

THE UNIVERSITY OF MANITOBA

DEVELOPMENT AND STRUCTURE OF CALLS IN YOUNG
AMERICAN COOTS (Fulica americana)

BY

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A dissertation submitted to the Faculty of Graduate Studies of
the University of Manitoba in partial fulfillment of the requirements
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ABSTRACT

The purpose of the study was to examine vocalizations of the American Coot (Fulica americana) from an ecological perspective, and to attempt to relate vocal behaviour to ecological, and other behavioural adaptations. Three aspects of vocal communication signals in young coots were studied. These included development of adult calls, potential cues for recognition in distress calls, and structure of calls in relation to transmissibility.

Recordings of laboratory-reared birds indicated that four call types were present after hatching including twitter, wit-ou, distress, and alarm calls. By about 8 weeks of age, juveniles used three call types, two derived from the wit-ou, and one derived from the distress call. Eleven adult calls were described. Of these calls, only two appear to be clearly derived from the distress call of chicks. Eight calls appear to be derived from the early wit-ou, and the origin of one call is unclear.

Analysis of distress calls for brood and individual differences showed that call length and minimum frequency differed significantly between broods. Significant individual differences were found for length, minimum frequency, maximum frequency, and frequency range. Coefficients of variation indicated that single cues are probably insuffi-

cient to distinguish individuals.

Measurement of pure tone attenuation and call attenuation indicated that call structure in young coots is related to transmissibility of vocalizations. High pitched twitters attenuate more rapidly than wit-ou, distress, or alarm calls which are lower pitched. These results are consistent with measurements of pure tones.

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GENERAL INTRODUCTION

1

Communication enables members of a species to interact and coordinate a wide range of activities (Scott 1968), presumably throughout all developmental stages from hatching or birth to adulthood. Any communication system involves a communicator, a signal, and a recipient (Klopfer and Hatch 1968). Analysis of such a system involves an understanding of the characteristics and information content of signals, the meaning of signals in light of their contexts, and their adaptive significance to interacting individuals (Marler 1961, Smith 1965, Smith 1977). This thesis is concerned mainly with the signal element, in particular, of vocal-auditory communication in young American Coots (Fulica americana). Though coots use vocalizations extensively in behavioural interactions, the only work to date on vocalizations (Gullion 1952) has been descriptive, lacking in quantitative analysis. This information is also limited to calls of adult coots. My study was designed to quantify characteristics of vocal signals during development from hatching to adulthood. Results are presented in three interrelated sections.

Vocal repertoires during three stages of development are examined in Part A. The purpose was not only to quantify calls, but more importantly to attempt to determine how vocal signals of the adult develop from those

present at hatching. Since both intraspecific interactions and communication signals change during an animal's development (Smith 1977), it is necessary to analyze communication systems throughout the ontogenetic period. Very little is known about what changes occur, or how they occur. Most studies of avian vocal-auditory communication have focused on adults, and ontogenetic studies have primarily been concerned with the influence of learning or genetics on vocal development (Lanyon 1960, Marler and Mundinger 1971). Since understanding communication involves a knowledge of the nature of selective influences on the signals (Klopfer and Hatch 1968), study of this aspect of communication is important at all developmental stages. This study has attempted to interpret changes in vocal behaviour in light of adaptations to the environment, and of other changes in behaviour during development.

Part B of the study focused on potential cues available for recognition in distress calls of young coots. Although studies have demonstrated individually distinct voices in adult birds (Beer 1970, Evans 1970a 1970b, White and White 1970), few studies have considered individual variation in the voices of the young (Miller and Emlen 1975, Noseworthy and Lien 1976). Studies of mammals, however, have indicated that individual recognition of distress calls of young by parents does occur (Espmark 1975, Petrinovich 1974), suggesting that the calls of the young

are individually distinctive. The further possibility that voices of the young may bear sibling resemblance appears not to have been examined. Cues that could provide information on both individual and family identity were therefore studied.

Part C of the thesis deals with the structure of vocalizations in relation to the habitat through which they are broadcast. Although several authors have discussed the potential for selective pressures on transmission of calls as a result of habitat structure (Emlen 1972, Moynihan 1967, Wilson 1975), studies providing quantitative data have been limited. Such studies (Chapuis 1971, Jilka and Leisler 1974, Morton 1975) have focused on bird song, and have not considered the possibility that functionally different calls within a single species might have quite different transmission characteristics, depending upon whether they normally function at close or long distances. While it has been suggested previously that calls functioning over different distances may differ in structure (Moynihan 1967), experimental evidence is lacking. The purpose of this study was to determine how long-distance and short-range calls of young coots differ, if at all, in transmissibility.

Part A. Development of Vocalizations
in the American Coot

Introduction

There have been many studies of vocal-auditory communication in birds, however most have dealt with adults. Of developmental studies done to date, the majority have involved passerine song (Immelmann 1969, Konishi 1964 1965a 1965b, Lanyon 1960, Marler and Mundinger 1971, Marler and Tamura 1977, Nottebohm 1972). There have been several studies of call development in passerines (see Marler and Mundinger 1971), but similar studies in non-passerines are rare. A relatively detailed description of vocal development for two gull species has been provided by Moynihan (1959). Other ontogenetic studies have involved Galliformes. Konishi (1963) has looked at the effect of deafening on call development in Domestic Chickens (Gallus gallus), and Guyomarc'h (1971) has done a spectrographic analysis of the development of maternal calls in Japanese Quail (Coturnix coturnix japonica). The use of spectrographic analysis is lacking for all or a major portion of calls present during development for any species (Lanyon 1960, Smith 1977).

In this study I examined vocal communication signals of a non-passerine species throughout major stages of

ontogeny. Calls of young laboratory-reared coots were⁵ studied during the first four weeks after hatching. In addition, calls of these birds as juveniles and calls of wild breeding adults were examined to determine how calls of young coots change during development into adult vocalizations.

Methods

The early development of vocalizations was followed in laboratory-reared coots. Use of captive birds enabled easy access as well as controlled conditions for recording and observation purposes. Four clutches of eggs were collected on 10 June 1975 from the Minnedosa pothole area of Manitoba. Pipping had begun in two of the clutches at the time of collection. Eggs were placed in a Brower forced air incubator and checked several times daily for hatched birds. Newly hatched chicks were individually marked with coloured leg bands and transferred, when dry, to holding pens. There was a hatching success of 88%, and a mortality rate of 28% after hatching.

Rearing Conditions

Holding pens were approximately 70 cm by 70 cm, consisting of 1.3 cm wire mesh sides and panelboard flooring

which could be removed and brushed clean. A 25 watt incandescent bulb at floor level provided heat in each pen. Each brood was held in a separate sound-attenuated room so that interbrood interactions were not possible.

Chicks were provided with water, and initially were fed by hand. Moistened chick or turkey starter was presented to newly hatched chicks from a spoon or finger. After several days a spoon full of moist food was placed on the pen floor, and replenished when necessary. When older birds appeared to be feeding independently at about 10 days of age, a dish of moistened food was left in each pen. Fresh food was provided daily.

When the youngest of a brood was at least 5 days old, birds were removed from the holding pens and released into a larger enclosure in the sound-attenuated rooms. Each of three broods containing from 5 to 8 birds was provided with a plastic pool about 1 m in diameter, containing free-running tap water. One of the smallest broods, containing 5 young was placed in a small 2 m by 3 m holding area, provided with bathing water in a 35 cm by 70 cm styrofoam container. The incandescent heat source was maintained until all birds were well feathered, at about 6 weeks of age. Hand feeding continued until the youngest in a brood was about 2 weeks old. At this time birds no longer approached me for food.

Recording Conditions

Tape recordings were made primarily with a Uher 4000 Report L tape recorder. Some recordings were also made with a Sony TC 106, and a Sanyo MR-920 tape recorder. Recordings were made in several situations. Vocalizations were recorded when chicks were being hand fed, when undisturbed in holding pens and enclosures, and when being held in the hand. Calls given during isolation were obtained by placing individuals in a separate room where auditory contact with broodmates was minimal.

Once birds were feeding independently, they showed fear of humans. Observations were then made using a Sony Video Recorder which was especially valuable for subadults.

Analysis of Calls

Vocalizations of each recorded call type were randomly selected for analysis from unedited tape recordings. They were then printed on sonagrams, once using the wide band setting, and once using the narrow band setting with a Kaye Electric Co. Model 675 Missilyzer. Call duration was measured from the wide band sonagrams, while frequency was measured from the narrow band sonagrams. For purposes of illustration, ink tracings of these sonagrams were produced, which combined characteristics of both wide and narrow band

sonagrams.

