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The Development of Acoustical Communication in the Mallard (Anas Platyrhynchos)

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THE DEVELOPMENT OF ACOUSTICAL COMMUNICATION IN THE MALLARD (*Anas platyrhynchos*)

by
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This Thesis submitted by Fredrick Dale Caswell in partial fulfillment for the requirements for the Degree of Master of Science from the University of North Dakota is hereby approved by the Faculty Advisory Committee under whom the work has been done.

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Department Biology

Degree Master of Science

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Date 30 November 1972

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ABSTRACT

Females begin calling on the nest before the young hatch and calling increases as the time of exodus approaches. Female calls, on the nest, are mainly in response to calls and movements of young. Females off the nest use a variety of calls and exercise complete control over the activity of the brood using mainly acoustical cues. Broody calls are significantly different between individual females and vary depending on the situation. As young develop, female communication to and control over the brood decreases. Young are extremely vocal except when being brooded or when in alert positions. Contact calls are common and distress calls are rare. These calls are end points of a graded system and intermediate calls occur. As young develop they become more independent and contact calls are eventually replaced by intention and aggressive calls. Development of the young is accompanied with a decrease in frequency (Hz) of the calls and a change in their structure to form a preliminary stroke and main note. Adult calls develop from the main note of contact calls by a decrease in its frequency below a threshold value and the addition of harmonics. During the juvenile to adult transition period, birds give juvenile, adult and intermediate calls. Juvenile calls were similar to those of adults by 18 to 19 weeks. By their first fall, birds are taking part in bouts of sexual displays and giving associated calls.

INTRODUCTION

The Mallard (Anas platyrhynchos) has been the most widely studied member of the family Anatidae, its sexual behaviour having been extensively studied by Lorenz (1941), Johnsgard (1955, 1960, 1965) Weidemann (1956, 1958), Ramsay (1956) and Labret (1961). These behavioural studies have dealt primarily with visual displays.

The role of sound in waterfowl communication has only been touched upon with most emphasis on imprinting (Klopfer, 1959; Klopfer and Gottlieb, 1962; Boyd and Fabricius, 1965; Gottlieb and Kuo, 1965; Bjärvall, 1968; Gottlieb, 1961, 1965, 1966, 1968; Lockner and Phillips, 1969; and Ramsay and Hess, 1971). Works dealing with specific calls of the mallard and their composition have been completed by Kear (1968) on newly hatched ducklings; and by Johnsgard (1971) and Abraham (1971) on those of the adult. Abs (1970) concentrated on the breaking of voice in juvenile domestic mallards. To date, however, there has been a minimal amount of work done on mallard behaviour in mid-and late summer.

The purpose of this study was to document changes in mallard vocalizations and associated behaviour from hatching to the time of first fall migration - the time at which adult sexual behaviour is apparent. Such a study is essential to an understanding of the conditions necessary for normal development of sexual behaviour.

METHODS AND MATERIALS

Research was conducted at Delta Waterfowl Research Station, Delta, Manitoba, Canada, from 23 April to 29 October 1971. Subject birds were wild stock obtained from eggs taken in 1969 near Saskatoon, Saskatchewan. On 23 April, three males and three females, individually marked with coloured leg bands, were placed in each of observation pens 1 and 2 (Figure 1A). Each pen measured 40' X 20' X 8' with a 3' high plywood base. To minimize external disturbance, burlap was strung over the sides above the plywood. Each pen had a 4' X 8' pond with continuous flowing water. Observations were made from an elevated blind.

Males and females were allowed to pair and initiate nests (Table 1). Males were removed just prior to hatching. Females were allowed to hatch and rear their broods in an undisturbed environment. Within two days of hatching, young were captured, pinioned and individually marked with wire leg bands. Due to the ducklings' rapid rate of growth, bands had to be changed every two weeks; at about six weeks they were replaced with coloured numbered plastic leg bands.

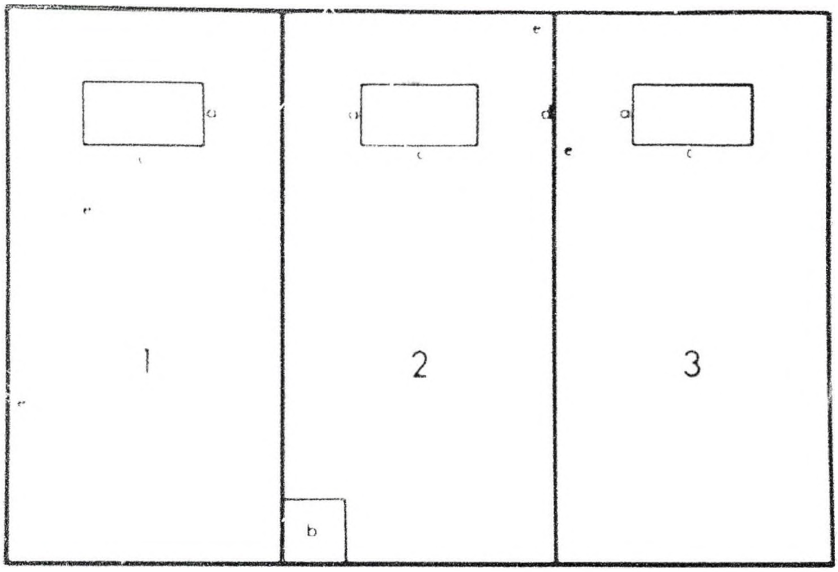
On 20 September all birds were individually marked with patagial tags (Anderson, 1963) and moved to a large flight pen (Figure 1B) to simulate fall flocking behaviour. This pen measured 127' X 51' X 16' and contained three large interconnected ponds with automatically controlled water level and flow. Birds were fed at centrally located feeding trays. They also obtained natural food from the ponds. Observations were made from an elevated blind which allowed an unobstructed view of all three ponds. Birds remained in this pen until freeze-up on 29 October.

A. Observation pens

B. Flight pen

Fig. 1.--Study pens.
a. Microphone position for individual recording
b. Blind
c. Feeding tray
d. Microphone position for all morning recording
e. Nest positions

A



B

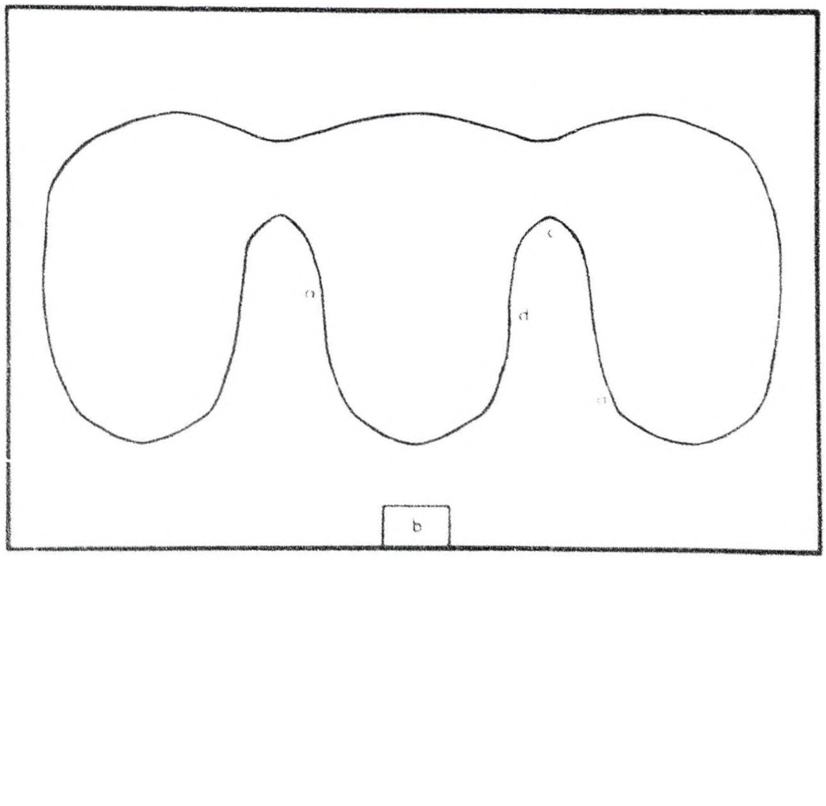


TABLE 1

KEY TO SUBJECT BIRDS AND HATCHING DATES OF BROODS

Number	Female	Pen	Male	Hatching Dates
1	Yellow	1	Yellow	Hatched brood 12 June
2	Blue	1	Red	Hatched brood 7 July
3	Red	1	Blue	Removed 15 June
4	Yellow	2	Red	Hatched brood 14 June
5	Blue	2	----	Removed 15 June
6	Red	2	Yellow	Removed to pen #3, 2 May; hatched brood 10 June

During the study data were collected throughout the day, weather permitting. Data were gathered from a total of 80 morning, 18 afternoon, and 29 evening observation periods, each period ranging from two to four hours. Calls were recorded on a Uher 4000 R-L tape recorder at three and three quarters inches per second using Uher 514 omnidirectional and Sennheiser 804 ultra-unidirectional microphones. Uher microphones were placed in the pens (Figure 1A and B) using 50' cables. The Sennheiser microphone was used to collect data from the blinds. In addition to recordings of individuals, all morning tapes were made once a week from one and one half hours before and until one and one half hours after sunrise. Prior to hatching, nests were individually monitored by placing a Uher microphone adjacent to them. Recordings were continued until females led young from nests. Associated behaviour of the birds was noted during the time of recordings.

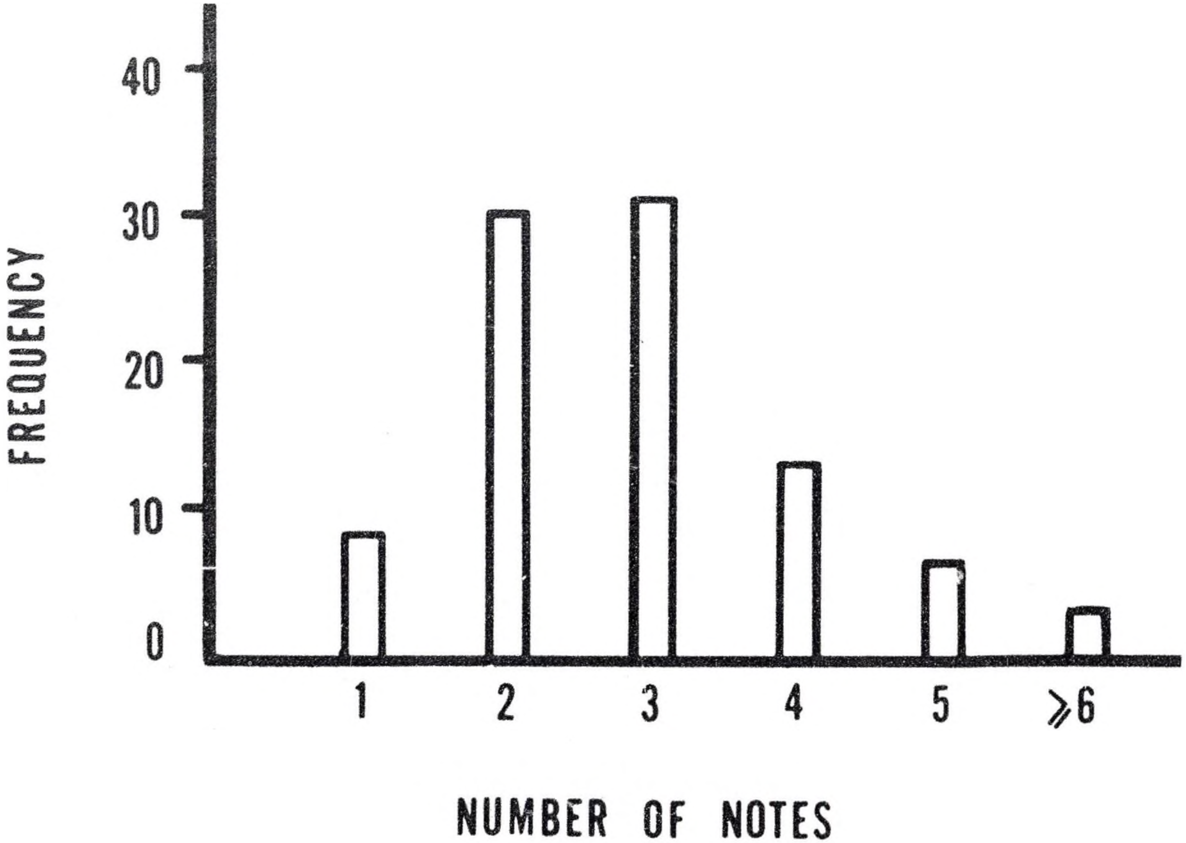
Sonographs of calls were made using a Kay electric sonograph 7029A at both narrow and wide band filter settings. In describing sonograph tracings, frequency was defined as the average frequency of the spectrum, and the spectrum as the area of the call where the greatest amount of energy was located.

BEHAVIOUR AND VOCALIZATIONS OF FEMALES WITH YOUNG

Females on the nest begin calling one to two days before the young hatch. Acoustical communication between female and young increases after eggs are pipped and continues until ducklings are led from the nest. This broody call consists primarily of two or three notes (Figure 2), which may be repeated several times. Broody calls at the nest may consist of preliminary stroke, preliminary stroke and note, or note alone (Figure 3), the preliminary stroke being most common early in the hatching sequence.

Although broody calls are variable, each female uses a distinct call (Table 2, Figure 3). At the nest, broody calls of female 2 consisted of a main note of 795 $\pm$ 118 Hz lasting for 36.6 $\pm$ 11.6 msec., and one overtone of 1428 $\pm$ 193 Hz. Broody calls of female 1 however, consisted of a preliminary stroke with a maximum frequency of 923 $\pm$ 162 Hz, a main note of 783 $\pm$ 44 Hz lasting for 49.5 $\pm$ 10.9 msec., and two overtones at 1443 $\pm$ 35 Hz and 2066 $\pm$ 161 Hz. Duration of the total call was 87.5 $\pm$ 9.4 msec. Analysis of variance of the common components of the female's broody call were significantly different ($F = 4.42$, $P < 0.05$ for one and 60 degrees of freedom). Calling of the hen on the nest with young appears to be in response to the calls and possibly movements of

Fig. 2.-- Number of notes in female broody call.


FREQUENCY
40
30
20
10
0
1
2
3
4
5
≥6
NUMBER OF NOTES

a. Broody call Female 1
b. Broody call Female 2
c. Alarm call Female 2
d. Alarm call Female 1
i. Preliminary stroke
ii. Main (fundamental) note
iii. First overtone

Fig. 3.--Spectrogram of female broody and alarm calls on nest.

