probably the whistle is caused by a sudden intake of air and the grunting sound is a result of compressed air being released. According to Johnsgard (1960), females giving the Inciting call will often elicit "Grunt-whistles" from males. Another courtship display in which a whistle is produced is the "Head-up-tail-up" display (Lorenz 1953; McKinney 1969). In the "Down-up" display, the whistle is given while the breast is at its deepest point in the water and the head is at its highest point. The whistle given by the male during the Down-up is lower in amplitude than the whistles given during the Grunt-whistle or Postcopulatory display. The reason is probably that the whistle is given from a different posture, and there are probably different physical stresses on the trachea. More detailed descriptions of these displays are given by Weidmann (1956), Johnsgard (1960), Lebret (1961), Raitasuo (1964), McKinney (1969), and Field (1970).

Postcopulatory whistle and grunting sound. The other occasion when a whistle is produced is after copulation, just before the male pulls his head back to the "Bridling" posture. One Postcopulatory Whistle was recorded on tape (fig. 11C). It was 150 msec long and in the 2.75–3.40 kHz range. The characteristics of this whistle were similar to those given in courtship situations. In most instances, the male emits the whistle while still grasping the female's crown feathers with his bill. After the male has dismounted completely, he nod-swims silently around the female. My observations suggest that the whistle is given only after a mounting in which the male actually thrusts his penis. I don't think there has to be intromission. Normally, a pair copulates once or twice a day. Copulations are usually several hours apart but in one instance a male was observed copulating with a female twice within a 1-min period. After each copulation, the male went through the full postcopulatory display, including the whistle. On several occasions, when males apparently were successful in "raping" a female on land or water, they also gave the full postcopulatory display including the whistle.

On several occasions copulations have been observed in game-farm Mallards at a distance of approximately 5–10 ft. In many instances when a whistle was given, a grunt, similar to the one following the whistle in the Grunt-whistle, followed. This leads me to believe that the grunt is a result of compressed air being released as Lorenz (1953) suggested.

Gasping. Another type of grunting sound other than that given during the "Grunt-whistle" and "Postcopulatory" display is the "Gasping" (Kuechen) produced by males during social courtship bouts. Lorenz (1953) was the first person to describe this peculiar sound. He noted that it can be imitated best by saying a three-syllabled *chachacha*, while breathing out, then in, then out. Lorenz suggested that "weak" drakes gave this sound while other members of the courtship group uttered the whistle. Von de Wall (1963) believed this behavior was an "expression of highly active participation in the display of the others." Although the sound was heard on several occasions, detailed observations were not made. A more thorough investigation, with the aid of social courtship experiments, should aid in providing a better understanding of the function of this sound.

Slow Raehb. The Slow *Raehb* of the male (fig. 10D and E) is produced in a variety of situations. Few records on species other than ducks can be found in the literature of instances in which a bird uses a similar note to both attract and alert a conspecific, yet this is what occurs in the Mallard. Lorenz (1953) has said ". . . I am never able to decide from the call whether a drake is calling or warning his mate." The calls are similar, but there does appear to be "intensity variants." If a bird is alarmed by a sudden noise, the call given most often is slightly lower and more rasping than the sound uttered in the presence of a female.

The sight of flying birds of prey will usually elicit a Slow *Raehb* from one or several males. A male, upon sighting a large hawk, raises his head and tilts it sideways, looking up at the sky. The nape feathers are ruffled while the other body feathers are sleeked. One or several notes may be given by an individual bird. Often nearby males will also give a Slow *Raehb*, but it is difficult to say whether they are responding to the initial calling bird or directly to the bird of prey. Unless a female is the first bird to sight the predator, she will seldom respond with any kind of vocalization. Males respond similarly to an approaching man or to the noise of a tractor. In the wintering house when they heard a door open, males often responded with outbursts of Slow *Raehbs*. The American and European races of the Green-winged Teal (*Anas crecca crecca* and *A. c. carolinensis*), which were housed with the Mallards, would also respond to the opening of a door. Their call, in this situation, was a high-pitched whistle. Apparently, the whistle is homologous to the Mallard's Slow *Raehb*. Of all the vocalizations of the Mallard, the Slow *Raehb* call is the most predictable. After a sudden disturbance, such as that caused by a man looking over the edge of the pen, a male will invariably call while swimming or flying away. The amplitude of the call varies slightly with the degree of alarm.