Calls recorded during the first 4 weeks after hatching were divided into 3 age groups. One represented the youngest birds sampled for a given call, one represented the oldest birds for which samples could be obtained, and the third group represented an intermediate age. Differences in the ease with which various call types could be recorded resulted in slight differences in absolute age categories between some calls. Approximately equal numbers of calls were analyzed from each of the broods at each age.

Characteristics of most call types of young coots were analyzed for age changes using a one way repeated measures analysis of variance (Hays 1973). Only the alarm call, where two rather than three age levels were compared, was tested using a dependent samples t-test (Hays 1973). In older birds where sex differences were compared, dependent samples t-tests were used (Hays 1973).

When describing calls of adult coots, names proposed by Gullion (1952) will be used where possible.

Sexing of Birds

To determine sex of captive birds, they were dissected, and the gonads were examined at the end of the study period.

Field Observations

Calls and activities of wild, adult coots were observed at the University Field Station (Delta Marsh), located at the south end of Lake Manitoba, during 1975 and 1976.

Prior to egg collection in June 1975, adult coots were observed for two weeks during May, usually from a canoe at Crescent Pond (Fig. 1). During 1976, observations were made from early May to mid-August. A small plastic boat equipped with a burlap blind enabled prenesting birds to be observed while vegetation was relatively low. During and after nesting a 5.6 m high wooden tower, placed within a nesting area, enabled observations of both adults and broods. Activities at nest sites were monitored using the boat and blind. Recordings during hatching were made by placing a Uher M539 microphone, camouflaged with burlap, at the edge of the nest. Its presence did not seem to alarm the birds.

Field Study Site. Figure 2 shows the area in which the wooden observation tower was placed. Predominant vegetation was Typha latifolia L. Of 10 nests located in the area, 8 were placed in this vegetation type. One nest was located in Phragmites communis Trin., and one nest was located in a flooded stand of Scolochloa festuacea (Willd.) Link. Recordings of brooding females, nearby males, and hatching young were made at nests 3, 8, and 9. Observations

Figure 1. Study area at Delta Marsh showing observation sites from which both adult and young coots were watched during 1975 and 1976.

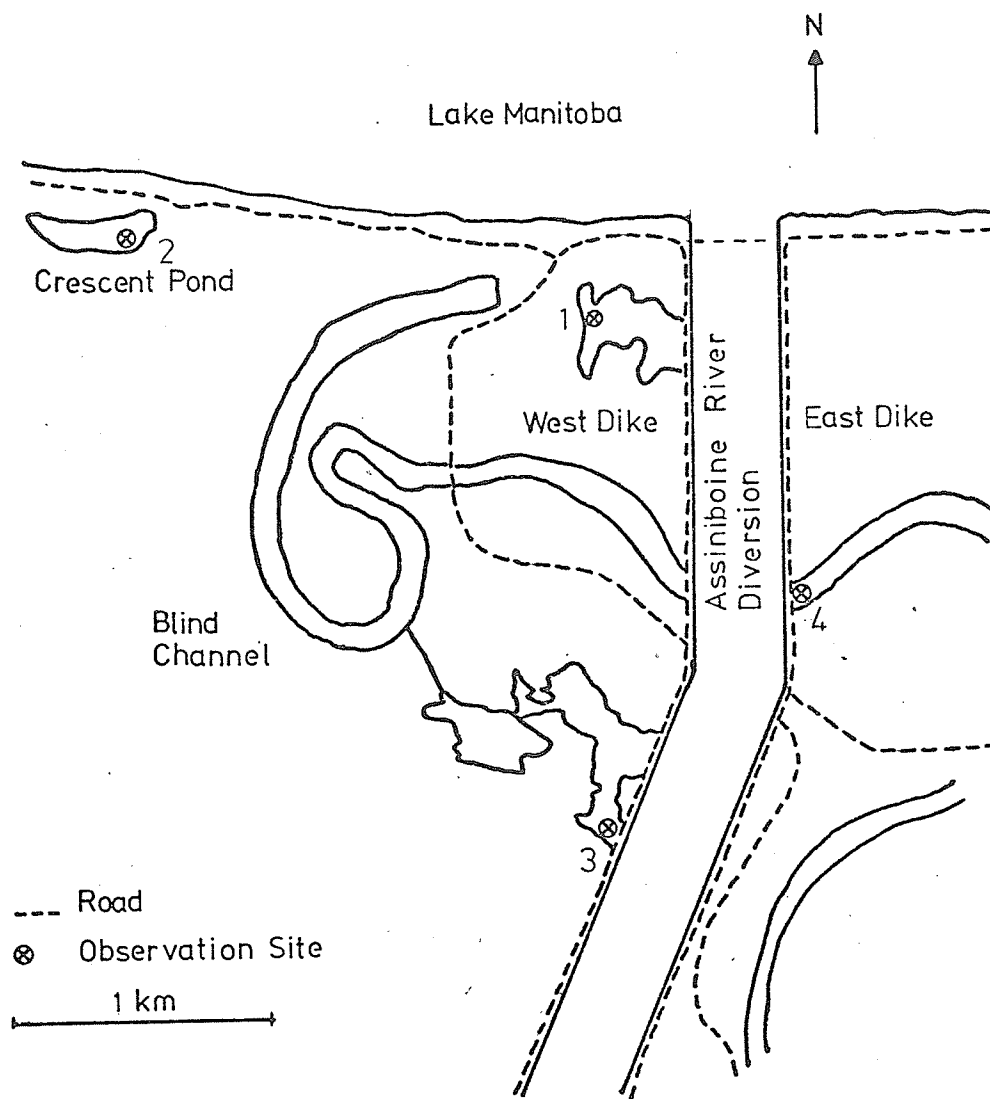
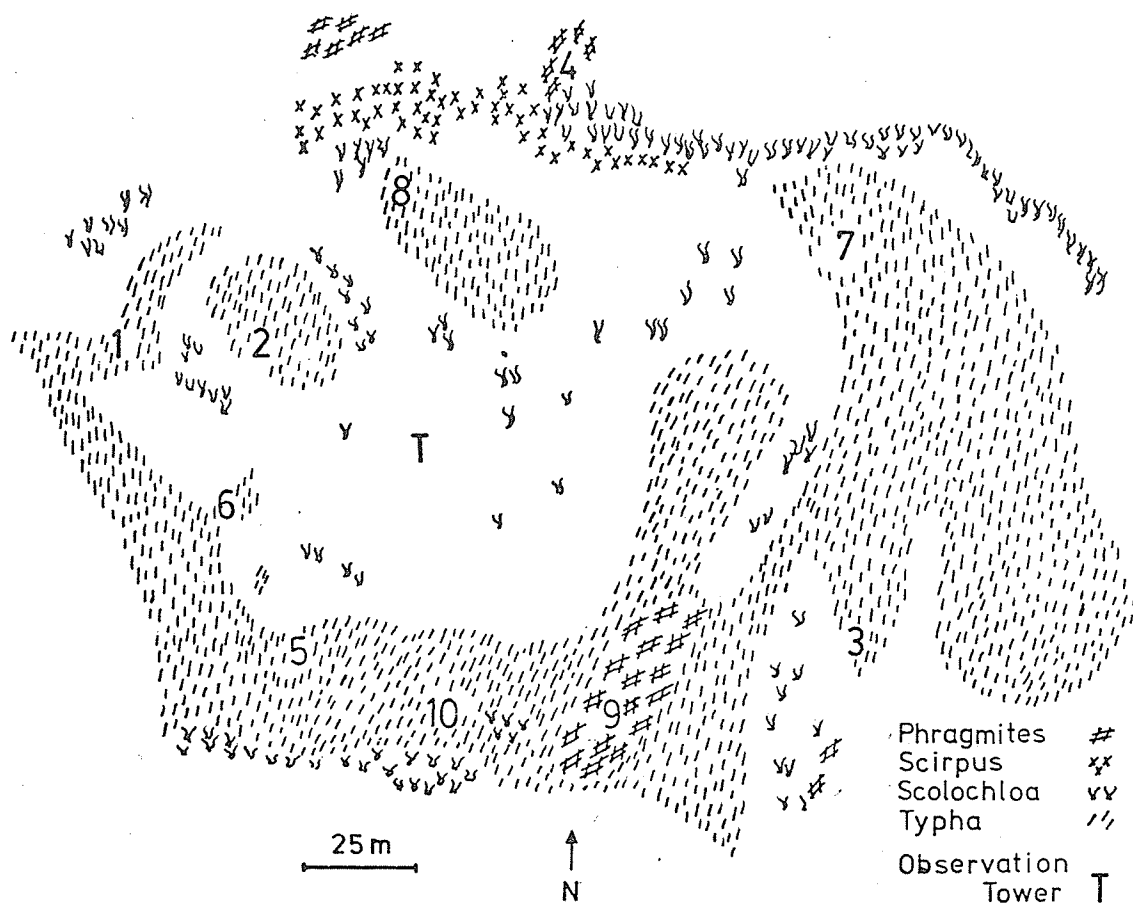


Figure 2. Sketch of nesting area (Site 1 in Figure 1) of coots in which the observation tower was placed. Numbers designate locations of nests of individual coots.



were made using 7x35 binoculars and a 15 power Bushnell spotting scope.