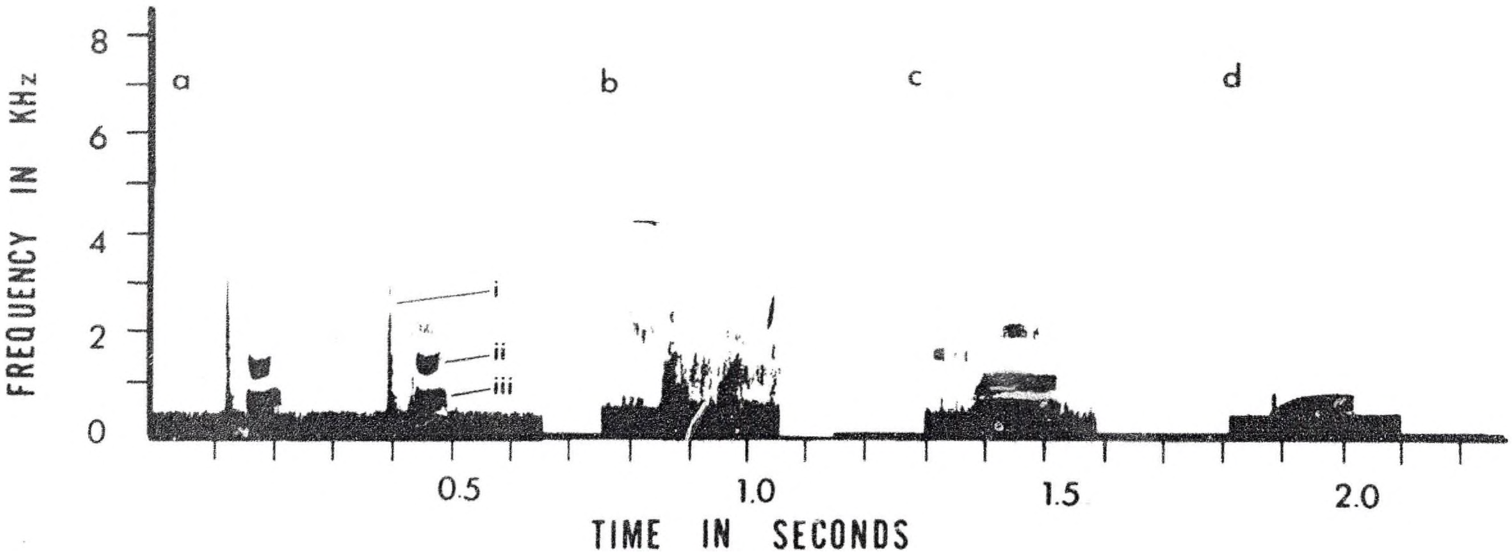

FREQUENCY IN KHz
8
6
4
2
0
a
b
c
d
i
ii
iii
0.5
1.0
1.5
2.0
TIME IN SECONDS

TABLE 2

NUMERICAL ANALYSIS OF FEMALE CALLS ON THE NEST WITH YOUNG
(Frequencies in Hz; time in msec.; N = sample
size; $\bar{X}$ = mean; S.D. = standard deviation)

			N	$\bar{X} \pm$ S.D.
Broody call Female 1				
	Frequency:	Preliminary stroke	17	923 ± 162
		Main note	17	783 ± 44
		First overtone	17	1443 ± 35
		Second overtone	17	2066 ± 161
	Time:	Duration of main note	17	49.5 ± 10.9
		Duration of call	17	87.5 ± 9.4
Broody call Female 2				
	Frequency:	Main note	16	795 ± 118
		First overtone	16	1428 ± 193
	Time:	Duration of call	16	36.6 ± 11.6
Alarm call Female 1				
	Frequency:	Preliminary stroke	2	813 ± -
		Main note	2	550 ± -
	Time:	Duration of call	2	128.5 ± -
Alarm call Female 2				
	Frequency:	Main note	8	704 ± 54
		First overtone	8	1214 ± 101
	Time:	Duration of call	8	146.3 ± 30.6

the young (Table 3). In tape recorded sequences, broody calls of females occurred during or immediately after calling of the young 74 per cent of the time. Another 15 per cent of the time calling of young stimulated movements of females such as adjusting eggs, young or breast feathers. Because soft calling of young went unrecorded it is possible that this figure should be higher. Generally after a hen gave broody calls, young

TABLE 3

FEMALE BROODY CALLS AND/OR MOVEMENTS IN RESPONSE TO YOUNG AT NEST

	During or Immediately After Calls of Young		No Calls of Young	
	No.	%	No.	%
Broody call only	79	74.2	8	7.5
Broody call and movement	8	7.5	5	4.6
Movement only	8	7.5	0	0
Total	95	89.2	13	12.1

called less frequently.

Females on nests sometimes give alarm calls which are lower in frequency and longer in duration than broody calls (Table 2, Figure 3). The call of female 2 consisted of a main note of 704 ± 54 Hz lasting for 146.3 ± 30.6 msec., and one overtone of 1214 ± 101 Hz. The call of female 1 consisted of a preliminary stroke with a maximum frequency of 813 Hz and a main note of 550 Hz lasting for 128.5 msec. The alarm call was usually given only once after which ducklings immediately became silent. They were given whenever females were disturbed. In the present study alarm calls could be elicited by hanging a white handkerchief out of the blind or by creaking a door.

As the time of exodus from the nest approaches, vocal communication between young and hen increases (McKinney 1969). While leading young from the nest, the hen gives a long series of rapidly repeating broody calls (leadership call, Weidemann, 1956) (Figure 4). Calling persists until females reach a place where the young can feed or rest. Whenever females begin moving again, they give the leadership call. The ducklings follow the hen in a fairly tight group and call nearly constantly. Once female and young reach an area where the young can feed, the number of broody calls decreases. Then females stand in alert positions and give periodic calls (alert calls, Table 4, Figure 5). While females feed, they communicate with the ducklings with another call (feeding alert call, Figure 5) which may be a modified alert call. These two calls may function to maintain the status quo.

The rate of female broody calling increases when she leads the young on a feeding excursion in the vegetation or away to be brooded. Generally the female leads the young to the brood site. However, females leaving young in the pond and going to prepare a brood site nearby were observed. Females then increased the rate of broody calling and the young left the pond to join the hens at the brood site. While preparing the brood site, females without young present periodically gave one to three notes, whereas females whose young were with them called more frequently. Preparation of a brood site consisted of the female turning around on one spot, poking under herself with her bill, and sometimes removing some pieces of vegetation. Females eventually stop turning and assume a half standing position with wings partially extended, allowing the young to be brooded. As females brood young, broody calling decreases and eventually ceases. After brooding the young for some time, females increase the rate of broody calling and lead them to the pond or on a feeding excursion in the vegetation.

Fig. 4.--Leadership call (rapid sequence of female broody calls)

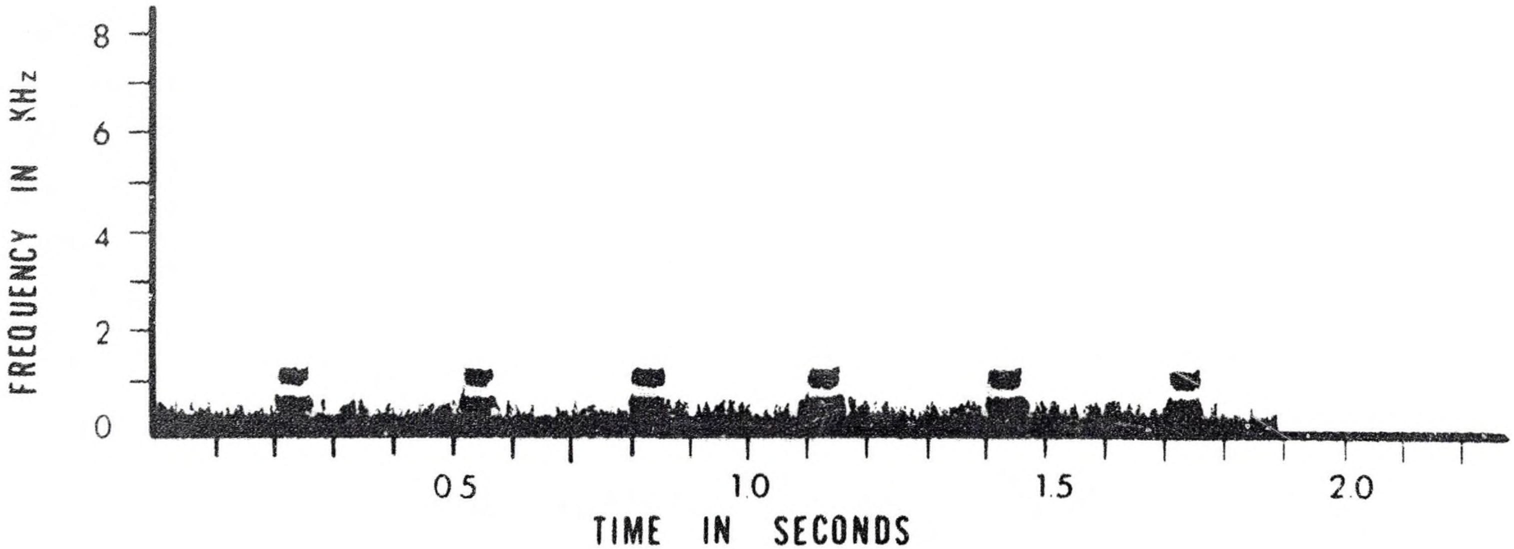

FREQUENCY IN KHz
8
6
4
2
0
0.5
1.0
1.5
2.0
TIME IN SECONDS

TABLE 4

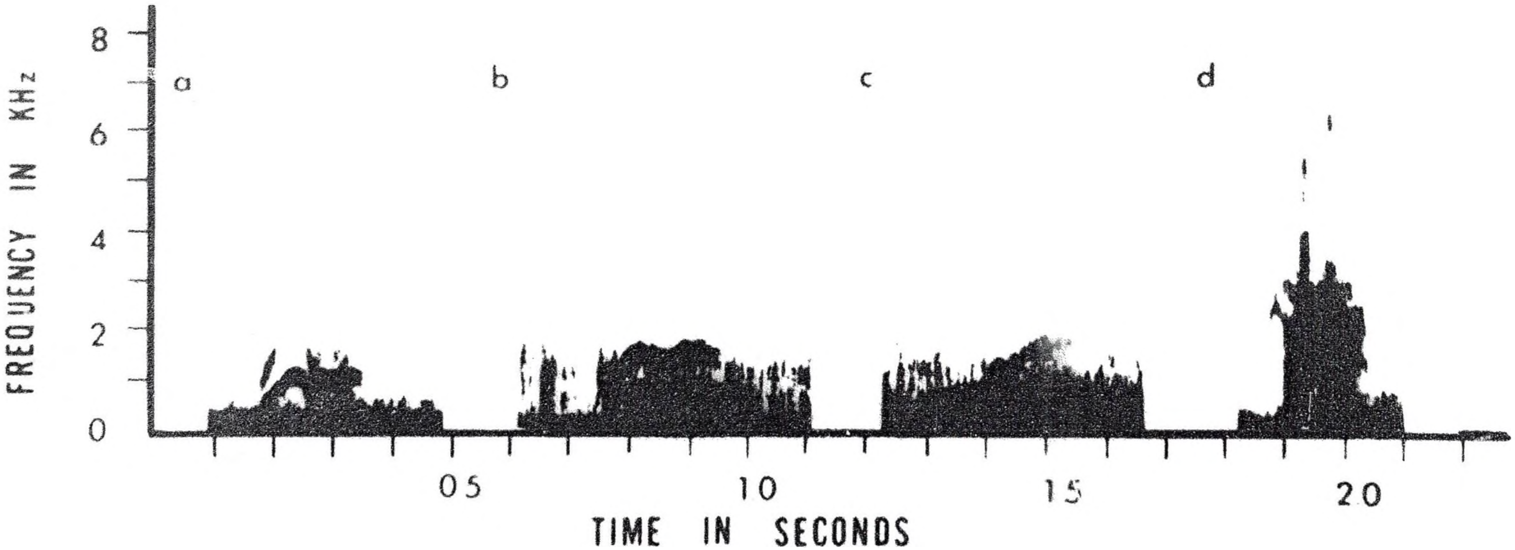
NUMERICAL ANALYSIS OF ALERT AND ALARM CALLS OF FEMALES WITH YOUNG OFF NEST (frequencies in Hz; time in msec.; N = sample size; $\bar{X}$ = mean; S.D. = standard deviation)

		N	$\bar{X} \pm$ S.D.
Alert Call Female 1			
Frequency:	Maximum preliminary section	7	1283 ± 72
	Main note	7	836 ± 218
	First overtone	7	1267 ± 142
Time:	Duration of note	7	46.3 ± 15.0
	Duration of call	7	106.4 ± 26.6
Alert Call Female 4			
Frequency:	Maximum preliminary section	10	1270 ± 48
	Main note	10	795 ± 69
	First overtone	10	1243 ± 60
Time:	Duration of note	10	61.3 ± 8.7
	Duration of call	10	131.7 ± 15.4
Low Level Alarm Female 1			
Frequency:	Main note	15	1059 ± 40
	First overtone	15	1372 ± 27
Time:	Duration of call	15	135.4 ± 12.6
High Level Alarm Female 2			
Frequency:	Fundamental	7	145 ± 21
	First overtone	7	361 ± 65
	Maximum	7	3215 ± 246
	Spectrum	7	1871 ± 186
Time:	Duration of call	7	194 ± 36.4

Females with young use two types of alarm calls: a low level alarm, which is almost a pure tone, and a high level alarm consisting of a deep quack (Table 4, Figure 5). Ducklings become silent and assume alert

a.	Alert call	Female <u>1</u>
b.	Feeding alert call	Female <u>1</u>
c.	Low level alarm call	Female <u>1</u>
d.	High level alarm call	Female <u>2</u>

Fig. 5.--Spectrogram of female calls off nest.


FREQUENCY IN KHz
8
6
4
2
0
a
b
c
d
05
10
15
20
TIME IN SECONDS

positions in response to the low level alarm. When hearing the high level alarm, ducklings moved immediately into vegetation.

After leaving the nest with their young, females generally utilize calls of a higher frequency. Analysis of variance shows F = 12.14, significant at $P < 0.01$ for one and 120 degrees of freedom. The frequency of the main note of female 1's broody call increased from 783 ± 44 Hz on to 1028 ± 294 Hz off the nest (Table 2 and 5), and low level alarm increased from 550 Hz on to 1059 ± 40 Hz off the nest (Table 2 and 4). Females further increase the pitch of the main note of the broody call when stressed. Analysis of variance shows F = 145, significant at $P < 0.01$ for one and 54 degrees of freedom. Table 5 illustrates that female 2's main note increased from 868 ± 106 Hz (under mild stress by the observer's presence in pen) to 1037 ± 61 Hz (under moderate stress by the observer cornering female and young). When under high stress, female calls fluctuate between broody calls, extended preliminary strokes, and some high level alarms. Young, at this time, are virtually under the hen.