Many situations occur in which the male appears to be using the Slow *Raehb* to attract the attention of a female or to announce his location. A bird circling a landing spot often gives this call. One often gets the impression that the bird expects an answer. A single male will do the same thing when approaching a set of decoys.

Another situation in which the male gives Slow *Raehb* call-notes is after his female has begun incubation. For a long time it was puzzling why single, loafing drakes in the flight pens were uttering these slow drawn-out *raehbs* late in the nesting season. These drakes appeared alert but not alarmed. This behavior appeared in the captive birds for a period of from 1 to 2 weeks. The function of the call became obvious only after I noticed that the calling males always had an incubating female nearby. Apparently, the males were indicating their locations to nearby incubating females. On occasion, the females seemed to respond to the calls by coming out of the nesting cover to join their calling mates.

During the second year of the flight-pen study, the number of Slow *Raehb* calls given by each individual was recorded for a 2-hr period every other day. Similar records were kept on the *Rabrab* call, Inciting call, Spring Persistent Quacking, Preflight calls, and Repulsion calls. There was a gradual decline in the frequency of all calls as the season progressed, but it was most marked in the case of the *Rabrab* and Inciting call. The frequency of Slow *Raehb* calling was always less than the frequency of *Rabrab* calling except in the late stages of incubation.

In the fall, winter, and early spring when females are giving Decrescendos, a male can be observed responding with Slow *Raehbs* to a particular calling female. The reverse is also true as was pointed out earlier when the Decrescendo was discussed. Males also give repeated Slow *Raehbs* during social courtship especially after "Head-up-tail-up" display, but detailed observations have not been made on these situations.

Rabrab call. The Rabrab call of the male is uttered in many different situations, but it is generally agreed that the call is associated with aggressive tendencies (Heinroth 1911) or with the presence of both escape and attack tendencies (Weidmann 1956). There is a wide gradation of sounds from the Slow *Raehb* to the rapidly uttered double-noted *Rabrab* (fig. 12). All *rab* sounds made by the drake, other than the drawn-out *raehb*, have been grouped under the label of *Rabrab* call. The grouping seems logical since there were no single-note, rasping sounds in the 130–270 msec duration range of any of the sonograms analyzed. Those single *rab* notes grouped under the heading *Rabrab* range from 50 to 130 msec. The duration of one, two, or three notes together plus the interval between notes can be from 50–500 msec. This section of the paper will include a discussion of all of these gradations.

The most familiar form of the *Rabrab* call is a double-noted sound, with emphasis on the second syllable (fig. 11A). These sounds are

uttered in a wide range of situations from a variety of postures. The most familiar posture is the "Bill-up" which is seen when two males are about to fight. As two males come together, their heads gradually rise to a point where their bills are pointing obliquely upward and slightly away from each other. The distance between their heads varies considerably, apparently depending on the strength of their aggressive tendencies. If the two birds turn toward each other, they lower their heads and bring them forward. During this movement, the double-noted *rabrabs* are often mixed with *rabs*, and *rabrabrabs*, and Slow *Raehbs* (fig. 11B and C).

Following this behavior, males often begin breast-to-breast fighting. Calling continues during the fight, the dominant bird doing most of the calling. If one male turns away and retreats, the other bird may chase him with head stretched forward and downward. The chasing bird gives *Rabrab* calls. The retreating bird runs away, with head extended, usually without giving calls. If, after a fight, the dominant bird does not chase, he may give the "Bill-up" display. Lockner and Maley (unpubl. data) have shown experimentally that the probability of the game-farm males giving this display is greatest when the mates are present. A good situation in which to observe male-male conflicts of this type is when several males are attempting to "rape" the same female.

The "Bill-up" display is not always followed by a fight. Sometimes the males merely turn away and swim off. This seems to occur more often in males which have been "displaying" at greater distances. For example, two birds 1–2 ft apart may swim along side by side for 50 ft, each giving the "Bill-up" display with accompanying *Rabrab* calls. Intermixed with the displays are often short bursts of ritualized drinking and preening movements. These side-by-side swims seem to break up when one of the birds faces away from the other. Bill-up *Rabrab* calls can also be heard from a whole group of males after they have been suddenly alarmed (Lorenz 1953; Weidmann 1956) or after a female has suddenly been introduced into a group of males which have been separated from females for several days.