Drought conditions (Table 1) eventually resulted in drying of the study area in 1976. Until this occurred, birds could be easily watched from the tower even when in stands of vegetation. Once drying occurred, coots moved to other areas of the marsh. Observations were then made of broods in channels from the dike roads (Fig. 1). These birds were watched until premigratory flocking occurred in mid-August.

Results

Calls of Chicks

Four major call types were identified in young laboratory-reared coots: twitter, wit-ou, distress, and alarm. All types may be given during hatching by wild coots. Immediately after hatching, laboratory-reared birds gave all call types without clear contexts. After the first day of age, the situations evoking call types became differentiated.

Twitter. Termed contentment or pleasure notes by Collias and Joos (1953), twitters were the most common call of young coots. Immediately after hatching chicks placed alone in pens gave these calls. After exposure to brood-

Table 1. Temperature and precipitation data for Delta Marsh during 1975 and 1976.

Month	Mean Temperature (C)				Precipitation (cm)	
	Minimum		Maximum		1975	1976
	1975	1976	1975	1976		
April	-8.5	-1.3	4.8	9.1	4.1	2.8
May	4.4	6.2	16.3	17.6	7.7	4.6
June	11.6	12.1	21.8	23.0	7.9	6.9
July	15.1	12.5	26.6	25.5	7.8	4.4
August	11.4	12.5	21.4	24.9	13.9	1.8

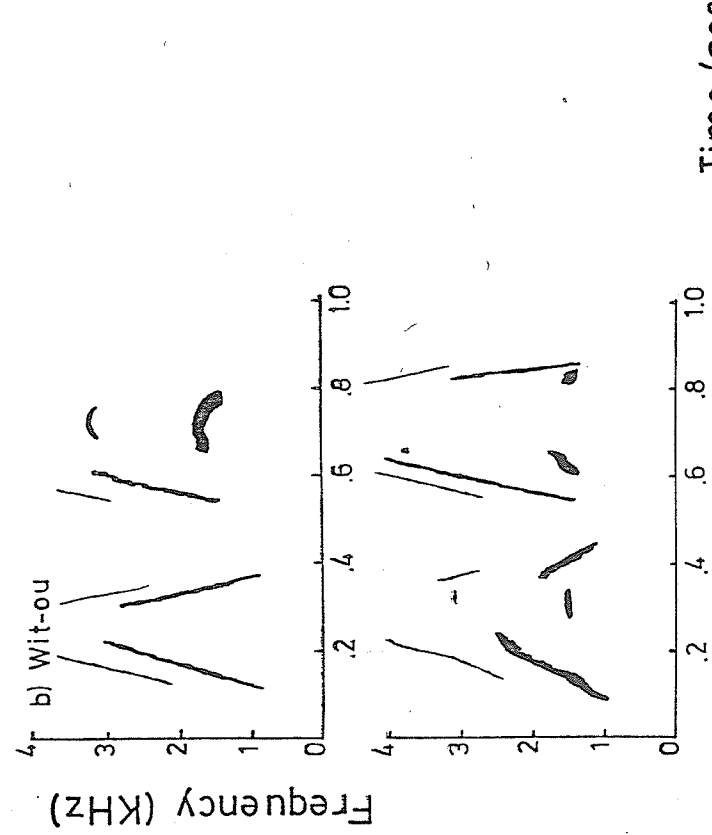
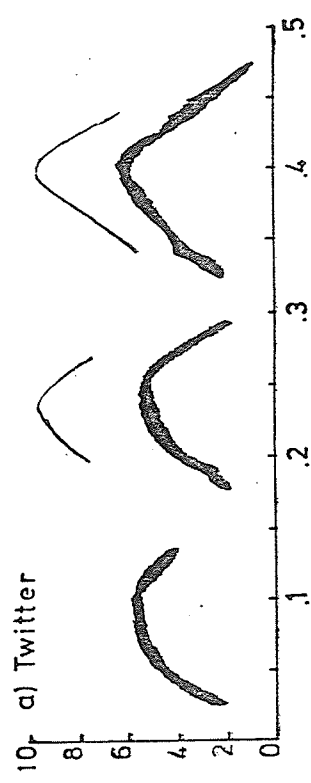
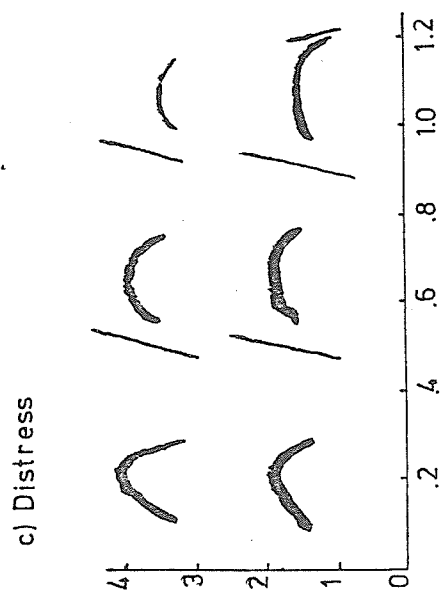
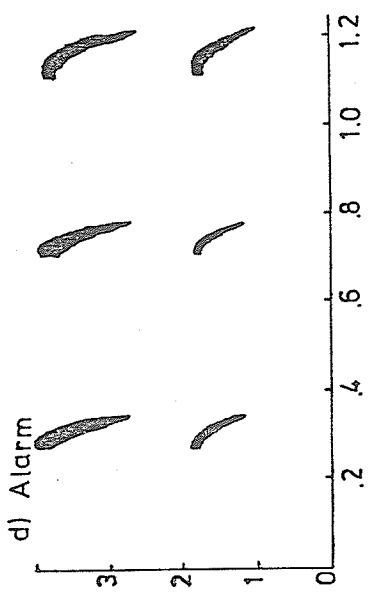
mates for about 24 hours, twitters were no longer given in isolation, but were given almost constantly among broodmates. They were also given during hand feeding sessions.

Twitters were low in intensity, and emitted with the bill closed. They were highest in pitch of all neonatal calls (Fig. 3). Call length (sec), and frequency (Hz) characteristics at three age periods are shown in Table 2. Twitters from most of the birds within a given brood were difficult to record after 3 weeks of age, because they were infrequently emitted. These are not included in the analysis.

Call length increased in the oldest birds, but overall age differences were not significant. Minimum frequency gradually, but significantly ($F_{2,78} = 5.8, p < 0.05$) increased with age after the first week. Maximum frequency remained stable for about the first 2 weeks, then dropped significantly ($F_{2,78} = 17.1, p < 0.001$) by the third week. Frequency range followed the same pattern as maximum frequency, showing a significant decrease ($F_{2,78} = 22.3, p < 0.001$) in the last week.

Call shape was classified by determining the relative occurrence of calls in which the frequency modulation (FM) pattern consisted of mainly ascending frequencies, of mainly descending frequencies, or both. Call shape remained essentially unchanged during the first two weeks of age (Fig. 4), with most calls showing both ascending and

Figure 3. Vocalizations of young coots recorded at 2 days of age.



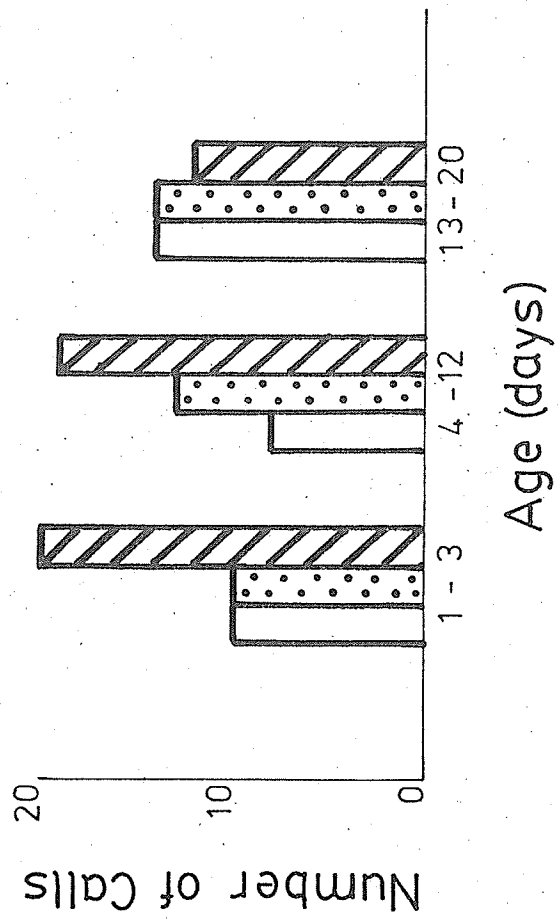
Time (sec)

Table 2. Age-related changes in characteristics of the four call types in young coots.