On several occasions a female took her brood to the vegetation, brooded them, and then silently returned alone after a short period of time. The young called briefly as she left and then became silent. In this situation it may be the lack of broody calling that caused the ducklings to remain behind. In one of these situations, the female fed for about 10 minutes and then began broody calling while on the pond. The young, which were about two meters away, left the brood site and joined the hen.

During the early stages of development, the hen initiates all of

TABLE 5

NUMERICAL ANALYSIS OF FEMALE BROODY CALLS OFF THE NEST WITH YOUNG
(frequencies in Hz; time in msec.; N = sample size
$\bar{X}$ = mean; S.D. = standard deviation)

		N	$\bar{X} \pm$ S.D.
Broody Call Female 1			
Frequency:	Main note	17	1028 ± 294
	First overtone	17	1882 ± 703
	Second overtone	17	2580 ± 972
Time:	Duration of call	17	56.2 ± 40.1
Broody Call Female 4			
Frequency:	Main note	8	973 ± 29
	First overtone	8	1259 ± 22
Time:	Duration of call	8	47.5 ± 6.7
Mild Stress Female 2			
Frequency:	Preliminary stroke	10	1670 ± 251
	Main note	13	868 ± 106
	First overtone	10	1511 ± 96
Time:	Duration of call	12	45.3 ± 4.2
Moderate Stress Female 2			
Frequency:	Main note	15	1037 ± 61
	First overtone	15	1411 ± 53
Time:	Duration of call	15	155.2 ± 21.9

the brood's activities. She broods the young at night, takes them to the pond in the morning, and leads them on feeding excursions to the vegetation and back to the pond. During the first few days after hatching, activity periods last about 30 minutes, after which the female leads the young to a brooding area. Each activity period consists of a hen taking her brood on a feeding excursion in the vegetation for a few minutes, then leading them back to the pond for a few minutes, and repeating this sequence several times before brooding the young. Alternation of feeding and brooding periods continue throughout the day. As young develop, the amount of time spent in feeding increases, and the amount spent in brooding decreases. Finally brooding ceases. At this time, young and female begin resting on the edge of the pond rather than walking to a brood site in the vegetation.

Communication between female and young decreases with the development of the brood. The amount of female calling steadily decreases until finally, when ducklings are seven to eight weeks old, communication of the female to the brood is insignificant (Table 6, Figure 6). This coincides with Dzubin's (1959) suggestion that females leave to molt, six to eight weeks after ducklings hatch. Females were observed giving preflight calls and attempting to fly as early as when ducklings were four weeks old.

CALLS OF NEWLY HATCHED MALLARD DUCKLINGS

A clutch of seven wild mallard eggs, collected near Minnedosa, Manitoba were hatched in an incubator. From the time eggs pipped, chicks were individually recorded at six hour intervals beginning 0600, 17 July and continuing until 1200, 19 July 1971. All ducklings were then hatched and dry. Recordings were made in the incubator, in the experimenter's lap and on a cold cement floor in order to obtain calls given in situations ranging from contentment to distress. Recording and analyzing methods were similar to those used for pen studies.

The ability of ducklings to vocalize develops about two to three

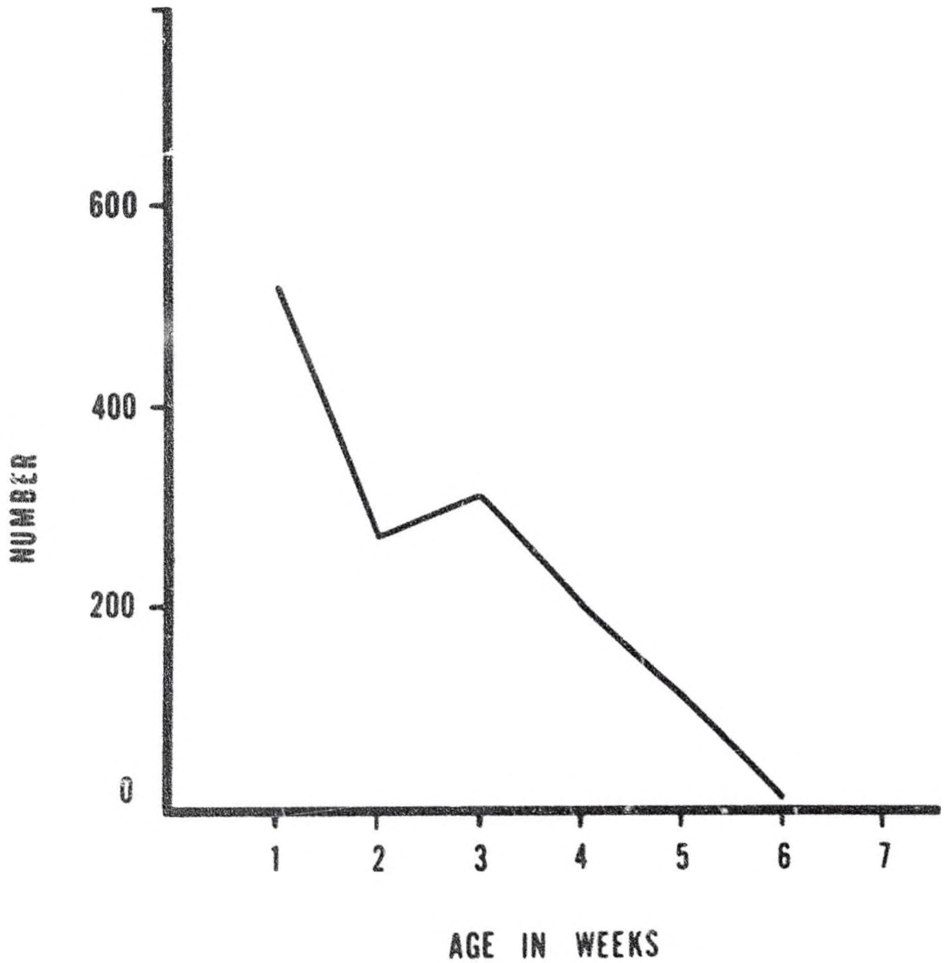
TABLE 6

TOTAL NUMBER OF FEMALE AND YOUNG CALLS COUNTED FROM ALL MORNING TAPES

Date	Age of Young in Weeks	Female Broody Calls	Young Calls Contact	Young Calls Intention	Total	Notes
18 June	1	534	1590	0	1590	
24 June	2	273	420	0	420	strong wind
1 July	3	315	2175	0	2175	
8 July	4	201	1965	0	1965	windy
15 July	5	114	2094	0	2094	
22 July	6	6	--	--	1830	
31 July	7	0	--	--	1527	windy
7 August	8	0	--	--	2670	
13 August	9	0	822	1644	2436	
20 August	10	0	574	1947	2493	
29 August	11	0	153	2106	2259	

-- Indicates data not available.

Fig. 6.--Total number of female calls from all morning recordings.


600
400
200
0
NUMBER
1
2
3
4
5
6
7
AGE IN WEEKS

days before hatching (Gottlieb and Kuo, 1965). Gottlieb (1965) has shown an increase in pre-hatching vocalization rates in response to broody calls. Kear (1968) recorded and illustrated by sonograph tracings, the clicks and cries emanating from mallard eggs about 12 hours before hatching. Clicks were described as being narrow vertical columns, cries as solid structures with a fundamental tone plus a series of overtones.

Newly hatched ducklings are able to emit sounds from about two to five KHz. These calls have been categorised as contentment and distress calls (Collias, 1962, McKinney, 1969). The contentment call is given when ducklings are "content" (warm, feeding, with brood mates), the distress call when they are "distressed" (cold, hungry, alone). Terms used synonymously with contentment calls are pleasure (Kear, 1968) and contact calls (Collias, 1962). In the pen study contact calls were commonly used and distress calls were rare.

The basic contact call of mallard ducklings appear on a sonogram as an inverted "U", the two sides of the "U" having an approximately equal distribution of sound energy (Figure 7A). These calls are variable in both frequency and duration (Table 7). Intervals between notes is irregular (Kear, 1968) and the number of notes in a call varies from one to seven; two to four being most common (Figure 8). Notes may also run together to form a trill.

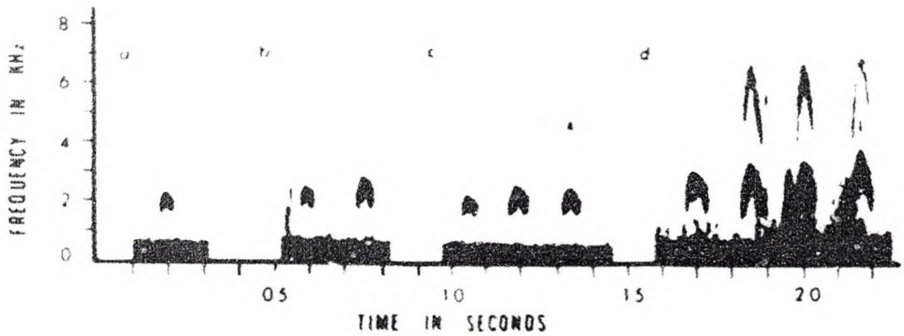
Notes within a group vary in frequency and time (Table 8). When two notes occur in series, the second normally has a higher frequency. When three occur, the second note has a higher frequency than the first, the third note may or may not be higher in frequency than the second.

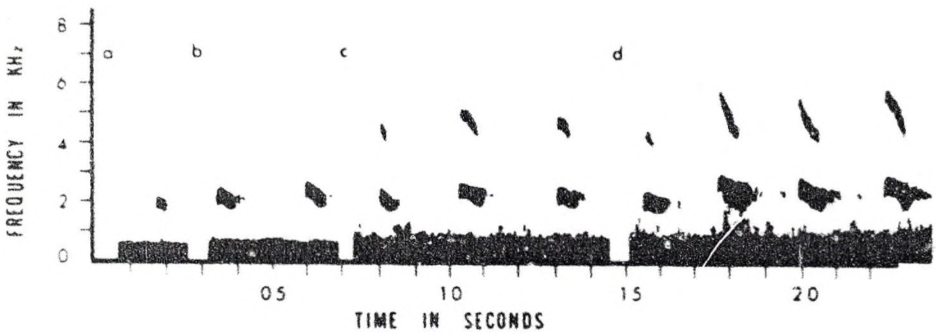
A. Contact calls

B. Intermediate calls

C. Distress sequence

Fig. 7.--Spectrograms of calls of newly hatched ducklings.
a. One note
b. Group of two notes
c. Group of three notes
d. Group of four notes


FREQUENCY IN KHz
TIME IN SECONDS
a
b
c
d


FREQUENCY IN KHz
TIME IN SECONDS
a
b
c
d

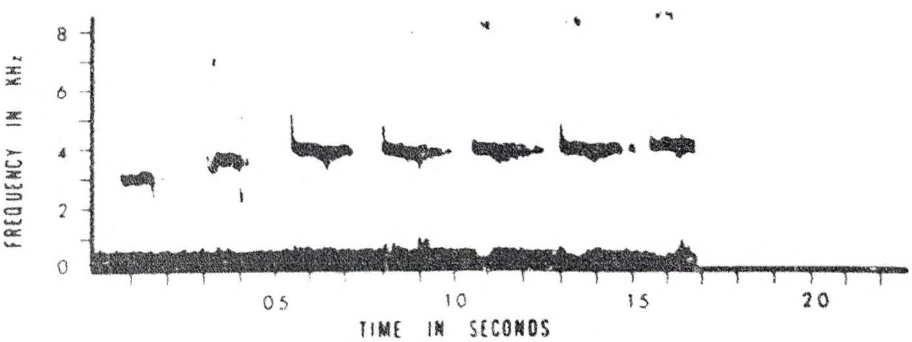

FREQUENCY IN KHz
TIME IN SECONDS

TABLE 7

NUMERICAL ANALYSIS OF A RANDOM SAMPLE OF CONTACT, INTERMEDIATE AND DISTRESS CALLS (frequencies in Hz; time in msec.; spectrum = frequencies containing most sound energy; N = sample size; $\bar{X}$ = mean; S.D. = standard deviation)

		N	$\bar{X}$ ± S.D.
Contact call			
Frequency:	Minimum spectrum	60	1844 ± 160
	Maximum spectrum	60	2840 ± 526
	Average spectrum	60	2335 ± 296
Time:	Duration of call	60	48.4 ± 10.2
	Interval	35	94.9 ± 18.1
Intermediate call			
Frequency:	Minimum spectrum	45	2131 ± 208
	Maximum spectrum	45	2555 ± 260
	Average spectrum	45	2344 ± 278
Time:	Duration of call	45	52.0 ± 13.7
	Interval	27	176.7 ± 24.2
Distress call			
Frequency:	Minimum spectrum	50	3435 ± 391
	Maximum spectrum	50	4134 ± 542
	Average spectrum	50	3800 ± 393
Time:	Duration of call	50	91.0 ± 11.4
	Interval	43	164.2 ± 19.9

In groups of four or more notes, there is usually an initial increase in frequency followed by a decrease in the latter notes. In all cases there is a change in frequency between subsequent notes of a series. There is a tendency for subsequent groups of notes to increase in frequency.

Mallard ducklings also give a series of calls similar to contact calls except that the main concentration of sound energy is extended and

Fig. 8.--Number of notes per group in contact calling.