One can also hear the *Rabrab* call from a male after a territorial pair is threatened by an approaching drake. The intruder may approach by land, water, or air. The territorial male responds with *Rabrab* calls, and at the same time the female often makes Inciting movements. If the territorial male happens to be separated from his female which is being threatened, upon returning, he and the female again display, even though the threat may have long passed. Such behavior has in some instances been termed a "greeting ceremony." Lorenz (1953) has labeled the whole performance a *Rabrab Palaver*, and in this situation he suggested that it may correspond to the "Triumph Ceremony" of geese and shelducks.

When a male gives *rabrab* notes in response to his female's Inciting, he often points his head away from her while calling. Lorenz (1966) suggested that this turning away of the head corresponds to the appeasement ceremony of Head-flagging in gulls. If a drake is exceptionally excited, he may redirect his aggression at an "innocent bystander" by pecking or threatening him.

It is difficult to obtain a clear recording of the various forms of the *Rabrab* call because it is seldom given when other birds present are silent. A calling male invariably seems to elicit *Rabrab* calls from an accompanying male. In instances in which the call has been stimulated electrically in the presence of a dominant companion, the dominant birds invariably reacted with a head-up posture and *Rabrab* call (Maley 1969).

The frequency of *rabrab* calling was greatest in the captive birds during the first month after the introduction of the birds into the flight pen. As the frequency of *rabrab* calling decreased, the sociability of all the birds increased. The peak calling period and gradual decline coincided fairly closely with the peak and decline of the Inciting call. The tapering-off was also evident in the Slow *Raehb*, and the daily frequency of Slow *Raehb* calling of most males was generally lower than the frequency of *Rabrab* calling. This is what I would expect since during the breeding period in the flight pens there are probably many more situations which would result in aggressive calling.

Drakes give calls intermediate between the *raehb* and *rabrab* in a variety of situations: while feeding; before, during, and after copulation; while making place-changes; while bathing; during mild encounters with other Mallards; and after a disturbance. The situations are very complex and further study is needed.

DUCKLING VOCALIZATIONS

Shortly before hatching, ducklings are able to vocalize and are responsive to maternal calls (Gottlieb 1968b, 1971; Hess 1972; Impekoven 1973). According to Gottlieb and Vandenbergh (1968), the ability to vocalize de-

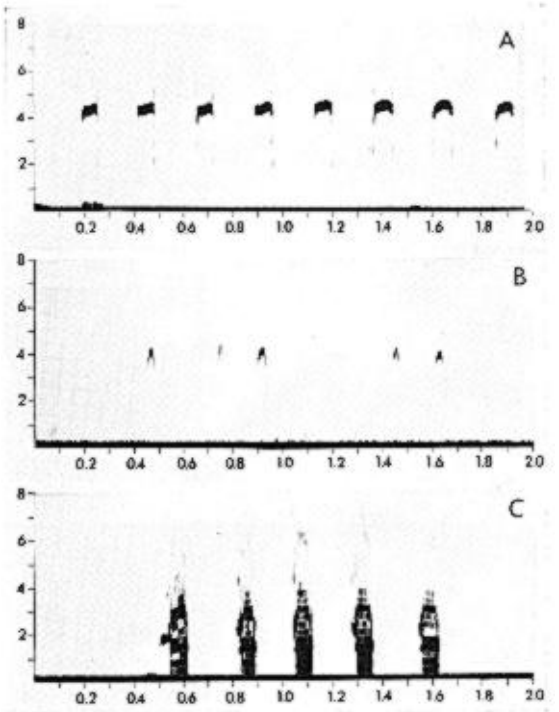

FIGURE 12. Audiospectrograms of sounds of ducklings: A, distress notes; B, contentment notes; and C, distress notes of 5-week-old Mallard.

veloped 3 and one-quarter days before hatching. The authors grouped these prenatal sounds into three categories which they suggested correspond to three types of calls of newly hatched ducklings: "distress," "contentment," and "brooding-like calls." Other investigators (Collias 1962; McKinney 1969) and I did not make the distinction of the third type of call in ducklings after hatching.

The contentment sounds are quiet, short notes uttered at irregular intervals. The emphasis appears to be slightly more on the ascending frequencies. Collias (1962) and Kear (1968) presented sonograms similar to figure 12B, illustrating the contentment notes of one-day-old Mallard ducklings. The ducklings utter these notes during feeding, while falling asleep, while bathing or preening, when the flock gathers together, when they are brooded by the mother, or after a "distressing" situation has passed. Probably the main function of these sounds is to help keep the brood together. According to Bjarvall (1968), the ducklings were almost completely silent during periods of inactivity.