Call Type	Age (days)	N	Mean Length (sec)	Mean Frequency (Hz)		
				Minimum	Maximum	Range
Twitter	1-3	40	.129(.022) ¹	1870(490)	5473(1147)	3603(1151)
	4-12	40	.126(.019)	1913(559)	5804(907)	3891(1096)
	13-20	40	.136(.065)	2250(586)	4660(928)	2410(892)
Wit-ou	2	20	.297(.050)	989(216)	2777(713)	1788(624)
	8-15	20	.346(.067)	950(148)	2353(624)	1403(517)
	21-28	16	.414(.073)	877(58)	2054(412)	1177(371)
Distress	2	28	.256(.030)	1347(223)	1953(203)	606(169)
	8-15	28	.384(.079)	1353(368)	2021(189)	668(376)
	21-28	23	.478(.105)	1127(239)	1720(297)	593(247)
Alarm	7	45	.131(.045)	1038(260)	1796(133)	758(261)
	16-20	22	.113(.028)	1145(254)	2371(434)	1226(407)
	30-34	22	.100(.037)	1566(285)	2362(201)	796(347)

¹ Numbers in parentheses are standard deviations.

Figure 4. Call shape of the twitter at three ages. Calls were classified by frequency modulation into three groups: mainly ascending , mainly descending , and equally ascending and descending .



descending frequencies. By the third week the proportion of all call types tended to be equal, however this change with age was not significant ($X^2 = 5.3$).

Coots gave twitter calls only during the first month after hatching. Older broods (brood D at 35 to 41 days, brood E at 34 to 41 days, brood C at 32 to 41 days, brood B at 31 to 35 days) gave distress calls rather than twitter calls while feeding, swimming, and resting in the enclosures.

Wit-ou. Under a variety of conditions birds gave a call which sounded like a 'wit-ou'. It often appeared similar to a twitter call in which the highest pitched portion, occurring about halfway through the call, was absent. While it may be merely a variation of the twitter, the different number of notes present, and the fact that it appears to grade into the typical distress call suggest that the wit-ou call can be treated as a distinct call type (Fig. 3).

The wit-ou call was given in several contexts. It was frequently heard when birds were together undisturbed, but was also commonly given after birds had been disturbed. In the latter case young coots gave the wit-ou call when returning to the open area of the pen after I left the enclosure. As separated birds returned to the pool area they frequently called though visual contact was possible. It was also given in the initial period of isolation by some birds. They would begin with this call type and then

grade into the typical distress call. The wit-ou thus appears to serve as a contact call in circumstances which do not warrant intense fear or escape responses, and could perhaps be termed a mild distress call.

Table 2 shows age-related changes in the wit-ou call. Call length increased significantly with age ($F_{2,38} = 15.9$, $p < 0.001$). While minimum frequency did not change, both maximum frequency and frequency range dropped significantly ($F_{2,38} = 9.8$, $p < 0.001$; $F_{2,38} = 7.3$, $p < 0.05$ respectively).

Wit-ou calls consisted of 2 to 4 notes (Fig. 3). The proportion of calls containing 2, 3, or 4 notes remained consistent with age (Fig. 5). At all ages, most calls were of 2 notes, 3-note calls were common, while 4-note calls were produced infrequently.

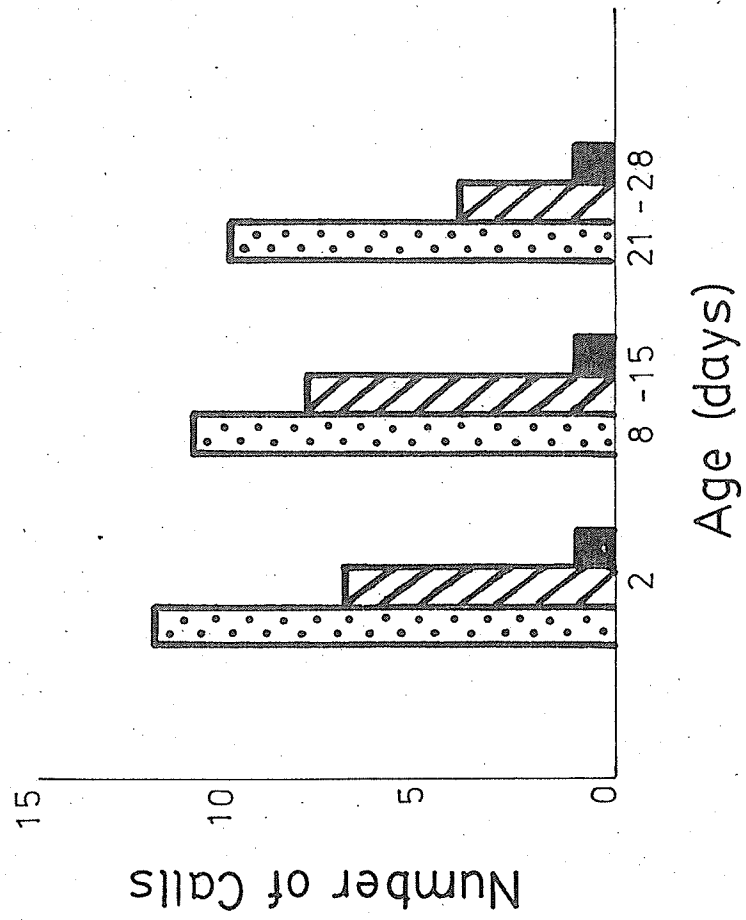
Unlike twitter calls, the wit-ou was not discontinued. It remained in the repertoire and, as will be discussed later, gave rise to many of the adult calls. It thus appeared to be an important call in the repertoires of both young and adults.

Distress. Once exposed to broodmates for about 24 hours, young coots emitted distress calls when placed in isolation (Fig. 3).

Two distress calls per bird were analyzed for 14 birds from 3 broods at 3 age periods (Table 1). Call length increased significantly with age ($F_{2,54} = 87.5$, $p < 0.001$). A significant decrease with age occurred for minimum

Figure 5. Proportion of wit-ou calls at three ages
containing 2 notes , 3 notes , or 4 notes





frequency ($F_{2,54} = 6.3$, $p < 0.05$), and for maximum frequency ($F_{2,54} = 16.5$, $p < 0.001$). Frequency range did not change.

Reflecting the close relationship with wit-ou calls, distress calls were emitted over a mean frequency range that was entirely within the range of wit-ou calls. Distress calls also often contained components of the wit-ou call (Fig. 3). From 1 to 3 notes may be present. The middle note of the 3-note call characterizes the distress call, being the only component of single note calls. In 2- or 3-note calls, the ascending initial note, generally inaudible, and the last descending note are also found in wit-ou calls. Figure 6a shows the frequency of occurrence of calls of 1, 2, or 3 notes. A significant difference with age was present ($X^2_{4} = 22$, $p < 0.05$). During the first two weeks most calls were of the 2-note type. By the third and fourth week calls containing 1 note were the most common. At any time, calls containing 3 notes were infrequent.

All distress calls contained at least one harmonic which was double the frequency of the fundamental note, which may be defined as the component of lowest frequency in a complex tone (Davis 1964). Some calls also contained tones which did not show this mathematical relationship with the fundamental (Fig. 7). This has been described as the two-voice phenomenon (Miller 1977, Miller and Gottlieb 1976) where two independent sound sources produce a call.

Figure 6. a) Number of distress calls containing 1 note  , 2 notes  , or 3 notes  at three ages.
b) Number of distress calls containing single voice  , or double voice  origin at three ages.