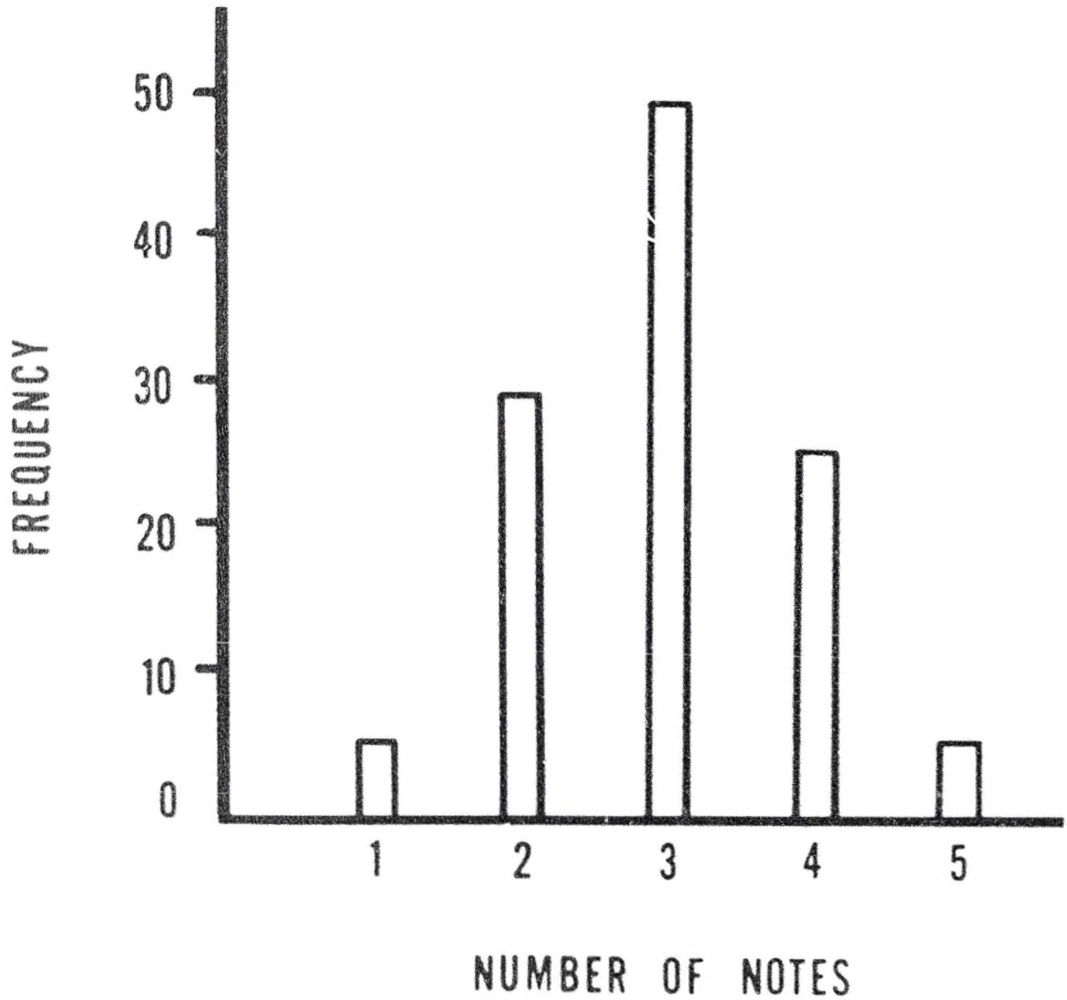

FREQUENCY
50
40
30
20
10
0
1
2
3
4
5
NUMBER OF NOTES

TABLE 8

FREQUENCY CHANGES WITHIN GROUPS OF DUCKLING CONTACT CALLS

Number of Notes Per Group	*All Notes Increase	**All Notes Decrease	No Change	Increase then Decrease
2	28	1	0	-
3	27	4	0	18
4	6	1	0	18
5	0	0	0	5
Total	61	6	0	41

* Increase - Each note has a higher frequency than the preceding.
** Decrease - Each note has a lower frequency than the preceding.

located in the peak or initial descending section of the note (Figure 7B). These notes share the following characteristics with the contact call: they are variable in frequency and time (Table 7), they occur in groups, and subsequent notes in a group vary as in contact calls. These notes appear to be intermediate between contact and distress calls. Kear (1968) suggests that the calls of young Anatidae grade into one another.

Distress calling of ducklings generally consists of evenly spaced notes that may extend into a sequence of as many as 20 to 30 notes (Table 7 Figure 7C). The concentration of sound energy is at the peak of the descending section of the note. Notes have a greater duration than in contact calls. The maximum frequency which ducklings attain (approximately five KHz) occurs during high level distress calling, the high frequency and long duration of each such note resulting in a harsh sound. Generally the first few notes of a distress sequence are the lowest in frequency; as the sequence proceeds, frequencies of subsequent notes increase and finally level off at the high level distress call. Distress calling may end abruptly or there may be a decrease in frequency of the notes at the end of the sequence.

Analysis of variance of high level distress calls of individual ducklings showed them to be significantly different ($F = 208$, $P < 0.001$ for four and 35 degrees of freedom). Not only does the average frequency of the spectrum differ between individuals, but so does the frequency distribution of energy with time (Table 9, Figure 9). The spectrum of the high level distress call of some ducklings decrease (duckling 1 from 4073 ± 93 Hz to 3714 ± 114 Hz; duckling 3, 4733 ± 184 Hz to 3577 ± 114 Hz; duckling 4, 4659 ± 148 Hz to 3939 ± 105 Hz) while for others it increases (duckling 2, 2901 ± 224 Hz to 3362 ± 179 Hz; duckling 5, 3105 ± 86 Hz to 3439 ± 102 Hz). No individual differences were observed in duckling contact calls.

POST-HATCHING DEVELOPMENT OF DUCKLING VOCALIZATIONS AND BEHAVIOUR

During early stages of development, ducklings were extremely vocal. They were silent only when in alert postures or when being brooded. Fabricius (1951) suggested that duckling vocalizations function to unite the brood. From hatching to seven weeks, contact calls were the most common type and were given almost constantly. Ducklings called most frequently when following females through plant cover. Lower calling rates occured when they were feeding in the plant cover or on the pond, or were resting.

When ducklings were two to three weeks old, they began initiating feeding bouts. Brooding by the female declined. Duckling alarm calls (Starkey, 1971) were first given when they were about two weeks old. The

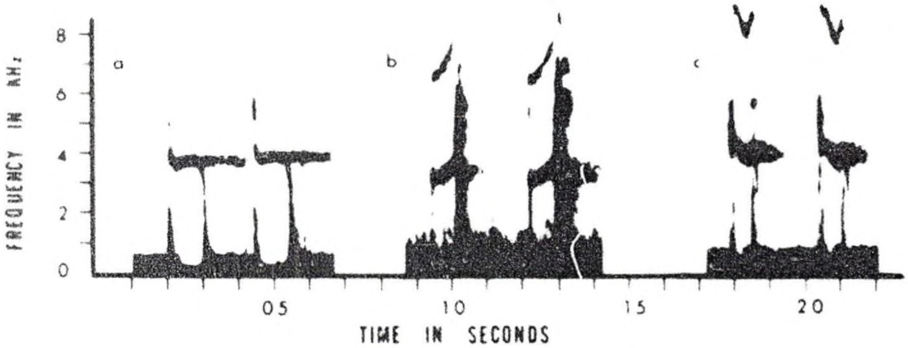
TABLE 9

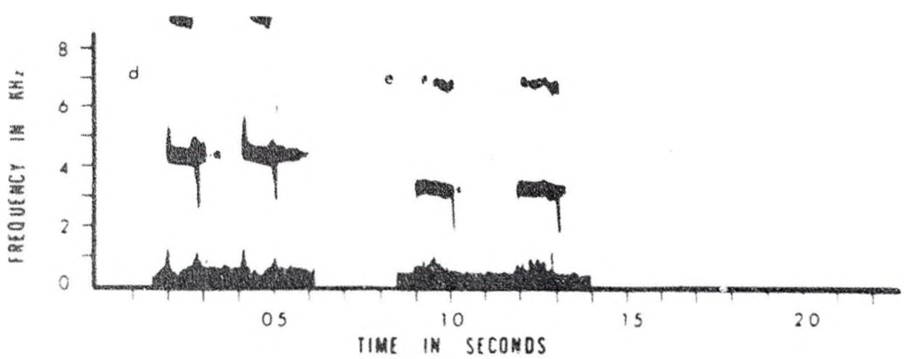
NUMERICAL ANALYSIS OF DISTRESS CALLS OF FIVE DUCKLINGS (frequencies in Hz; time in msec.; spectrum = frequencies containing most sound energy; N = sample size; $\bar{X}$ = mean; S.D. = standard deviation)

		N	$\bar{X} \pm$ S.D.
Duckling 1			
Frequency:	Beginning spectrum	12	4073 ± 93
	Ending spectrum	12	3714 ± 114
	Average spectrum	12	3885 ± 100
Time:	Duration of call	12	100.9 ± 5.8
	Interval	12	146.3 ± 7.7
Duckling 2			
Frequency:	Beginning spectrum	8	2901 ± 224
	Ending spectrum	8	3362 ± 179
	Average spectrum	8	3631 ± 92
Time:	Duration of call	8	84.9 ± 9.5
	Interval	5	187.3 ± 6.5
Duckling 3			
Frequency:	Beginning spectrum	14	4733 ± 184
	Ending spectrum	14	3577 ± 114
	Average spectrum	14	4141 ± 107
Time:	Duration of call	14	87.2 ± 5.1
	Interval	11	108.2 ± 12.4
Duckling 4			
Frequency:	Beginning spectrum	9	4659 ± 148
	Ending spectrum	9	3939 ± 105
	Average spectrum	9	4280 ± 129
Time:	Duration of call	9	87.1 ± 4.4
	Interval	6	146.3 ± 8.1
Duckling 5			
Frequency:	Beginning spectrum	15	3105 ± 86
	Ending spectrum	15	3439 ± 102
	Average spectrum	15	3272 ± 86
Time:	Duration of call	15	97.7 ± 7.7
	Interval	14	172.4 ± 15.5

a. Duckling 1
b. Duckling 2
c. Duckling 3
d. Duckling 4
e. Duckling 5

Fig. 9.--High level distress calls of individual ducklings.


8
6
4
2
0
FREQUENCY IN KHz
a
b
c
0 5
1 0
1 5
2 0
TIME IN SECONDS


8
6
4
2
0
FREQUENCY IN KHz
d
e
0 5
1 0
1 5
2 0
TIME IN SECONDS

alarm call consisted of a spectrum of frequencies increasing with time, resulting in a whistle-like sound (Table 10, Figure 10). Alarm calls were recorded from ducklings two to eight weeks old. These calls elicited responses from both ducklings and females and appeared to be given for both aerial and ground disturbances. Following an alarm call, ducklings usually stopped contact calling and assumed alert postures. Females also became alert.

TABLE 10

NUMERICAL ANALYSIS OF DUCKLING ALARM CALLS (frequencies in Hz; time in msec.; N = sample size; $\bar{X}$ = mean; S.D. = standard deviation)

		N	$\bar{X} \pm$ S.D.
Frequency:	Minimum	12	1673 ± 312
	Maximum	12	2420 ± 311
	Average	12	2031 ± 267
Time:	Duration of call	12	102.4 ± 15.6

The frequency of all duckling calls decrease with age (Tables 11 and 12, Figure 11). The average frequency of contact calls while feeding is consistently lower than those where the ducklings were disturbed (Table 11, Figure 11A). Abs (1970) correlated the drop in frequency of distress calls of developing domestic male mallards with an increase in tracheal length. Accompanying the decrease in frequency of contact calls is a change in call structure. In young females, the spectrum shifts to a section of the descending part of the call. The modification of the call in this manner is a gradual process, and at any given time each

Fig. 10.--Spectrogram of duckling alarm calls.

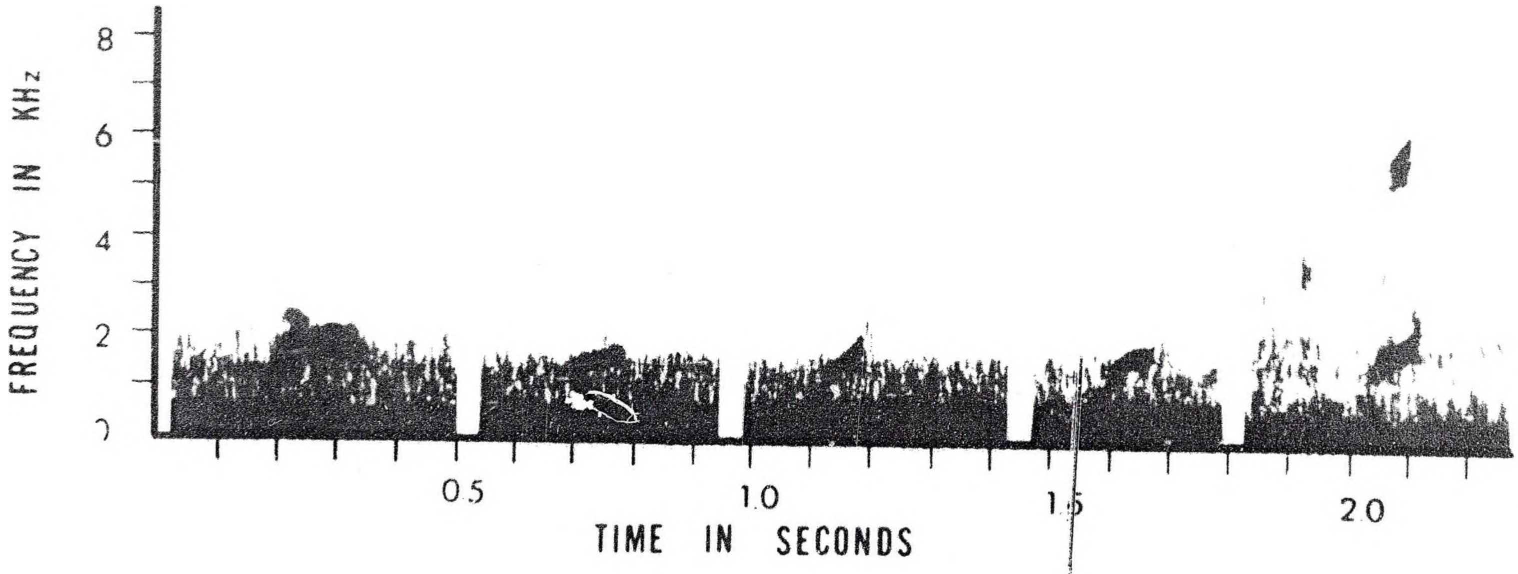

FREQUENCY IN KHz
8
6
4
2
0
0.5
1.0
1.5
2.0
TIME IN SECONDS

TABLE 11

CHANGE IN MAXIMUM FREQUENCY OF CALLS OF YOUNG WITH AGE (frequencies in Hz; N = sample size; $\bar{X}$ = mean; S.D. = standard deviation)

Age in Weeks	Situation	N	$\bar{X} \pm$ S.D.
1	Feeding	15	3204 ± 198
	Disturbed	15	3502 ± 313
2	Feeding	20	3001 ± 270
	Disturbed	20	3303 ± 223
3	Feeding	20	2427 ± 218
	Disturbed	20	2769 ± 271
4	Feeding	20	2421 ± 320
	Disturbed	20	2958 ± 308
5	Feeding	20	1989 ± 299
	Disturbed	20	2635 ± 411
6	Feeding	20	1945 ± 280
	Disturbed	20	2183 ± 327
7	Feeding	20	1634 ± 304
	Disturbed	20	1830 ± 278

series of calls may contain the contact call with both the inverted "U" and the modified form. Not only did the frequency of calls change with age, but so did the rate of calling. As ducklings developed, the amount of contact calling decreased in all situations.