Distress notes are harsher in quality than contentment notes, and more evenly spaced (compare fig. 12A and B). The spectrograms of distress cries presented by Collias (1962) showed a wide range in frequencies and an emphasis on the descending frequencies. The sonogram of the 4-day-old duckling shown in figure 12A differs slightly from Collias' sonagrams, but the grating quality of the call is still evident. There are different intensities of distress notes, and those illustrated are probably the harshest and loudest calls possible. They were recorded from a bird held in hand.

The ducklings utter distress cries when they are wet, hungry, cold, alarmed, or separated from their parent. They frequently utter these calls from an erect posture. Lorenz (1953) has labeled the distress cry given from an erect posture the "whistle of desertion." He feels that the one-syllabled call-note (Slow *Raehb*) of the male develops ontogenetically from this call.

Dement'ev et al. (1952) reported that sex may be determined by call from the earliest age, since females utter two beat whistles compared to the male's one beat whistle. Several attempts were made to sex 1–4-week-old ducklings by voice, but no differences could be detected. During weeks 4–12, the ducklings undergo a "break-in-voice." During weeks 4–6, some individuals can utter alternately a clear, loud *piiii* or a rasping *raehb* for males or *quack* for females. The transition in voice change is gradual. Abs (1969) has shown that the drop in mean frequency from 3.5 kHz/sec at first day of hatching to about 1.5 kHz/sec at 8 weeks of age for drakes is correlated with the growth of the trachea.

Detailed observations were not conducted on the development of calls, but a few recordings were made of calls from disturbed 5- and 6-week-old ducklings (fig. 12C). The quality of these calls is quite different from those of either ducklings or adults.

DISCUSSION

Little has been written about the relative importance of vocal versus visual signals in Anatidae. The research emphasis on visual displays may have led to neglect of the importance of vocalizations in duck communication. A synopsis of the vocal repertoire of the Mallard is presented in table 7. The variety of probable functions listed in this summary suggests that vocalizations play an important role in many aspects of Mallard behavior, i.e., courtship, copulation, care of young, avoidance of danger, hostile encounters, pair contact, integrating flock activities, etc.

While circumstantial evidence has suggested these probable functions, it is impossible, without experimental study, to determine precisely the information conveyed by

TABLE 7. Synopsis of Mallard vocalizations.

Type of call	Seasonal distribution	Place	Situation	Probable function
Female:				
Inciting	Sept.–June; infrequent July and August	Air, water, or land	During pair-formation; response to threatening drake; when showing preference for drake; upon return of mate; after hostile encounters	Shows preference for certain drake and rejection of another
Decrescendo	Sept.–April; all year except during July for unmated females	Water, land; rarely in flight	Response to mate's Slow *Raehb*; response to a female uttering same call; response to flying conspecific	Indicates location to conspecifics, especially to separated mate; possibly advertises "availability" to nearby males
Spring Persistent Quacking	April and May	Air, water, or land	During prelaying period after pair settles on breeding home range	Advertises presence of female preparing to nest
Repulsion	May and June	Air, water, or land	Response of female that has started incubating to male intent on raping her	Possibly repels threatening drakes; attracts males to female requiring fertilization of renest clutch
Calls of the Broody Female	May–July	Land or water	While incubating or leading broods	Auditory imprinting of ducklings; maintains contact between female and members of brood
Single Quacks	All year	Air, water, or land	Response to calling conspecifics; while alighting or swimming into group of conspecifics	Attract or indicate location to conspecific
Preflight Call	All year; more frequently in fall	Land or water	When about to fly of her "own free will"	Indicates readiness to fly and provides mutual stimulation for simultaneous take-off of group
Alarm	All year	Air, water, or land	Impending danger or after sudden disturbance	Alerts conspecifics
Male:				
Slow *Raehb*	All year; but less frequent during molt	Air, water, or land	Impending danger; response to conspecific calling; when alighting in flock of birds; while on loafing spot and female on nest; during social courtship	Alert or attract conspecific; indicates location to mate
Rabrab	Frequent Oct.–June; infrequent from July–Sept.	Water, land, ? in air	Characteristic of male-male hostile encounters; upon returning to mate; after sudden scare; after Down-up courtship display; quiet version given without bill uptilting component before making place-changes, before and after flight, before, during, and after copulation	Acts as part of threatening, courting, and greeting display; milder version of call indicates readiness to copulate; probably important in conveying graded hostile signals.
Courtship Whistle and Grunting Sounds	Sept.–June: absent July; infrequent Aug.	Water	Accompany Grunt-whistle and Down-up courtship display	Draws attention to male giving display
Postcopulation Whistle	Oct.–July; absent Aug. infrequent Sept.	Water; infrequently on land	After apparently successful copulation or rape	Unknown