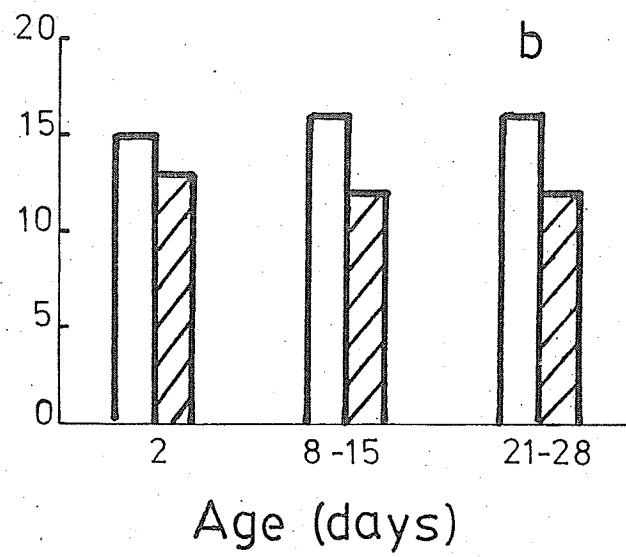
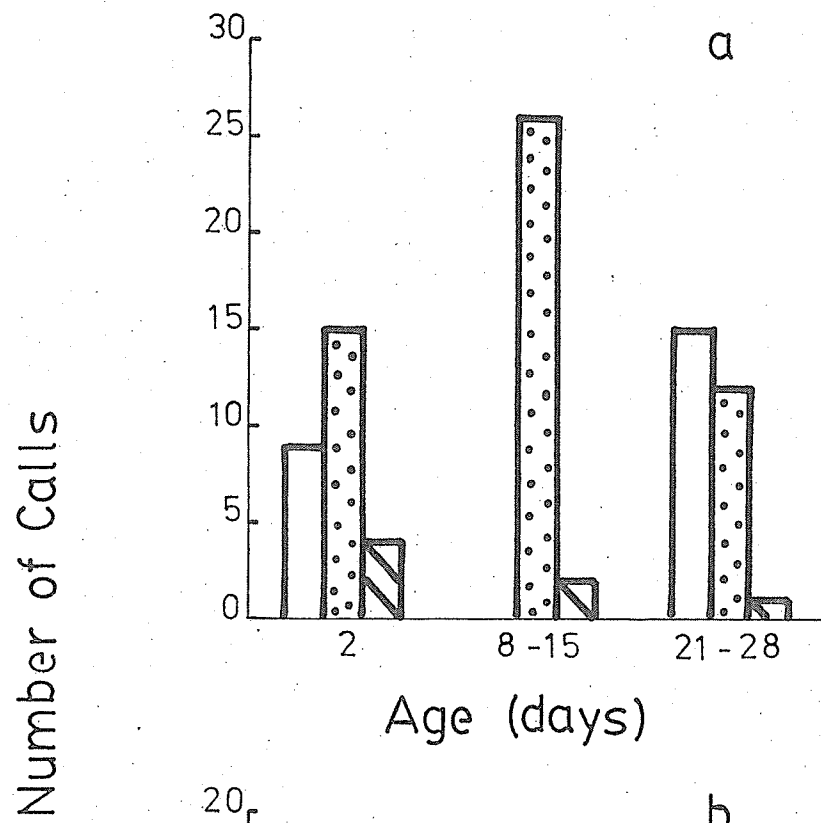


Figure 7. Distress calls of 15 day old coots showing double voice (a), and single voice (b) origin.



Calls of single or double voice origin occurred in similar proportions at all ages (Fig. 6b).

Like the wit-ou call, the distress call remained in the repertoire of young coots, and, as will be shown, develops into some of the adult calls.

Alarm. Although birds sometimes gave this call for no apparent reason, the alarm call in laboratory-reared coots was given most typically in response to being held in the hand. Wild birds were observed giving alarm calls in the nest after hatching and also, when older, in response to Forster's Terns (Sterna forsteri) hovering overhead, as well as in response to attacks by parents and other adult coots.

Since recordings of this call (Fig. 3) were made less regularly than for other call types, data are less complete. Results for 1 week of age (Table 1) were obtained from 2 broods. Data for 16 to 20 days, and 30 to 34 days of age were obtained from a third brood.

Call length decreased, but not significantly. Minimum frequency increased significantly ($t_{21} = 5.2, p < 0.001$), while maximum frequency did not change. Frequency range decreased significantly ($t_{21} = 3.8, p < 0.05$).

Alarm calling of laboratory-reared coots in response to being held in the hand continued until about 2 months of age, when the fleshy portion of the frontal shield (callus) became orange in colouration. While escape and

defense responses such as kicking and pecking were given after this time, alarm calls were not. In contrast, birds tended to be silent. Like twitter calls, alarm calls dropped out of the vocal repertoire.

Observations of Young Wild Coots

In wild birds the twitter and wit-ou calls were heard both during and after hatching. Once the young had left the nest, I rarely heard these calls, presumably due to their low intensity and the fact that brood observations were made from too great a distance to pick up these calls. Distress calls, which were normally given at a greater intensity, were often heard, though chicks could not always be located visually from the observation tower. On several occasions lone chicks were seen giving distress calls either when no adults could be seen, or when they were approaching an adult.

Alarm calling by chicks was heard several times. On two occasions a tern was hovering or diving nearby, and this seemed to be the focus of the bird's response. Other observations were of adult coots attacking chicks. While it was not possible to tell whether attacking birds were parents, there were five observations of a bird feeding a young coot and then attacking it. In several other incidents the chick approached the adult which then attacked

it. Occasionally an adult actively charged a chick. In each case observed, young coots gave alarm calls in response to the attacking adults.

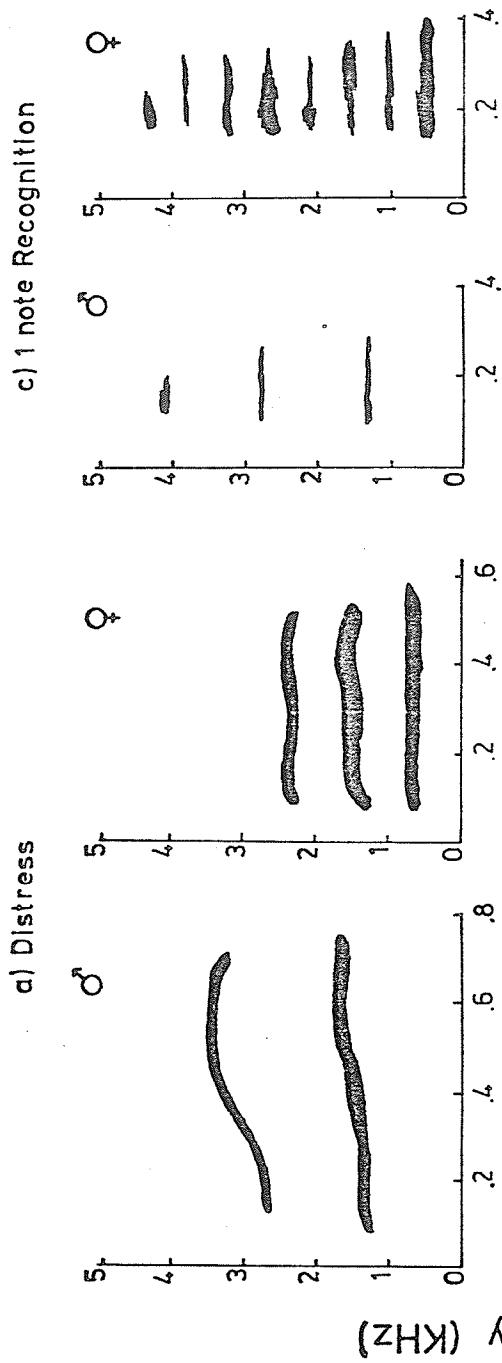
Juvenile Vocalizations

From 19 August to 27 August calls of juveniles were recorded in the lab. On 19 August birds of the four broods ranged in age from 51 to 69 days. Of calls initially present after hatching, only two remained in distinct form. Twitters were occasionally given briefly, but no longer formed an important part of the vocal repertoire. Alarm calls were no longer given when held in the hand. Only one bird, age 49 days, gave alarm calls during this time. All others remained silent, while attempting to escape. Predominant calls were those derived from the wit-ou and distress calls.

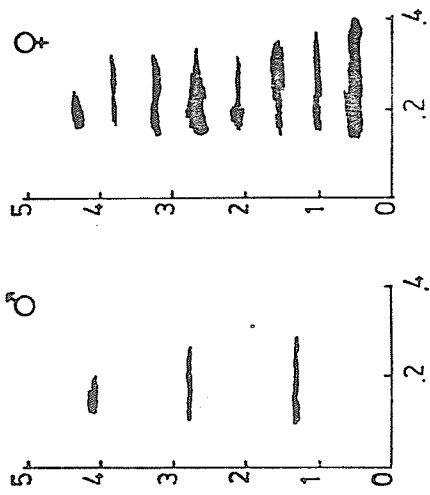
Distress Call. The most common call given during August was the distress call. The context in which it was used differed from that typical of young chicks, the distress call replacing the twitter when birds were feeding and resting (Fig. 8a).