The time of day at which young were active changed as they developed. This is shown for 11 weeks using the total number of calls, counted from all morning recordings as an indicator of activity (Figure 12). Young were consistently more active after, than before, sunrise (Figure 12A). Generally, activity increased during each consecutive one hour period of the three hours of recording (Figure 12B). As young developed, they were

TABLE 12

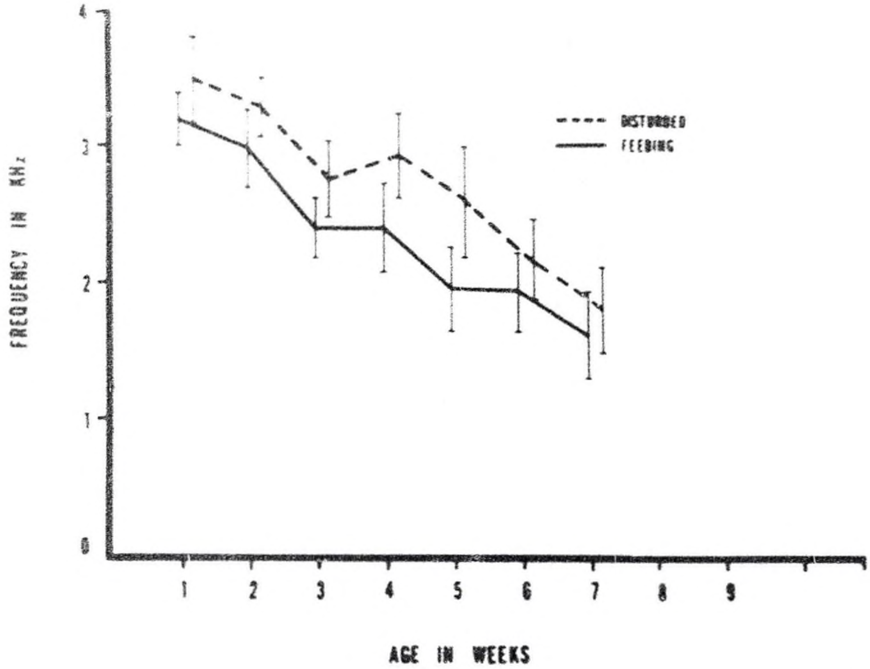
NUMERICAL ANALYSIS OF CALLS OF YOUNG WITH AGE (frequencies in Hz; time in msec.; N = sample size; $\bar{X}$ = mean; S.D. = standard deviation)

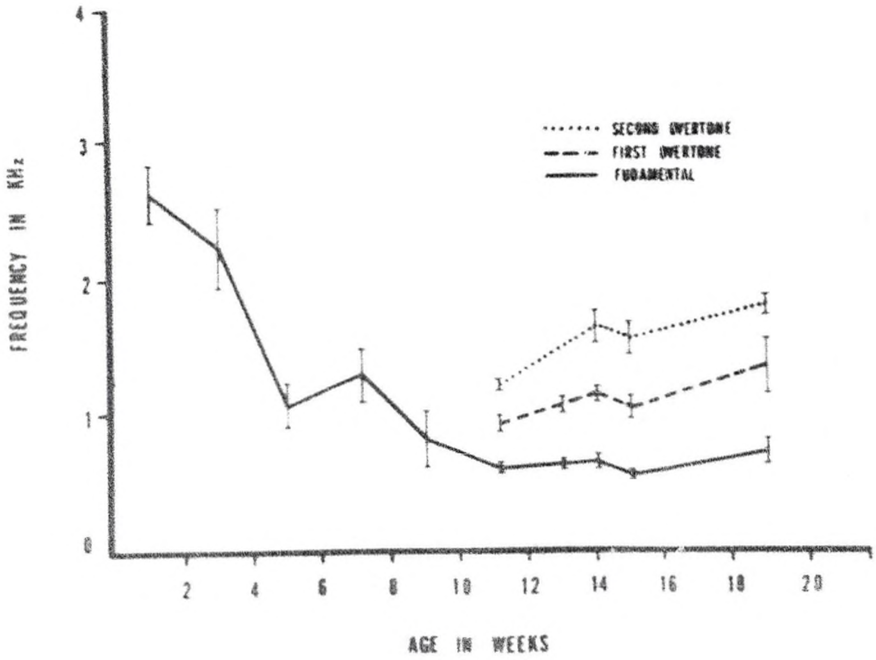
Age in Weeks			N	$\bar{X} \pm$ S.D.
1	Frequency:	Average	46	2669 ± 207
	Time:	Duration of call	31	51.8 ± 9.1
3	Frequency:	Average	35	2236 ± 266
	Time:	Duration of call	27	59.4 ± 23.0
5	Frequency:	Average	22	1073 ± 143
	Time:	Duration of call	22	60.6 ± 10.7
7	Frequency:	Average	25	1292 ± 197
	Time:	Duration of call	25	50.9 ± 10.6
9	Frequency:	Average	17	818 ± 204
	Time:	Duration of call	17	65.4 ± 16.7
11	Frequency:	Preliminary stroke	8	1099 ± 276
		Fundamental	14	841 ± 42
		1st overtone	14	1766 ± 44
		2nd overtone	10	2659 ± 65
		3rd overtone	5	3584 ± 175
	Time:	Duration of note	13	56.9 ± 6.7
		Duration of call	8	101.2 ± 4.8
13	Frequency:	Fundamental	17	627 ± 36
		1st overtone	15	1076 ± 60
14	Frequency:	Fundamental	14	645 ± 61
		1st overtone	15	1143 ± 69
		2nd overtone	7	1676 ± 113
15	Frequency:	Fundamental	15	556 ± 30
		1st overtone	15	1051 ± 81
		2nd overtone	7	1567 ± 107
		3rd overtone	5	2029 ± 108
19	Frequency:	Fundamental	11	711 ± 86
		1st overtone	11	1347 ± 215
		2nd overtone	3	1787 ± 49

A. Average frequency of "loop" structure calls

B. Most common calls. ("loop" structured up to 10 weeks)

Fig. 11.--Change in frequency of calls of developing young. (I = ± one standard deviation)


DISTURBED
FEEDING
FREQUENCY IN KHz
AGE IN WEEKS
0
1
2
3
4
1
2
3
4
5
6
7
8
9

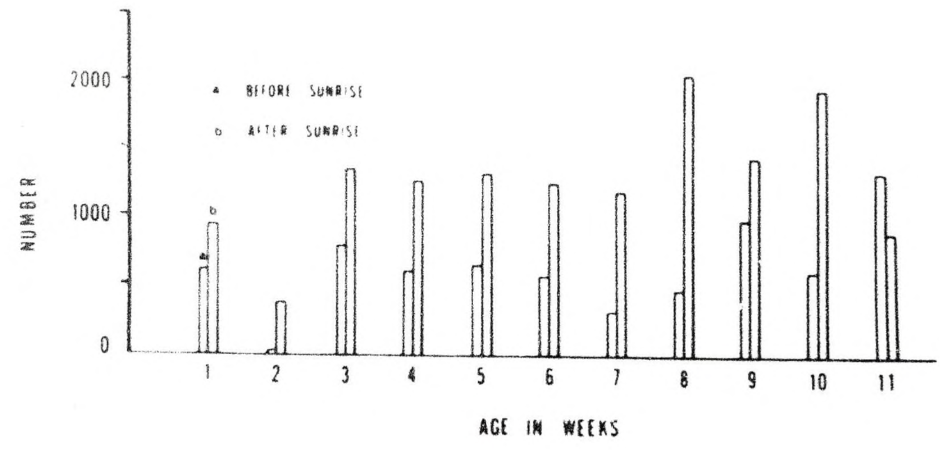

SECOND OVERTONE
FIRST OVERTONE
FUDAMENTAL
FREQUENCY IN KHz
AGE IN WEEKS
0
1
2
3
4
2
4
6
8
10
12
14
16
18
20

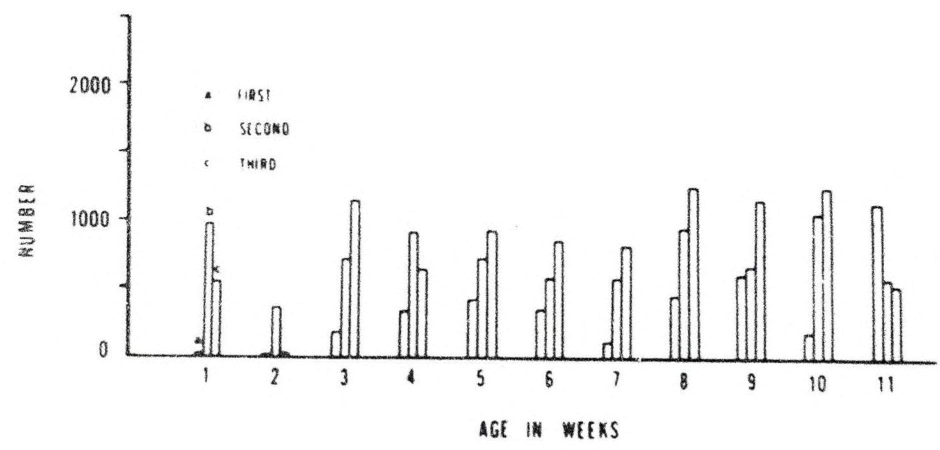
A. Two one and one half hour periods

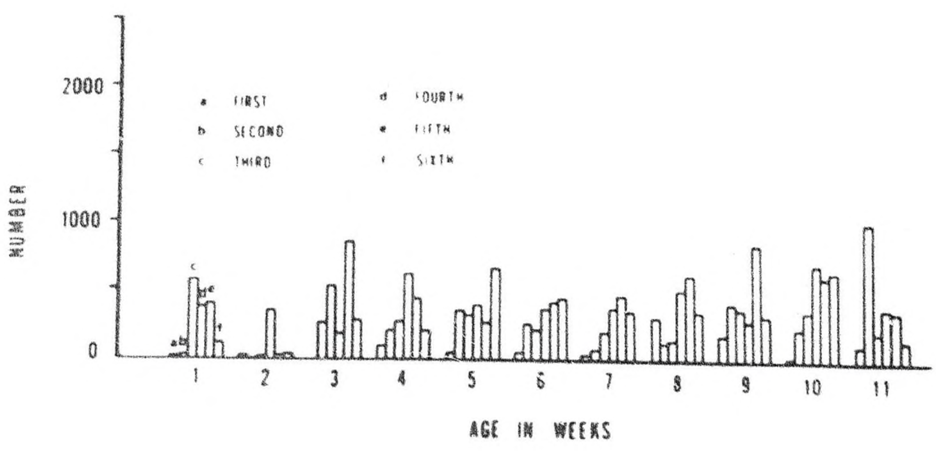
B. Three one hour periods

C. Six one half hour periods

Fig. 12.--Change in activity of developing young.
(From one and one half hours before to one and one half hours after sunrise.)


2000
1000
0
NUMBER
a BEFORE SUNRISE
b AFTER SUNRISE
1 2 3 4 5 6 7 8 9 10 11
AGE IN WEEKS


2000
1000
0
NUMBER
a FIRST
b SECOND
c THIRD
1 2 3 4 5 6 7 8 9 10 11
AGE IN WEEKS

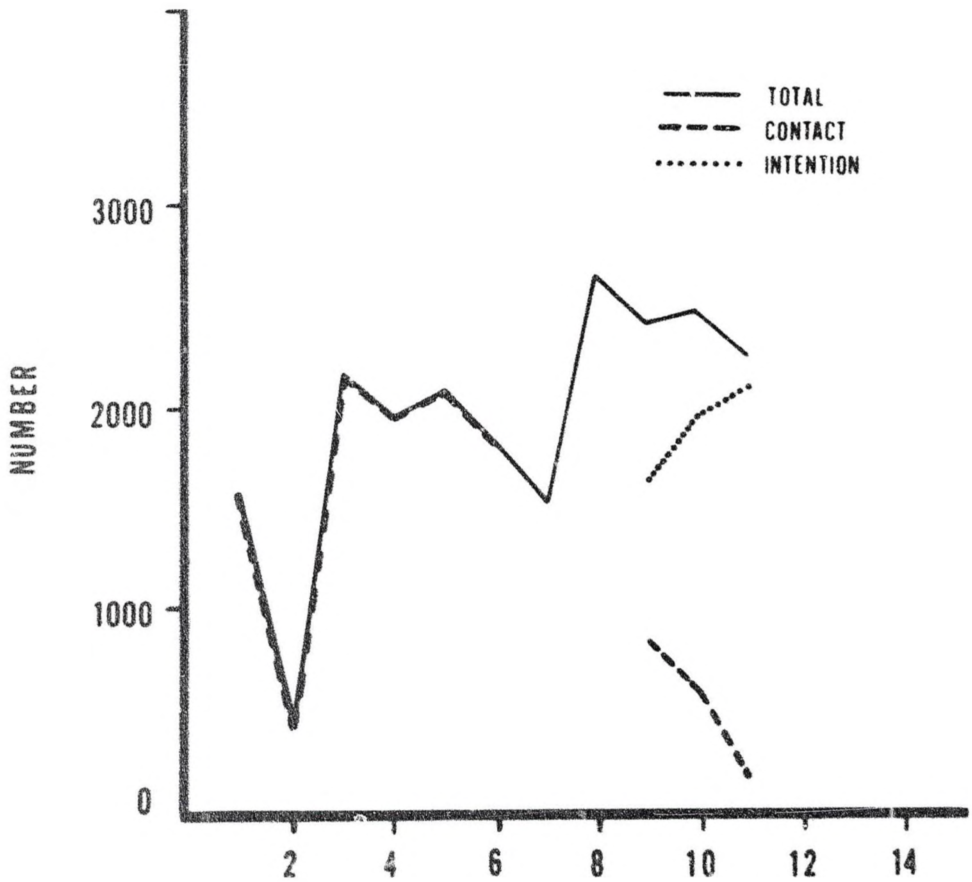

2000
1000
0
NUMBER
a FIRST
b SECOND
c THIRD
d FOURTH
e FIFTH
f SIXTH
1 2 3 4 5 6 7 8 9 10 11
AGE IN WEEKS

active earlier in the morning. Figure 12C shows that initially young were not very active early in the morning, however, by four weeks they were active as early as one and one half hours before dawn. Generally the activity increased as dawn approached and tended to drop-off near the end of the recording period.

Ducklings become more independent as they develop. Members of a brood were observed feeding alone on the pond at five weeks; and by seven weeks aggression between members of the brood was evident. While on the pond, ducklings occasionally chased and nipped siblings. Their aggressive encounters developed into bouts of aggressive activity by nine weeks. By seven weeks ducklings were giving calls associated with pre-flight intention movements. The total number of these calls per unit time increased from about the time ducklings began flying at seven to eight weeks until approximately 12 weeks.

As ducklings increased in age and degree of independence, the rate and type of calling changed. Over an 11 week period, the total number of calls in an all morning recording increased and there was a marked shift from contact to intention calling (Table 6, Figure 13). Initially contact calls were almost exclusively given. The peak in contact calling occurred at about five weeks of age just prior to the onset of intra-brood aggression. Aggressive and intention calls were not definitely distinguishable when juveniles were six to eight weeks of age. By the time definite bouts of pre-flight intention movements became frequent (at about eight to nine weeks), intention calling was easily distinguishable and common; and by 11 weeks it had virtually replaced contact calling. By 10 weeks, when adults began calling bouts from a pen just north

Fig. 13.--Total number of duckling calls from all morning recordings.