vocal displays. Lockner and Phillips (1969) and I have presented experimental evidence for one function of the female Mallard's Decrescendo call. It is to this call that I would like to devote my discussion.

Lorenz (1953), writing about the Decrescendo, stated that "all female ducks . . . can make a very peculiar sound which . . . represents the same homologous instinctive behaviour in all forms." I am not sure that "all" duck species have a homologue of the Decrescendo call, but certainly most *Anas* spe-

cies do (Johnsgard 1965). Since the call is in the vocal repertoire of so many species, it is an excellent vocal display for comparative study.

In the Mallard the Decrescendo call typically consists of from 1–20 notes, with the strongest accent on the first or second note. The distinctive physical characteristics of the call are: (1) decreasing amplitude of successive notes; (2) smaller frequency range in later notes; (3) shorter duration of the last few notes; and (4) increase in interval duration between successive notes. Although there is considerable variation in call structure, I have found that females consistently give calls of typical patterns. Many females in fact can be recognized easily by the form of their Decrescendo call alone.

Three stimuli which will elicit calls from females are: (1) Slow *Raehb* calls of mates; (2) another female giving a Decrescendo; and (3) the sight of another Mallard on the wing. The call apparently functions in individual recognition, especially identifying the calling bird to its separated mate.

Although the Decrescendo is probably the duck vocalization that has been studied most, there are still many unanswered questions. Why do some females give calls more readily than others? Why do some species give Decrescendos more frequently than others? What is the function of Decrescendos given in response to those of another female? Why is there such a marked diurnal rhythm for this call? How much learning is involved during development? Since the call is so well suited for experimental analysis and can be elicited from captive birds under laboratory conditions, these questions should be answerable.

Since the original study was completed, I have carried out further mate-separation experiments using game-farm Mallards. These birds gave many more Decrescendo calls than the wild Mallards studied for my thesis research. The significance of this difference in calling rate is unknown, but it suggests that there may be a strong genetic component influencing the frequency of calling or possibly an earlier rate of learning. Extensive comparative studies of the many wild and domestic stocks of Mallard-like ducks might be especially instructive in leading to a further understanding of the functions of this important vocalization.

SUMMARY

This study examines the behavioral significance of the vocal displays of the Mallard. Calls of each sex are different in physical structure and are discussed separately under the headings of female and male vocalizations. The vocal repertoire of each sex is described quantitatively as well as qualitatively and probable functions are proposed. Spectrographic illustrations are provided and information is given on the seasonal distribution and daily rhythm of certain calls.

ACKNOWLEDGMENTS

This research was completed in partial fulfillment of of the Master of Science degree at the University of Minnesota. For stimulating my interest and suggesting the project, for his advice throughout the study, and for his criticism of the final paper, I would like to express my appreciation to Frank McKinney. I would also like to thank Richard E. Phillips and Lew Oring for their criticisms of the paper.

I am grateful to Joe Ball, Julie Barrett, Ron Barrett, Noel Christianson, and Rebecca Field for their observational help; Lew Oring for the use of his sonagraph machine and for his advice in operating it; the Minnesota State Department of Conservation for their help in trapping the wild birds and for providing the wintering quarters at the Carlos Avery Game Farm; William H. Marshall and Alvar Peterson for their courtesies at the Cedar Creek Natural History Area; and the late Hugh House for his help in caring for the birds.

The project was financed by the USPHS Grant No. NB-06981 and AEC Contract AT(11-1)-1332, COO-1332-74.

LITERATURE CITED

Abs, M. 1969. Zur bioakustik des "stimmbrauchs" bei hausenten. Verh. Zool. Ges. Zool. Anz., Suppl. Bd. 33, p. 298–301.

Abs, M. 1970. Acoustical properties of the bulla ossea and vocal behavior of domestic drakes (*Anas platyrhynchos*). Abstract Proc. XV Int. Ornithol. Congr., Hague.