By 5 August, when birds were 37 to 55 days of age, some distress calls became low pitched and nasal. Presumably this indicated the onset of sexual dimorphism in call structure which has been described by Gullion (1950). Low

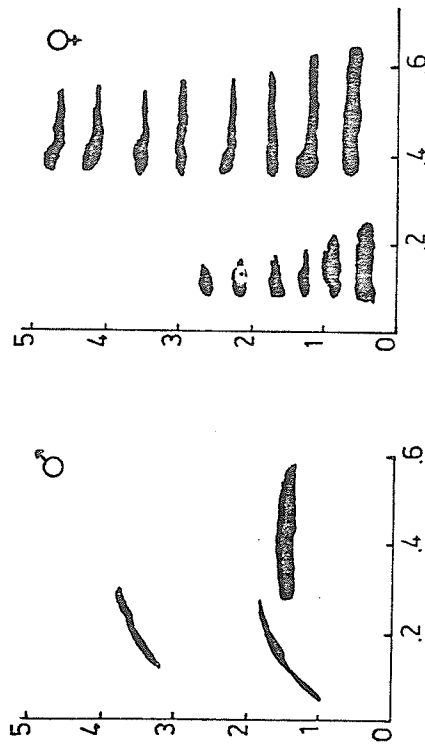
Figure 8. Juvenile vocalizations of the coot recorded at
2 to 3 months of age.



c) 1 note Recognition



b) 2 note Recognition



Time (sec)

pitched nasal calls were emitted by females, while higher pitched calls were emitted by males (verified later by dissection).

Call length did not differ between males and females. Males had a significantly higher minimum frequency ($t = 8.9$, $p < 0.001$), as well as maximum frequency ($t = 9.7$, $p < 0.001$) (Table 3). Frequency range was also significantly greater for males ($t = 6.0$, $p < 0.001$).

Unlike calls given by chicks less than 1 month old, the distress call now had a flatter shape, especially in females, and contained only one note. There was no longer any gradation detectable between the wit-ou and the distress call.

Recordings made in September, when birds were 82 to 100 days of age, indicated that the distress call now was given less frequently. Although it becomes an important adult call, distress calls appeared to have only a short-term function in juveniles.

Two-note Recognition Call. This call, which was more often heard from females, was apparently derived directly from the wit-ou call of chicks. This will be further discussed in a later section. When given by males, this call still resembled, to my ear, the 2-note wit-ou call given by chicks. In females, the call was perceptibly lower pitched (Fig. 8b), and sounded like the 'punk-unk' described by Gullion (1952) for adults.

Table 3. Characteristics of vocalizations of male and female juvenile coots.

Call Type	Sex	N	Mean Length ¹ (sec)	Mean Frequency (Hz)		
				Minimum	Maximum	Range
Distress	Male	20	.690(.198) ²	1215(266)	1764(363)	549(221)
	Female	12	.618(.201)	612(225)	832(249)	228(65)
1-note	Male	16	.202(.049)	1278(349)	1629(468)	352(210)
Recognition	Female	17	.232(.062)	425(226)	678(292)	252(107)
2-note	Male	5	.493(.133)	1426(282)	3094(1060)	1668(815)
Recognition	Female	16	.629(.142)	453(243)	721(254)	268(69)

1. Call length may be overestimated for juvenile calls. As a result of increased intensity of calls, reverberation may have occurred. Other measurements were not affected.
2. Values in parentheses are standard deviations.

Sex differences in the 2-note recognition call (Table 3) were not analyzed as too few calls were obtained to permit statistical testing, but differences in frequency characteristics were quite large. Females tended to give lower pitched and longer calls than males. While never a predominant call type, the 2-note recognition call was retained in the repertoire.

One-note Recognition Call. The single note recognition call described by Gullion (1952) for adult coots was also present in juveniles. Next to the distress call, it was the most frequently heard call type in birds of 51 to 69 days of age (Fig. 8c). Like the 2-note recognition call, it also appears to be derived from the wit-ou call as is discussed more fully below.

As in the distress call, sex differences were apparent (Table 3). Minimum frequency was significantly higher for males ($t = 7.8$, $p < 0.001$), as was maximum frequency ($t = 6.6$, $p < 0.001$). Neither call length, nor frequency range differed between the sexes.

Recordings taken during September showed that this call type became more frequent, eventually becoming more common than the distress call.

Adult Vocalizations

To assess the overall ontogeny of coot calls, vocali-

zations of wild adult coots were observed, recorded, and where possible analyzed in the same way as calls of developing young. As in previous sections low pitched nasal calls were classed as female, and higher pitched calls were classed as male.

Recognition Notes. Prior to, and after establishing territories, the most commonly heard call given by adult coots was the short clucking call described by Gullion (1952) as recognition notes (Fig. 9a). These calls were typically given when birds were feeding and swimming through vegetation, apparently to maintain auditory contact. Used not only between adults, they were also given by adults caring for young. Adults were typically heard clucking while young coots followed behind or foraged nearby. Recognition notes were rarely associated with aggressive encounters (Table 4).

Both sexes gave brief notes with a relatively wide range of frequency. Maximum frequency and frequency range were variable (Table 5). This suggests that results of analysis using sonograms may show less sexual dimorphism than is apparent by ear, especially for the nasal quality of the female. Apparent pitch differences to the human ear may result from more subtle differences in relative distribution of energy over the frequency range of the calls. Unlike some other call types, recognition calls had no clear overtone structure.

Figure 9. Vocalizations of adult coots recorded at Delta Marsh from May to July.

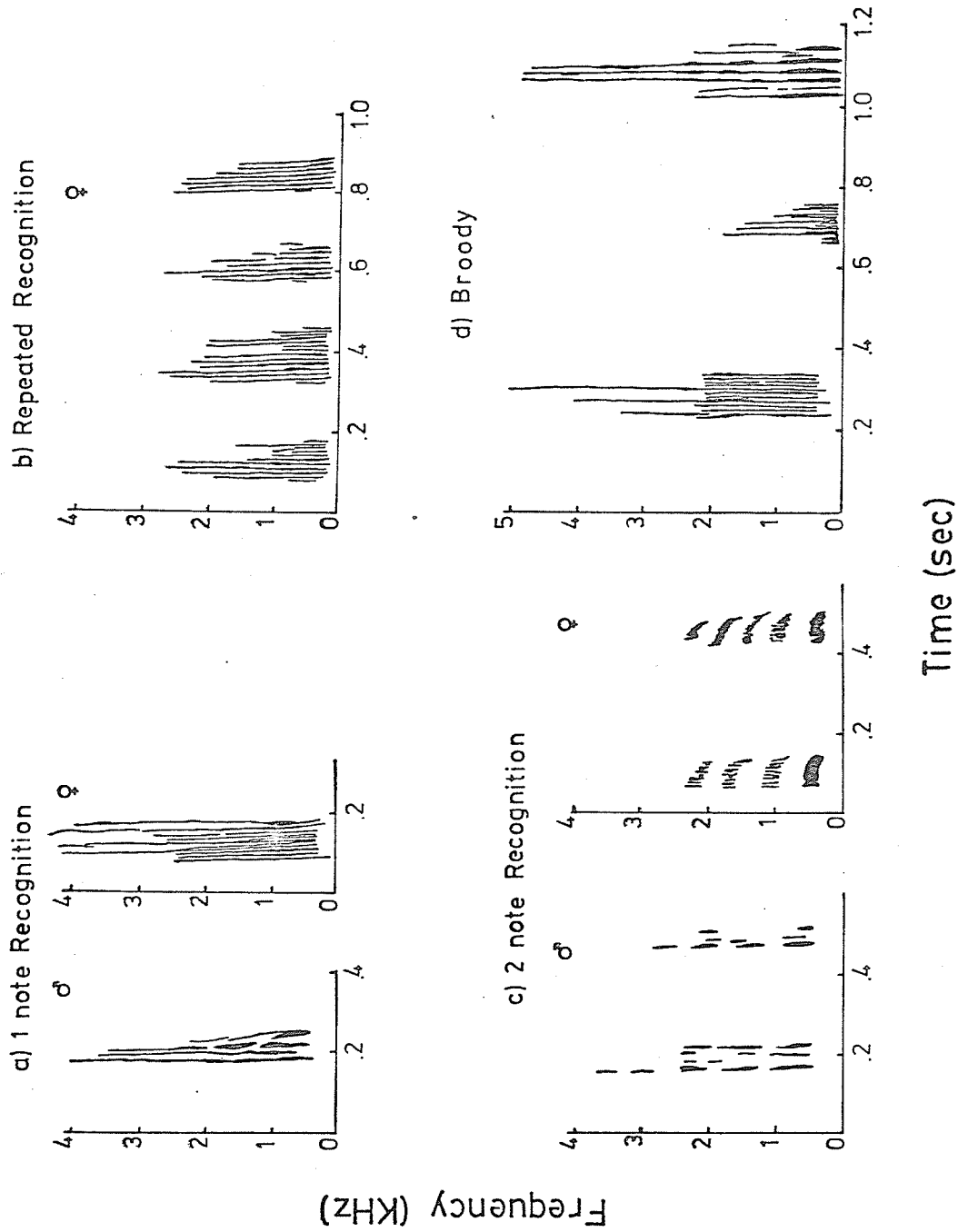


Table 4. Frequency of occurrence of major adult calls of both sexes in non-aggressive and aggressive contexts during the initial territorial phase of breeding.