TOTAL
CONTACT
INTENTION
NUMBER
3000
2000
1000
0
2
4
6
8
10
12
14
AGE IN WEEKS

of the study pens. Juveniles in study pens faced the calling adults, began intention calling, and moved to the north end of the pen. This continued and increased for three weeks until the adults were removed. The juveniles then continued to give intention calls, until removed a week later, but did not move to the north end of the pen. This suggests that one of the functions of sexual calling, in late summer and fall, may be to attract birds to a common location for the formation of flocks.

The age at which juveniles develop adult calls is variable and hard to determine. Within a brood, individuals vary in their stage of development. In one brood, it was observed that one male had developed more pronounced plumage characteristics than the other, and attempted to give adult calls more than a week before the other male.

It appears that the extent to which juvenile calls have attained adult characteristics depends not only on the bird's ability to produce adult calls, but also on its motivational state at the time of calling. During the transition from juvenile to adult calling, it is not uncommon for a bird to give intention calls similar to adults and yet a week later give definite juvenile intention calls. Likewise with other calls, during this transitional period, any individual can give juvenile, adult and/or intermediate calls. Nevertheless, the age at which adult calls and visible sexual behaviours were first noted was recorded.

Definite quacks and short decrescendos were recorded from nine week old females. These calls, however, did not appear to be commonly used by females until they were more than 18 weeks old. Males were first observed nod-swimming at 16 weeks but definite bouts of sexual displays and associated calls were not observed until they were 18 weeks old.

Males gave definite grunt whistles, head-up-tail-up displays and associated raehb calling during these bouts of sexual activities. At this time, females were also observed inciting. Generally, contact calling of young had ceased by 11 - 12 weeks, and by 18 - 20 weeks the birds were regularly giving adult calls and associated behaviour.

When the birds were first introduced into the large flight pen each brood remained as a unit, feeding and resting alone. Inter-brood aggression was common and within a few days a hierarchy related to age was established, the oldest brood being dominant. The first sexual behaviour observed was displayed to brood-mates. These units slowly broke down and birds were displaying in mixed groups before freeze-up. Broods remaining as a unit for such a long time, however, may not be common in the wild.

DEVELOPMENT OF ADULT CALLS

A. FEMALE CALLS

Female adult calls develop from the basic contact call of the duckling. Accompanying the decrease in frequency, the inverted "U" characteristic of the contact call gradually changes so that the descending section of the call contains most of the sound energy and extends to form a "foot like" structure (Table 13, Figure 14). The spectrum of the call decreases from 2118 $\pm$ 113 Hz at three weeks to 1902 $\pm$ 74 Hz by six weeks (Table 13, Figure 15). Both frequency and form continue to change, eventually leading to a low frequency vocalization with two parts: a brief ascending part forming the preliminary stroke, and a descending portion that forms the main note, as shown for seven week old females (Table 13, Figure 14). The ascending part has a maximum frequency of

TABLE 13

NUMERICAL ANALYSIS OF THE DEVELOPMENT OF FEMALE CALLS (frequencies in Hz; time in msec.; spectrum = frequencies containing most sound energy; N = sample size; $\bar{X}$ = mean; S.D. = standard deviation)

Age in Weeks			N	$\bar{X}$ ± S.D.
Calls with spectrum in descending section (foot like)				
3	Frequency:	Maximum	17	3040 ± 136
		Spectrum	17	2118 ± 113
	Time:	Duration of call	17	75.9 ± 3.7
5	Frequency:	Maximum	15	2835 ± 231
		Spectrum	15	2020 ± 109
	Time:	Duration of call	15	87.1 ± 4.6
6	Frequency:	Maximum	19	2649 ± 136
		Spectrum	19	1902 ± 74
	Time:	Duration of call	19	81.8 ± 6.1
Calls given with associated intention movements				
7	Frequency:	Maximum preliminary stroke	11	2090 ± 334
		Spectrum	14	1275 ± 107
	Time:	Duration of note	11	73.9 ± 10.0
		Duration of call	14	140.6 ± 6.1
9 (a)	Frequency:	Maximum preliminary stroke	10	901 ± 17
		Fundamental	10	726 ± 29
		First overtone	10	1507 ± 65
		Second overtone	3	2065 ± 0
	Time:	Duration of note	10	51.2 ± 6.6
		Duration of call	10	100.7 ± 4.6
9 (b)	Frequency:	Maximum preliminary stroke	10	906 ± 72
		Fundamental	10	1479 ± 67
		First overtone	10	2621 ± 42
	Time:	Duration of note	10	51.2 ± 4.8
		Duration of call	10	84.8 ± 3.8
10	Frequency:	Maximum preliminary stroke	11	775 ± 42
		Fundamental	11	404 ± 28
		First overtone	11	1373 ± 83

TABLE 13--Continued

Age in Weeks			N	$\bar{X}$ ± S.D.
10		Second overtone	11	2410 ± 57
		Third overtone	11	3536 ± 114
	Time:	Duration of note	11	53.8 ± 6.0
		Duration of call	11	93.2 ± 6.0
11	Frequency:	Maximum preliminary stroke	5	915 ± 46
		Fundamental	5	447 ± 23
		First overtone	5	1389 ± 160
		Second overtone	5	2532 ± 118
	Time:	Duration of note	5	56.9 ± 5.9
		Duration of call	5	96.5 ± 5.9
12	Frequency:	Maximum preliminary stroke	3	1006 ± 99
		Fundamental	3	879 ± 22
		First overtone	3	1771 ± 91
		Second overtone	3	2666 ± 67
	Time:	Duration of note	3	54 ± 4.2
		Duration of call	3	96.5 ± 8.4

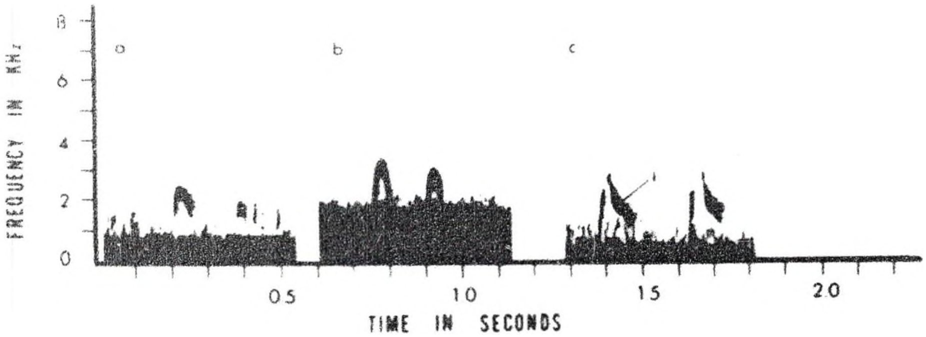
2090 ± 334 Hz, the spectrum of the main note being 1275 ± 107 Hz.

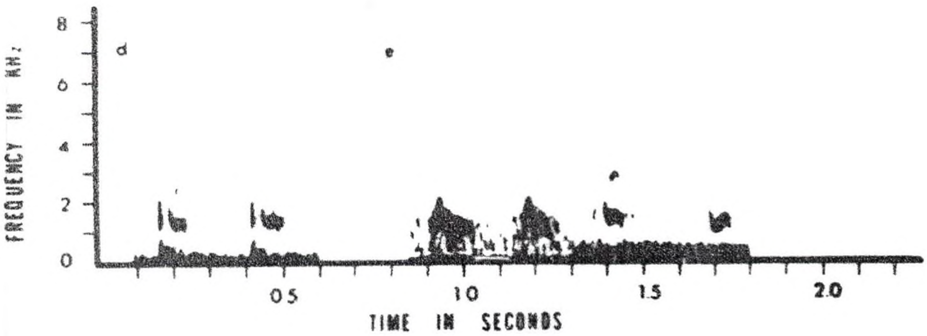
Adult female calls develop mainly from the descending section of the call. As the main note decreases in frequency, harmonics are added (Table 13, Figure 15). Greenwalt (1968) suggested that each species has a threshold frequency below which the fundamental produces harmonics. The value of this threshold frequency, however, is variable and is controlled by the penetration of the external labium into the bronchial lumin.

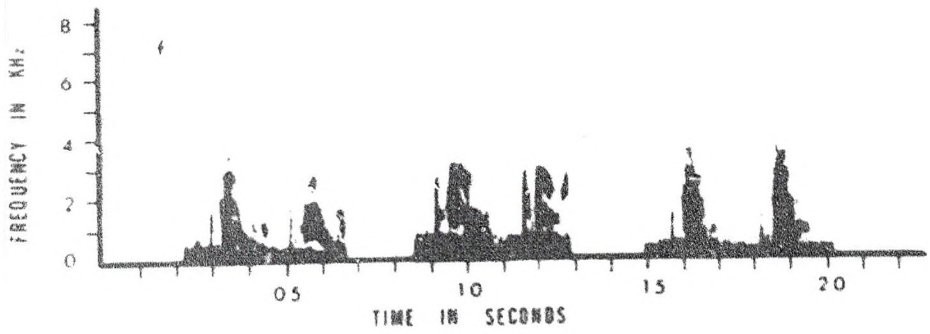
By using the first recognizable concentration of energy as the fundamental frequency, it can be shown that as the fundamental of intention calls decreases, harmonics are added. Table 13 and Figure 15 show that females can alter the fundamental frequency and harmonic content. During

a. One week
b. Three weeks
c. Five weeks
d. Seven weeks
e. Nine weeks
f. Eleven weeks
i. Foot like structure

Fig. 14.--Spectrograms of the development of female calls.

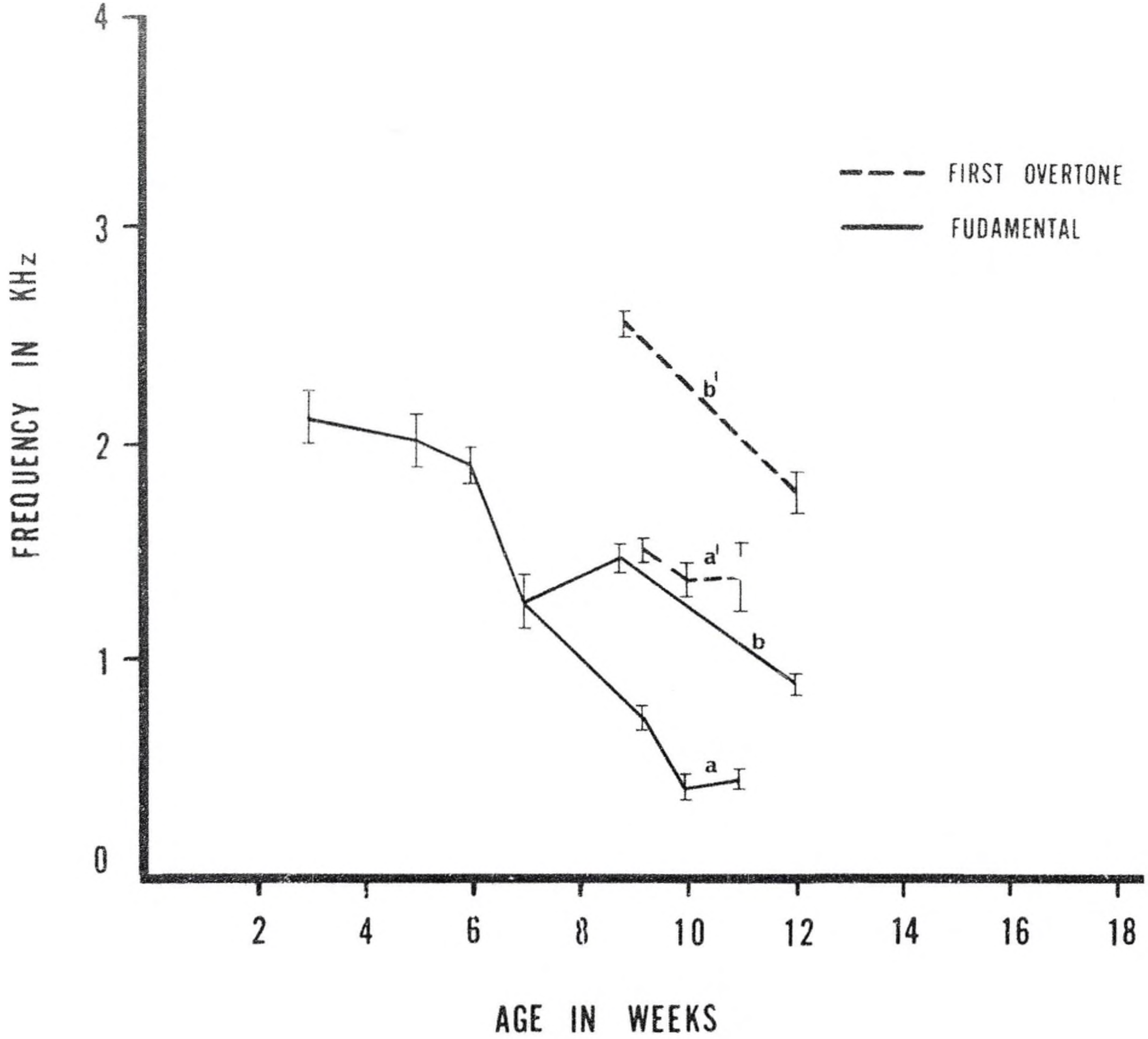

a
b
c
FREQUENCY IN KHz
TIME IN SECONDS


d
e
FREQUENCY IN KHz
TIME IN SECONDS


f
FREQUENCY IN KHz
TIME IN SECONDS

a.a'. Fundamental and overtone for: 9(a), 10 and 11 weeks.
b,b'. Fundamental and overtone for: 9(a) and 12 weeks.

Fig. 15.--Frequencies of developing female calls.
(I = ± one standard deviation)


FIRST OVERTONE
FUDAMENTAL
FREQUENCY IN KHz
AGE IN WEEKS
0
1
2
3
4
2
4
6
8
10
12
14
16
18
a
b
a'
b'

two different bouts of intention calling, nine week old females gave calls containing a fundamental frequency of 726 $\pm$ 29 Hz(a) with two overtones at 1507 $\pm$ 65 Hz(a') and 2065 Hz; and also calls with a fundamental frequency of 1479 $\pm$ 67 Hz(b) and one overtone at 2621 $\pm$ 42 Hz(b'). The calls recorded at 10 and 11 weeks appeared to be with the group with the lower fundamental (a, a') whereas the calls at 12 weeks with the higher fundamental group (b, b').