Barrett, J. 1973. Breeding behavior of captive Mallards. M.S. Thesis. Univ. of Minnesota, Minneapolis.

Bartonek, J. C., and C. W. Dane. 1964. Numbered nasal discs for waterfowl. J. Wildl. Mgmt. 28:688–692.

Bateson, P. P. G. 1966. The characteristics and context of imprinting. Biol. Rev. 41:177–220.

Bjarvall, A. 1968. The critical period and the interval between hatching and exodus in Mallard ducklings. Behaviour 28:141–148.

Boyd, H., and E. Fabricius. 1965. Observations on the incidence of following of visual and auditory stimuli in naive Mallard ducklings (*Anas platyrhynchos*). Behaviour 25:1–15.

Collias, N. E. 1962. The behaviour of ducks. *In* E. S. E. Hafez [ed.] The behaviour of domestic animals. Williams & Wilkins Co., Baltimore.

Collias, N. E., and E. C. Collias. 1956. Some mechanisms of family integration in ducks. Auk 73:378–400.

Dane, B., C. Walcott, and W. H. Drury. 1959. The form and duration of the display actions of the Goldeneye (*Bucephala clangula*). Behaviour 14:265–281.

Dane, B., and W. van der Kloot. 1964. An analysis of the Goldeneye Duck (*Bucephala clangula* (L.)). Behaviour 22:282–328.

DEMENT'EV, G. P., N. A. GLADKOV, AND U. A. ISAKOV. 1952. Birds of the Soviet Union. Vol. 4. (Translated from Russian).

DZUBIN, A. 1957. Pairing display and spring and summer flights of the Mallard. Blue Jay 15: 10–13.

FIELD, R. 1970. An analysis of social courtship in the Mallard (*Anas platyrhynchos*). M.S. Thesis. Univ. of Minnesota, Minneapolis.

FRITH, H. J. 1967. Waterfowl in Australia. East-West Press, Honolulu.

GOTTLIEB, G. 1965. Components of recognition in ducklings. Nat. Hist. 74:12–19.

GOTTLIEB, G. 1968a. Species recognition in ground-nesting and hole-nesting ducklings. Ecology 49: 87–95.

GOTTLIEB, G. 1968b. Prenatal behavior of birds. Quart. Rev. Biol. 43:148–174.

GOTTLIEB, G. 1971. Development of species identification in birds: An inquiry into the prenatal determinants of perception. Univ. of Chicago Press, Chicago.

GOTTLIEB, G., AND J. G. VANDENBERGH. 1968. Ontogeny of vocalization in duck and chick embryos. J. Exp. Zool. 168:307–326.

HEINROTH, O. 1910. Beobachtungen bei einem Einbergerungsversuch mit der Brautente (*Lampronessa sponsa* L.). J. Ornithol. 58:101–156.

HEINROTH, O. 1911. Beitrage zur biologie namentlich ethologie und psychologie der Anatiden. Verh. Int. Ornithol. Kongr. (Berlin, 1910), p. 589–702.

HESS, E. 1972. "Imprinting" in a natural laboratory. Sci. Amer. 227:24–31.

HOCHBAUM, H. A. 1944. The canvasback on a prairie marsh. Amer. Wildl. Inst., Washington, D.C.

HOCHBAUM, H. A. 1955. Travels and traditions of waterfowl. Univ. of Minnesota Press, Minneapolis.

HORI, J. 1963. Three-bird flights in the Mallard. Wildfowl Trust 14th Ann. Rept., p. 124–132.

IMPEKOVEN, M. 1973. Response-contingent prenatal experience of maternal call in the Peking Duck (*Anas platyrhynchos*). Anim. Behav. 21:164–168.

JOHNSGARD, P. A. 1960. A quantitative study of sexual behavior of Mallards and Black Ducks. Wilson Bull. 72:133–155.

JOHNSGARD, P. A. 1961. Tracheal anatomy of the Anatidae and its taxonomic significance. Wildfowl Trust 18th Ann. Rept., p. 58–69.

JOHNSGARD, P. A. 1965. Handbook of waterfowl behavior. Cornell Univ. Press, Ithaca.

JOHNSGARD, P. A. 1971. Observations on sound production in the Anatidae. Wildfowl Trust 22nd Ann. Rept., p. 46–59.