Call Type ¹	Context	
	Non-aggressive	Aggressive
1-note Recognition	16	6
2-note Warning	21	10
3-note Warning	13	5
Perturbation	2	19

1. All names of calls are those used by Gullion (1952)



Table 5. Characteristics of adult calls for which recordings were obtained from both males and females.

Call Type	N	Sex	Mean Length (sec)	Mean Frequency (Hz)		
				Minimum	Maximum	Range
1-note	10	Male	.059(.021) ¹	282(207)	2383(515)	2101(492)
Recognition	9	Female	.083(.017)	336(129)	1956(983)	1620(943)
2-note	6	Male	.331(.083)	305(84)	890(131)	585(209)
Recognition	6	Female	.360(.078)	304(89)	637(40)	333(114)
Perturbation	5	Male	.400(.061)	574(22)	778(34)	204(53)
	12	Female	.333(.135)	294(59)	727(166)	433(156)

1. Values in parantheses are standard deviations.

Occasionally this call was heard as a rapidly repeated series with a mean of 4.0 calls/sec (N=26) (Fig. 9b). The function of this form of the recognition call was not determined.

Two- and 3-note recognition calls were also heard, typically in the same context as the 1-note recognition call. According to Gullion's description (1952) the 2-note call sounds like 'punk-ut' or 'punk-kuk' (Fig. 9c). He describes the calls as warning notes. However my field observations (Table 4) indicated that like the single note recognition calls, the 2- and 3-note calls were usually associated with non-aggressive contexts. Birds often gave all three call forms in a series, interchanging call types. Since the three forms were given in similar contexts, and interchanged, the 2- and 3-note calls are here being considered as recognition notes.

Data presented for the 2-note calls (Table 5) indicate that sexes differed mainly in maximum frequency and frequency range. These characteristics were less variable than in single note calls. Also in comparison to single note recognition calls, the 2-note calls contained a more defined overtone structure. Up to 4 overtones were apparent in some calls, but the most common number was 2.

Like the single note recognition call, the 2- and 3-note calls were sometimes given as a rapidly repeated series with an average of 3.0 calls/sec (N=18). Repeated calls

were heard from both males and females.

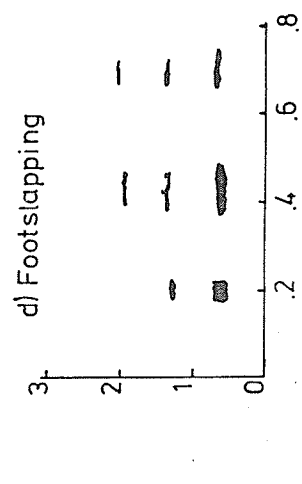
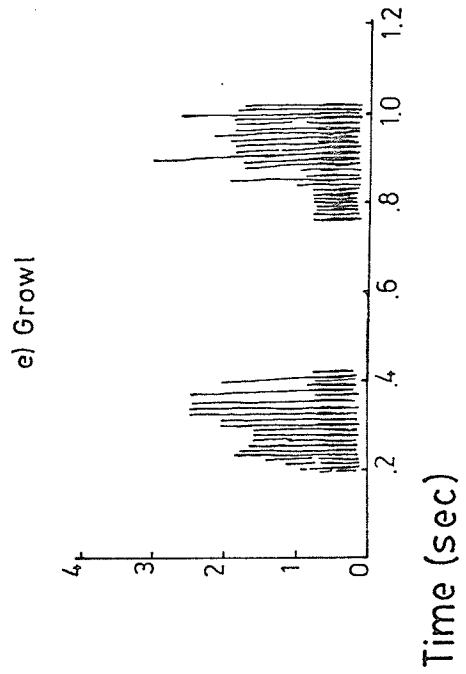
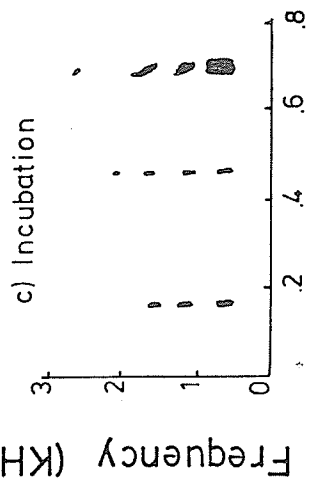
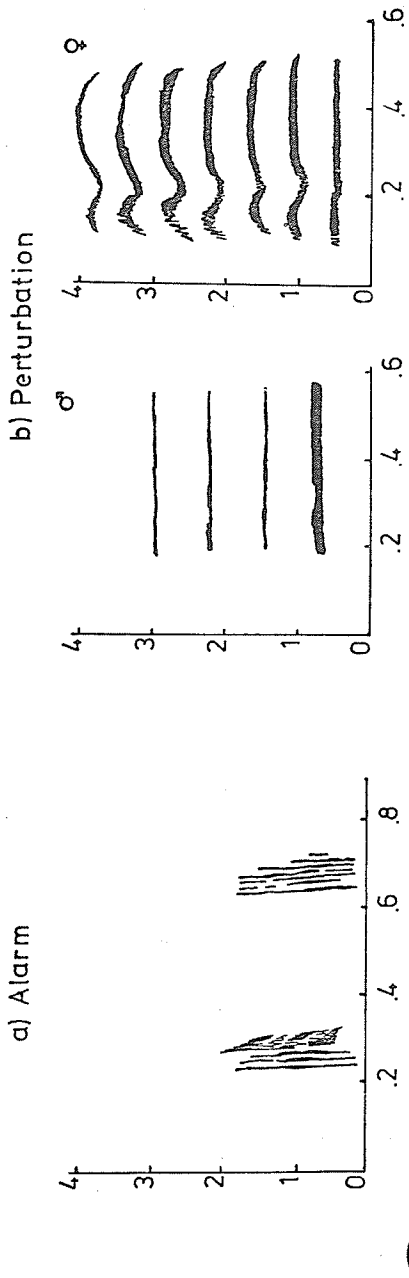
Broody Calls. When pipping began, females gave soft, low intensity clucking sounds over the hatching young (Fig. 9d). Data were obtained for 12 calls from 3 females. Calls were brief (Mean length=.093 sec, S.D.=.030), but usually longer than recognition notes. Minimum frequency averaged 151 Hz (S.D.=98), well below that obtained for female recognition notes. As in recognition calls, maximum frequency was high (Mean=2507 Hz), and quite variable (S.D.=1327). Frequency range was also wide (Mean=2356 Hz) and variable (S.D.=1324). Like recognition notes, overtone structure was not defined.

Alarm Notes. Gullion (1952) indicated that recognition notes and alarm notes are similar except for a vigorous movement of the head associated with the latter. Alarm notes do appear similar on sonagrams (Fig. 10a), but to my ear sounded louder and sharper than recognition notes. Alarm notes were given by both sexes, but only recordings of male calls were obtained.

Call length averaged .096 sec (S.D.=.010) for 5 calls. Mean minimum frequency was 159 Hz (S.D.=111), while maximum frequency averaged 1911 Hz (S.D.=131). Frequency range averaged 1752 Hz (S.D.=115).

Perturbation Notes. During periods of territorial dispute, involving both sexes, calls described by Gullion (1952) as 'perturbation notes' were commonly heard. At

Figure 10. Vocalizations of adult coots recorded at Delta Marsh from May to July.



Delta Marsh they were usually associated with aggressive encounters, although generally not during actual fighting. (Table 4). They were typically long single notes (Fig. 10b) that appeared similar to distress calls of young birds. Unlike single note recognition, broody, and alarm calls, there were 1 to 5 clear overtones, with 4 being the most common. Both males and females gave this call, females tending to use a lower minimum frequency than males (Table 5). Like recognition notes, perturbation calls were sometimes given as a rapidly repeated series at an average of 2.2 calls/sec (N=17) by both sexes.