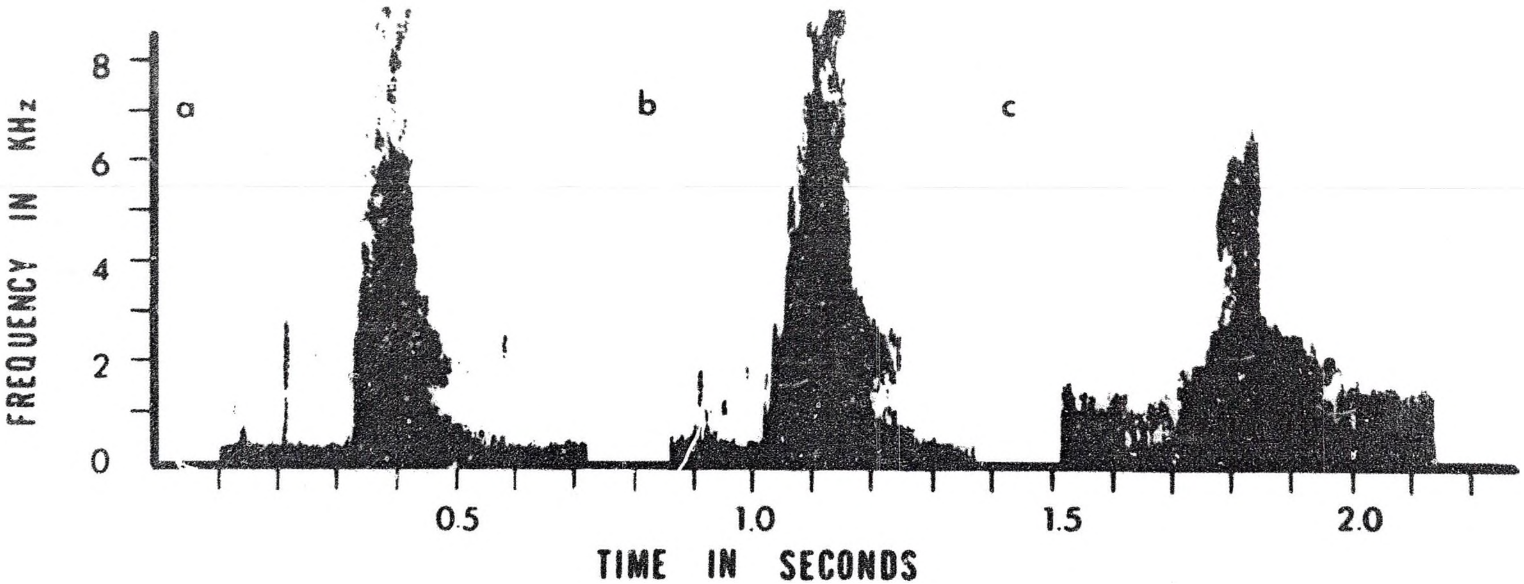
By 10 to 11 weeks female intention calls generally contained a fundamental of about 400 Hz with two to three overtones, although a greater harmonic content was sometimes found. At this time, intention calls were similar to the adult pre-flight calls described by Abraham (1971).

Other calls of females also appeared to develop from the main note of the contact call. An extended transitional period for the development of quack and decrescendo calls were not observed. It may be that when females first gave these calls, they were almost in adult form. These calls are composed of a low fundamental frequency and a series of harmonics, the fundamental frequency being formed from the main note of the contact call. Notes of these different calls vary in terms of fundamental frequency, number of harmonics, duration of each note, and amount of sound energy utilized. The number and spacing of notes is important in the formation of the total call. For a description of adult female calls and their ranges of variation see Abraham (1971).

First quacks given by juvenile females were almost in adult form and appeared to be formed from the main note of the basic contact call. Quacks from juvenile females are shown in Figure 16. Due to the small sample

a. Twelve weeks
b. Sixteen weeks
c. Eighteen weeks

Fig. 16.--Spectrogram of quacks of juvenile females.


FREQUENCY IN KHz
8
6
4
2
0
a
b
c
0.5
1.0
1.5
2.0
TIME IN SECONDS

size of juvenile quacks no attempt was made to test if they were significantly different. By 18 weeks the quack consists of the main note with low fundamental frequency ($<$ 200 Hz) and a series of harmonics. This may be similar to the adult mallard call analyzed by Greenwalt (1968) which had a fundamental frequency of 179 Hz, the 12th harmonic being dominant.

Decrescendo and inciting calls recorded from 16 to 18 week old females also contained only portions derived from the main note of the basic contact call (Table 14, Figure 17). The decrescendo had a fundamental frequency of about 462 $\pm$ 24 Hz and a series of harmonics with the concentration of energy at 2105 $\pm$ 90 Hz. This is similar to an adult decrescendo analyzed by Johnsgard (1971), with a fundamental frequency of 585 Hz and a maximum amplitude between 1500 and 2500 Hz. Johnsgard (1971) stated that the fundamental frequency of the inciting call appeared to be lower than the decrescendo. Inciting calls of 18 week old females contained a fundamental frequency of 337 $\pm$ 45 Hz and a spectrum located at about 1978 $\pm$ 91 Hz.

B. MALE CALLS

Until the male raehb was easily distinguishable, calls associated with intention movements were used in tracing the development of male calls. These calls appear to develop from the contact call in a way similar to female calls. There is a decrease in frequency with age, and the characteristics of the call change, initially forming a preliminary stroke and a main note.

The development of the calls is shown in Table 15 and Figure 18 and 19. Male calls at six weeks, averaging 2329 $\pm$ 130 Hz, had decreased

TABLE 14

NUMERICAL ANALYSIS OF ADULT CALLS OF JUVENILE FEMALES (frequencies in Hz; spectrum = frequencies containing the most sound energy; time in msec.; N = sample size; $\overline{X}$ = mean; S.D. = standard deviation)

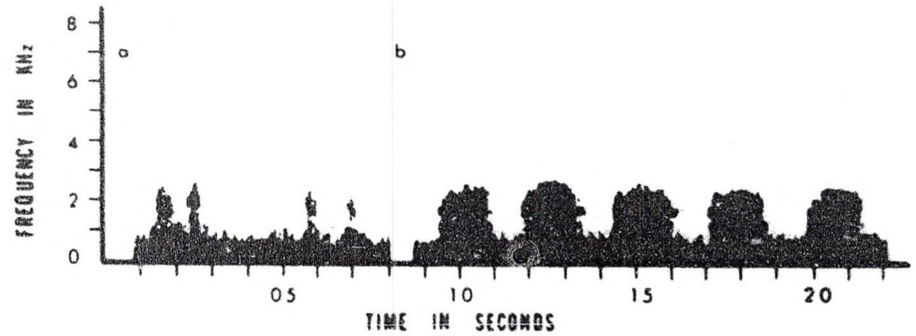
		N	$\overline{X}$ ± S.D.
Decrescendo of 16 week olds			
Frequency:	Fundamental	6	462 ± 24
	First overtone	6	841 ± 48
	Second overtone	6	1291 ± 29
	Third overtone	6	1671 ± 57
	Maximum	6	2754 ± 218
	Spectrum	6	2105 ± 90
Time:	Duration of call	6	150 ± 13.7
Inciting of 18 week olds			
Frequency:	Fundamental	6	337 ± 45
	First overtone	6	637 ± 23
	Second overtone	6	908 ± 50
	Maximum	6	2637 ± 96
	Spectrum	6	1978 ± 91
Time:	Duration of call	6	40.2 ± 7.6

and changed by nine weeks forming calls containing a preliminary stroke of 1736 ± 316 Hz and a main note of 1258 ± 120 Hz. The higher frequency of the main note (1981 ± 109) at 10 weeks (Table 15) may reflect variably in the motivational state of birds when calling and not be characteristic of the development of the call.

By 11 weeks definite raehb calls were heard. They consisted of a main note (562 ± 64 - 909 ± 494 Hz) and one overtone (1846 ± 28 - 1954 ± 204 Hz). The preliminary stroke was absent or minimal. By 14 weeks, the main note appeared to be lost and only an overtone (1493 ± 131 Hz) was present (Figure 19). The overtone had become diffuse and the spectrum

a. Juvenile inciting
b. Juvenile decrescendo
c. Adult inciting
d. Adult decrescendo

Fig. 17.--Spectrograms of inciting and decrescendo of females


a
b
FREQUENCY IN KHz
0
2
4
6
8
05
10
15
20
TIME IN SECONDS

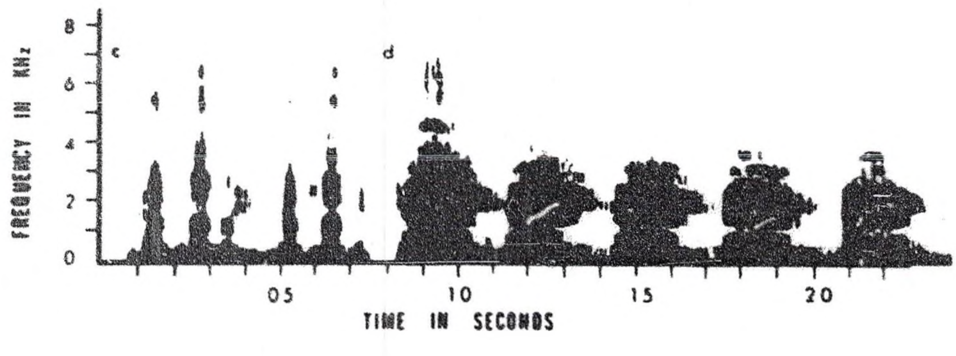

c
d
FREQUENCY IN KHz
0
2
4
6
8
05
10
15
20
TIME IN SECONDS

TABLE 15

NUMERICAL ANALYSIS OF THE DEVELOPMENT OF MALE CALLS (frequencies in Hz; time in msec.; spectrum = frequencies containing most sound energy; fundamental = first recognizable frequency; N = sample size; $\bar{X}$ = mean; S.D. = standard deviation)

Age in Weeks			N	$\bar{X}$ ± S.D.
6	Frequency:	Average of call	6	2329 ± 130
	Time:	Duration of call	6	78.8 ± 4.2
7	Frequency:	Average of call	13	2015 ± 68
	Time:	Duration of call	9	149.1 ± 25.7
9	Frequency:	Maximum preliminary stroke	16	1736 ± 316
		Fundamental	16	1258 ± 120
		First overtone	10	2448 ± 158
	Time:	Duration of note	16	87.4 ± 21.6
		Duration of call	16	121.3 ± 19.7
10	Frequency:	Maximum preliminary stroke	14	1887 ± 99
		Fundamental	14	1981 ± 109
	Time:	Duration of fundamental	14	128 ± 9.8
Recognizable as Raehb calls				
11(a)	Frequency:	Fundamental	13	909 ± 494
		First overtone	8	1954 ± 204
	Time:	Duration of call	6	125.7 ± 7.5
11(b)	Frequency:	Fundamental	6	562 ± 64
		First overtone	6	1846 ± 28
	Time:	Duration of call	6	125.7 ± 7.5
14	Frequency:	Minimum	15	983 ± 89
		Maximum	15	1810 ± 135
		Spectrum	15	1493 ± 131
15	Frequency:	Minimum	8	835 ± 150
		Maximum	8	1834 ± 148
		Spectrum	8	1323 ± 134
16	Frequency:	Minimum	4	1143 ± 70
		Maximum	4	2320 ± 84
		Spectrum	4	1680 ± 56

TABLE 15--Continued

Age in Weeks			N	$\bar{X} \pm$ S.D.
16	Time:	Duration of call	4	252.5 ± 37.1
18	Frequency:	Minimum	6	1142 ± 176
		Maximum	6	2315 ± 152
		Spectrum	6	1641 ± 245
	Time:	Duration of call	6	247.1 ± 76
19	Frequency:	Minimum	10	1379 ± 151
		Maximum	10	2082 ± 218
		Spectrum	10	1710 ± 195
	Time:	Duration of call	10	153.6 ± 127.1
		Duration of Rabrab	6	58.5 ± 8.9
		Duration of Raehb	4	296.3 ± 69.3

appeared to reach a low of 1323 ± 134 Hz at about 15 weeks. It then increased, reaching 1710 ± 195 Hz by 19 weeks. This frequency is similar to the first concentration of energy at 1851 ± 115 Hz of adult male calls (Table 16, Figure 20).

TABLE 16

NUMERICAL ANALYSIS OF ADULT MALE CALLS (frequencies in Hz; time in msec.; spectrum = frequencies containing most sound energy; N = sample size; $\bar{X}$ = mean; S.D. = standard deviation)

		N	$\bar{X} \pm$ S.D.
First concentration of energy			
Frequency:	Minimum	13	1431 ± 141
	Maximum	13	2263 ± 113
	Spectrum	13	1851 ± 115
Time:	Duration of call	13	160 ± 76.8
	Duration of Rabrab	10	129.4 ± 9.1
	Duration of Raehb	3	300 ± 12.7

a. Six weeks
b. Seven weeks
c. Nine weeks
d. Eleven weeks
e. Fourteen weeks
f. Sixteen weeks
g. Eighteen weeks

Fig. 18.--Spectrograms of developing male calls.