KEAR, J. 1968. The calls of very young Anatidae. Vogelwelt Beihefte 1:93–113.

KLOPFER, P. 1959. An analysis of learning in young Anatidae. Ecology 40:90–102.

LEBRET, T. 1958. Inciting ("Hetzen") by flying ducks. Ardea 46:68–72.

LEBRET, T. 1961. The pair formation in the annual cycle of the Mallard, *Anas platyrhynchos* L. Ardea 49:7–157.

LOCKNER, R., AND R. PHILLIPS. 1969. A preliminary analysis of the decrescendo call in female Mallards (*Anas platyrhynchos* L.). Behaviour 35: 281–287.

LORENZ, K. 1953. Comparative studies on the behaviour of the Anatinae. Avicult. Mag., London, p. 1–87.

LORENZ, K. 1958. The evolution of behavior. Sci. Amer., 199:67–78.

LORENZ, K. 1966. On aggression. Harcourt, Brace & World, Inc.

MALEY, M. 1969. Electrical stimulation of agonistic behavior in the Mallard. Behaviour 36:138–160.

MCKINNEY, F. 1961. An analysis of the displays of the European Eider *Somateria mollissima mollissima* (Linnaeus) and the Pacific Eider *Somateria mollissima* v. *nigra* Bonaparte. Behaviour, Suppl. VII.

MCKINNEY, F. 1965a. The comfort movements of Anatidae. Behaviour 25:120–220.

MCKINNEY, F. 1965b. The spring behavior of wild Steller Eiders. Condor 67:273–290.

MCKINNEY, F. 1967. Breeding behaviour of captive Shovelers. Wildfowl Trust 18th Ann. Rept., p. 108–121.

MCKINNEY, F. 1969. The behaviour of ducks. *In* E. S. E. Hafez [ed.] The behaviour of domestic animals. Williams & Wilkins Co., Baltimore.

MCKINNEY, F. 1970. Displays of four species of Blue-winged Ducks. Living Bird 9:29–64.

ORING, L. W. 1964. Behavior and ecology of certain ducks during the post breeding period. J. Wildl. Mgmt. 28:223–233.

ORING, L. W. 1968. Vocalizations of the Green and Solitary Sandpipers. Wilson Bull. 80:395–420.

PHILLIPS, J. C. 1922–26. A natural history of the ducks. Vol. 2, p. 25–26. Houghton Mifflin, Boston.

PHILLIPS, R. E., AND A. VAN TIENHOVEN. 1962. Some physiological correlates of Pintail reproductive behavior. Condor 64:291–299.

RAITASUO, L. 1964. Social behaviour of the Mallard, *Anas platyrhynchos*, in the course of the annual cycle. Paper on Game Res. 24:1–72.

SIEGEL, S. 1956. Nonparametric statistics. McGraw Hill Co., New York.

SIMMONS, K. E. L. AND U. WEIDMANN. 1973. Directional bias as a component of social behaviour with special reference to the Mallard, *Anas platyrhynchos*. J. Zool. 170:49–62.

SLUCKIN, W. 1964. Imprinting and early learning. Methuen, London.

SMITH, R. I. 1963. The social aspects of reproductive behavior in the Pintail (*Anas acuta acuta*, L.). Ph.D. Thesis, Utah State Univ., Logan.

SMITH, R. I. 1968. The social aspects of reproductive behavior in the Pintail. Auk 85:281–296.

SOWLS, L. K. 1955. Prairie ducks. Wildl. Mgmt. Inst., Washington, D.C.

STEPHEN, W. J. D. 1963. Some responses of female Mallards to disturbance by man. J. Wildl. Mgmt. 27:280–283.

VON DE WALL, W. 1963. Bewegungsstudien an Anatinen. J. Ornithol. 104:1–15.

WEIDMANN, U. 1956. Verhaltensstudien an der Stockente (*Anas platyrhynchos* L.) I. Das Aktionssystem. Z. Tierpsychol. 13:208–271.

WEIDMANN, U. 1958. Verhaltensstudien an der Stockente (*Anas playtrhynchos* L.) II. Versuche zur Auslasung und Pragung der Nachfolge-und Anschlussreaktion. Z. Tierpsychol. 15:277–300.

WEIDMANN, U., AND J. DAILEY. 1971. The role of the female in the social display of Mallards. Anim. Behav.. 19:287–298.

Accepted for publication 28 March 1974.