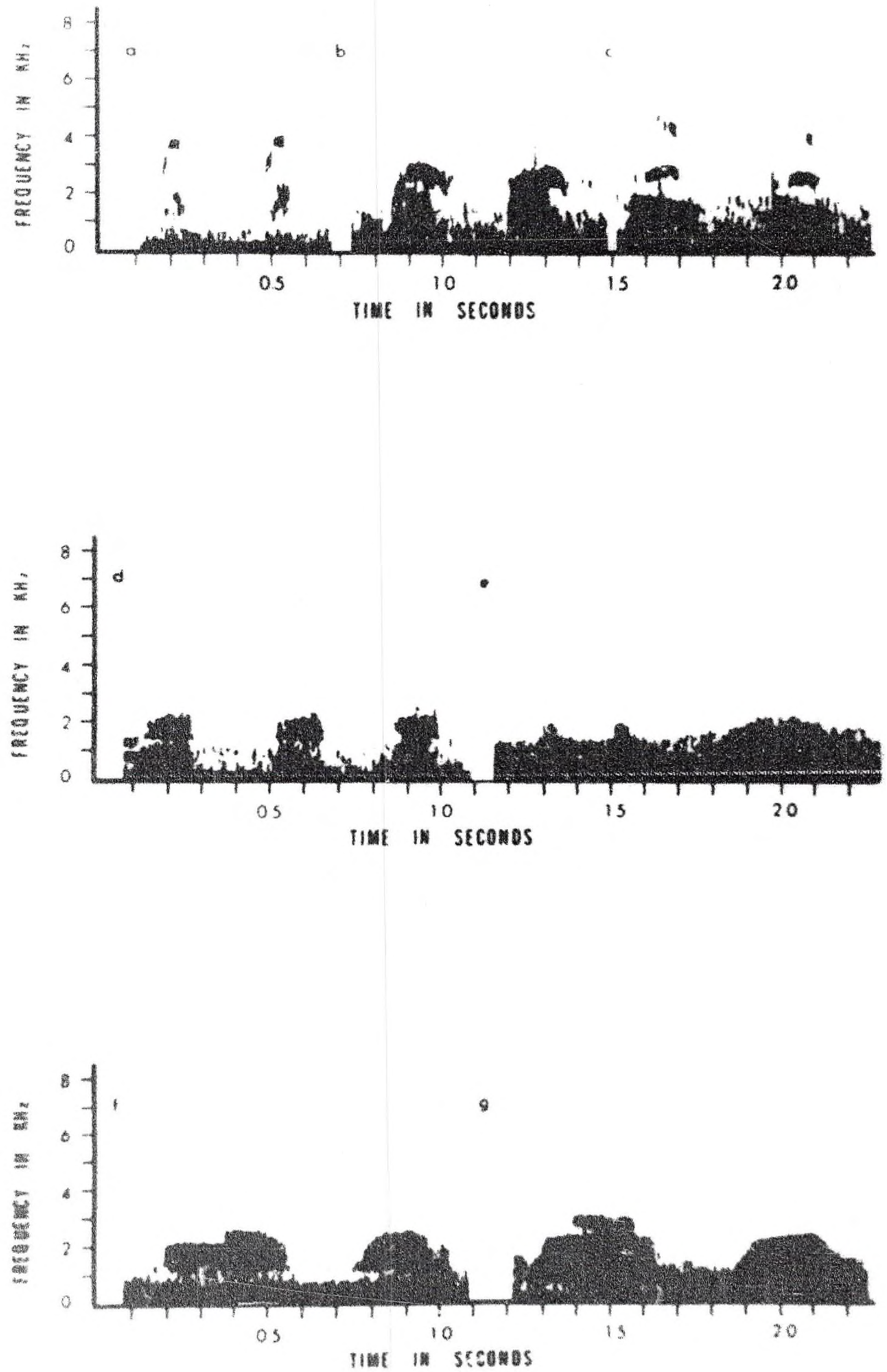
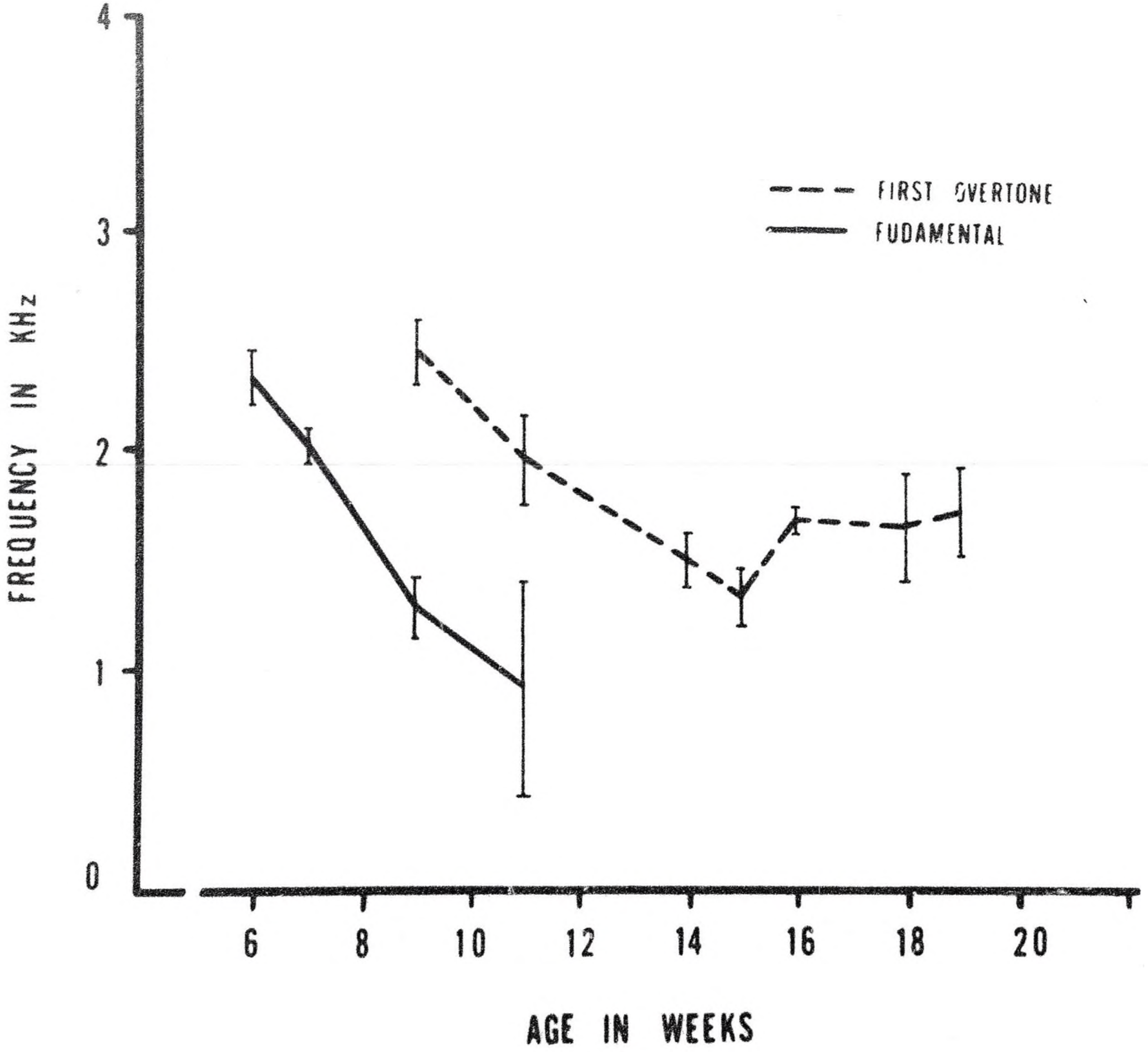
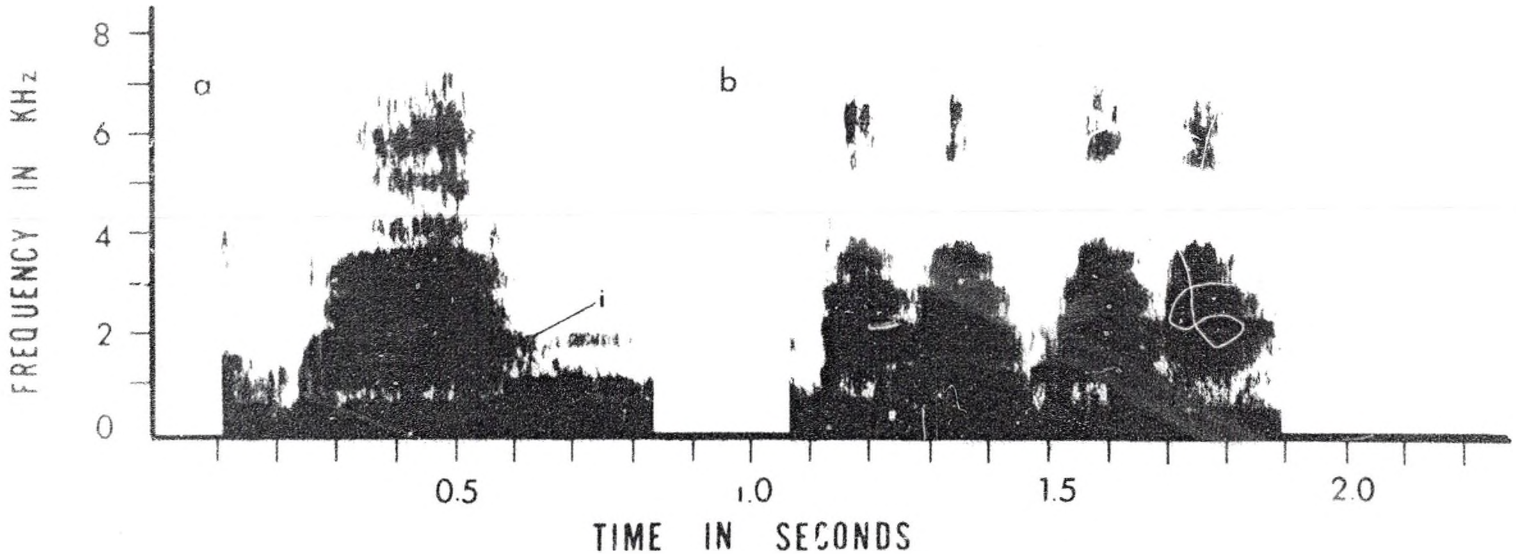

FREQUENCY IN KHz
TIME IN SECONDS
0
2
4
6
8
0.5
1.0
1.5
2.0
a
b
c
d
e
f
g

Fig. 19.--Frequencies of developing male call.
(I = $\pm$ one standard deviation)


FIRST OVERTONE
FUDAMENTAL
FREQUENCY IN KHz
0
1
2
3
4
6
8
10
12
14
16
18
20
AGE IN WEEKS

a. Raehb
b. Rabrab
1. First concentration of energy

Fig. 20.--Spectrograms of adult male calls.


FREQUENCY IN KHz
0
2
4
6
8
a
b
i
0.5
1.0
1.5
2.0
TIME IN SECONDS

Duration of long raehb calls of 19 week old males (296.3 ± 69.3 msec.) were similar to that of adult males (300 ± 12.7 msec.), however the duration of rabrab calls were not. Duration of adult rabrab calls averaged 129.4 ± 9.1 msec. while those of 19 week old males averaged 58.5 ± 8.9 msec.

DISCUSSION

Female calling initiates brood acitivity, providing information about the external environment. Ducklings call almost constantly, providing the hen with information about their state of being and/or location. One of the few times in the mallard's life cycle that sound communication is of primary importance is when female and broods are interacting. At this time relatively little information is conveyed via other modalities.

Besides providing information about the ducklings' external environment, the female broody calls appear to function in maintaining the brood as a unit. These calls are important for short range communication. For example, when plant cover is dense, ducklings may not be aided by visual cues and have to rely solely on the females' acoustical cues. In such a situation, the increased rate of female broody calling compensates for the lack of visible information.

The basic calls of newly hatched ducklings, contact or contentment (Figure 7A) and distress calls (Figure 7C), appear to be at the ends of a graded system. In the transition from basic contact to distress calls, frequency increases and the spectrum shifts until maximum modification is attained with the high level distress call. This gradation probably reflects a gradual change in the motivational state of the ducklings from "pure contentment" to "extreme distress". An increase in the rate of contact calling and in the frequency of subsequent groups of notes, may also indicate a change in the motivational state. Utilization of a graded system allows ducklings to communicate varied information about their motivational state to both female and brood mates.

Contact calls also function to maintain the brood as a unit (Fabricius, 1951). The nature of the basic contact call, an inverted "U" structure, repeated in groups, and low in frequency, is well suited for general location over a short distance. Contact calling of the brood mates allows the female or any duckling to locate the brood. According to Collias (1962) duckling distress calls attract the female to the young. The high level distress calls, which is of high frequency, amplitude, and regularly repeated, provides good location cues. As the harmonic content, and number of repetitions varies on a continuum from contentment to distress, so does the locatability of the calls.

Call structure is important for preservation of the brood. Female and young calls are low in amplitude and nearly free of harmonics. These are effective only at close range, and do not give away brood location to potential predators. The only calls with high amplitude and harmonics are distress calls of young and high level alarm calls of females. These calls are given in the presence of imminent danger when concealment of the brood's location is of less relative importance.

Individual differences observed in female broody calls and young distress calls reveals a potential for individual recognition. Although mixing of broods has been reported (Titman, 1969), its incidence may be reduced by acoustical cues. Aggression by females and their broods to members of other broods was observed, indicating that individual recognition does take place. The ability of the birds to recognize a strange duckling is probably established through a combination of visual and acoustical cues. This ability is important, as the probability of broods' success probably decreases above a certain size.

The decrease in number of female broody calls as young develop may be important in shifting control of the brood's activities from the female to members of the brood. This shift must occur before females leave their young and molt. After the young are able to fly, maintenance and control of the brood unit may no longer be advantageous. Thus reduction in the number of contact calls and finally their replacement by intention calls may reflect an increased independence of juveniles accompanied by a decrease in control of the brood as a unit.

Maturation of ducklings is accompanied by a decrease in frequency and a change in structure of their calls. Adult calls develop from part of the basic contact call. There is a reduction in the fundamental frequency below the threshold value accompanied by the addition of harmonics, (Table 13 and 15). The addition of harmonics to calls is not prominent until birds are able to fly. This is important because harmonics would make the birds more vulnerable to predators. Finally, adult calls are formed which have low fundamental frequencies and a series of harmonics. Birds gave adult calls consistently in the fall when they were interacting aggressively and sexually in flocks. The use of the harmonic domain for adult calls is important in drawing attention to an individual bird during sexual displays; and probably forms the basis for individual recognition by sound.

Sexual displays and associated calls of birds in the fall seem to partially function in the attraction of conspecifics. This may be important in the formation of fall flocks prior to migration. Mallard calls carry a long distance on a clear night and would function well in attracting juveniles and lone birds to flocks.

SUMMARY

Development of acoustical communication of the mallard was studied in pens from 23 April to 29 October 1971. Females were allowed to hatch and raise their young in an undisturbed environment. Birds were individually marked and recorded as individuals and in groups.

Females began broody calling two to three days before hatching and communication increased as time of exodus from the nest approached. Female calls on nests were mainly in response to calls and movements of young.

Broody calls were found to be significantly different between individual females and varied in different situations. On the nest, females mainly gave broody and alarm calls while off the nest they gave broody, alert and low and high level alarm calls. Females initiated brood activity by acoustical communication. As young developed, the communication of females to and control over the brood decreased and finally ceased by six weeks.

Calls of newly hatched ducklings ranged from two to five KHz. They are termed contact and distress calls. These calls appeared to be part of a graded system with intermediate calls present. Individual differences were observed in duckling distress calls.

Broods of ducklings were extremely vocal, being silent only when in alert positions or when being brooded. Contact calls were common and distress calls rare. Ducklings gave alarm calls by two weeks of age. As they developed ducklings became more independent and active earlier in the morning. Intrabrood aggression became evident by seven weeks.

Frequency (Hz) of calls decreased and structure changed as ducklings developed. The number of contact calls decreased and eventually were replaced by intention and aggressive calls. Juveniles were attracted to adult calls.

Adult calls developed from duckling contact calls. The contact call changed so that it formed two parts: an ascending preliminary section forming a stroke and a descending section forming a main note. The frequency of the main note decreased and harmonics were added. During the transition period, birds gave [illegible], adult and intermediate calls. Degree of maturity of call appeared to depend on the duckling's motivational state at the time of calling.

Adult calls were definitely distinguishable by nine weeks, however, bouts of adult displays and calls were not common until 16 to 18 weeks of age. Female calls were formed from the main note and overtones whereas male calls seem to be formed from only overtones of the main note. By 18 to 19 weeks the calls were similar to adult calls examined by other workers.

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