Other Call Types. Several less frequently heard calls were given by adult coots. One such call, which may be termed the 'incubation call', consisted of a rhythmic series of short moderately intense notes (Fig. 10c). Gullion (1952) describes what appears to be this call given by males during change in incubation duties. On at least 6 occasions when I heard the call, the male was at or near the nest, usually with the female. The call was heard 3 times when a male gave it while following closely behind a female. Attempted copulation was seen once at this time. The proximity of the nest was not known on these latter 3 occasions. Observations agree with those of Gullion for this call type.

Values for call characteristics were determined from a sample of 20 notes. Length averaged .035 sec (S.D.=.012).

Minimum frequency was 494 Hz (S.D.=86), and maximum frequency averaged 793 Hz (S.D.=59). Mean frequency range was 299 Hz (S.D.=77). Overtone structure was well defined.

Another infrequently heard call, recorded only from males, was a low intensity plaintive note associated with foot-slapping (Fig. 10d). Gullion (1952) stated that males "standing on display platforms . . . giving steadily repeated 'puhk' . . . often slapped the platform with one foot". The few recordings made on my study area indicated that both short and long notes may be given. Call length averaged .099 sec (S.D.=.038). Mean minimum frequency was 543 Hz (S.D.=105). Maximum frequency was 749 Hz (S.D.=80), and frequency range averaged 206 Hz (S.D.=62). Values were obtained from a sample of 5 calls. Calls contained from 1 to 3 overtones.

Function of the 'foot-slapping' call was difficult to determine. The few observations made of the call occurred at the nest, late in the incubation stage. While such a call was not observed in females, Gullion (1952) describes females as giving low calls associated with platform slapping when copulation was not about to occur.

A third relatively uncommon call, given by females while I was in the blind adjacent to a nest, was the growl (Fig. 10e). This call was described by Gullion as being given by parents when intruders approach the nest. Mean call length was .226 sec (S.D.=.033). Minimum frequency

averaged 146 Hz (S.D.=49), while maximum frequency averaged 630 Hz (S.D.=17). Mean frequency range was 485 Hz (S.D.=48). Values were determined from a sample of 5 calls.

All calls described above, except the broody call, have been discussed by Gullion (1952). Calls described by Gullion (1952), but not observed in my study include the intimidation note, and courtship notes. Further discussion of ontogeny of vocalizations will be confined to calls which were observed in this study.

Ontogeny

Tracing the probable ontogeny of vocalizations was necessarily interpretive. While some calls showed a relatively direct path of development, others were less clear-cut. In general, relationships between call types were determined by structural and contextual similarity. Interpretations presented in this section were based on the calls described above from three broad ontogenetic stages: chick (up to 4 weeks), juvenile (2 to 3 months), and adult (during the breeding season). Most observations of chicks and juveniles are of captive birds, while those of adults are of wild birds.

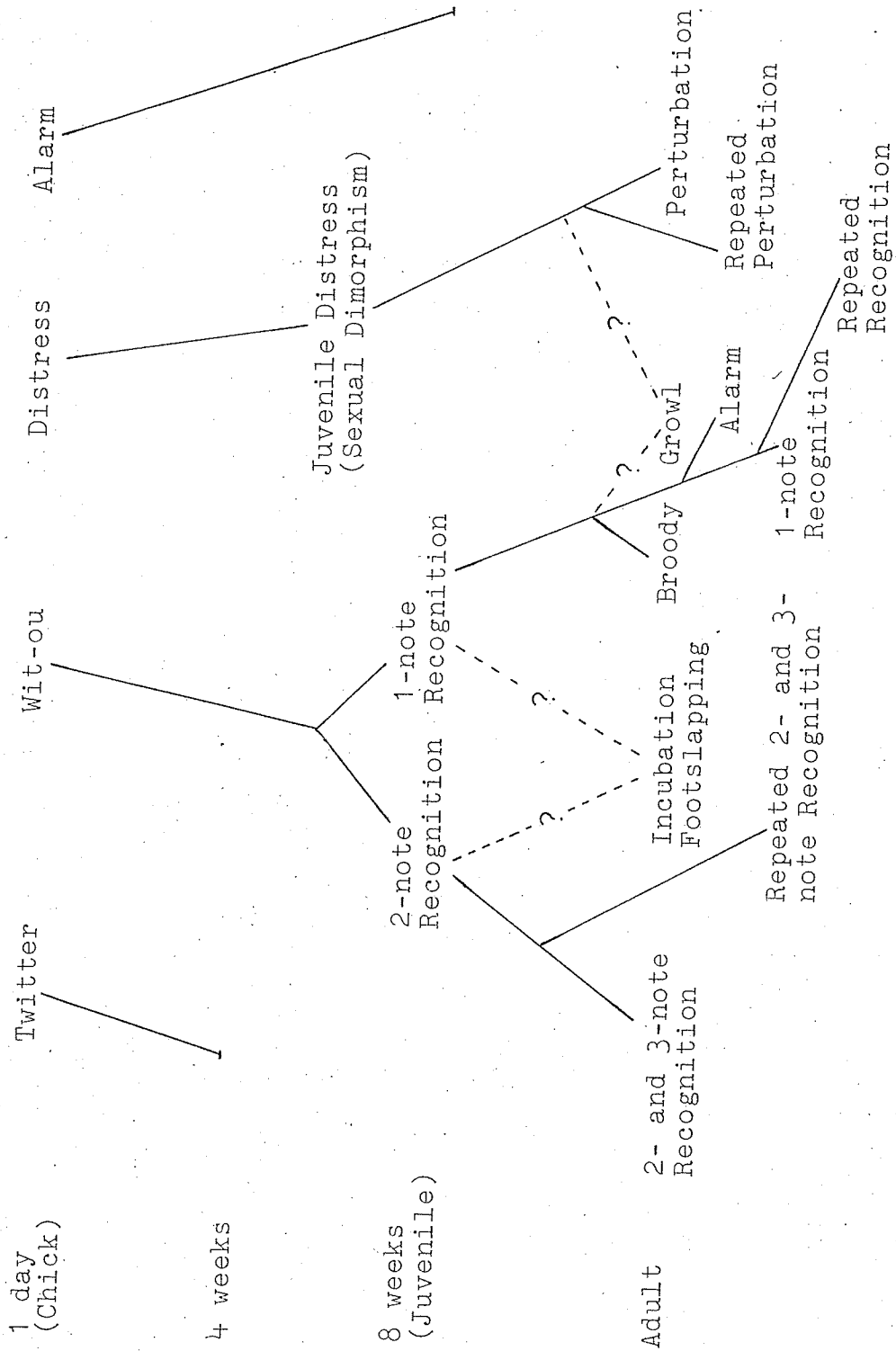
Development of Juvenile Calls. During the first month of life, coots had a stable vocal repertoire containing the twitter, wit-ou, distress, and alarm calls. During the

next two months, vocal repertoires underwent a series of changes. Twitters were discontinued. Chicks stopped giving distress calls in isolation, and gave them in the context of the twitter. Sexual dimorphism in call pitch began at about 6 weeks of age, and alarm calls were discontinued at about 8 weeks of age.

During the juvenile stage of development birds used three main calls, two of which may be classed as recognition calls, one as a juvenile distress call. The juvenile distress call, used during feeding and resting, was still recognizably like the main distress call note used by chicks, though much longer (Figs. 3 and 8). Recognition calls of juveniles appeared to develop directly from the wit-ou call of chicks. To my ear, the 2-note recognition call of juvenile males still sounded similar to the 2-note version of the wit-ou (Figs. 3 and 8). While call shape changed especially in females, similarities both in structure and rhythm remained, the main changes being in pitch. Comparison between the single and the 2-note recognition calls (Fig. 8) suggests that the single note call is merely one note of the 2-note call. The probable ontogenetic origins of the three main juvenile calls from those present in younger birds are shown diagrammatically in Fig. 11.

Development of Adult Calls. Eight of the 11 types of adult vocalizations indentified in this study can be grouped on the basis of structural affinity, into three main cate-

Figure 11. Diagrammatic illustration of the ontogeny of vocalizations in the coot.



gories (Fig. 11). All single or multiple short note adult calls are broadly similar in duration and appear to have closer structural affinities to the juvenile recognition calls than to the longer juvenile distress call. Of these short-note calls, the broody, recognition (and its repeated form), and alarm calls exhibit a closer resemblance to the single note juvenile recognition call than to the double note call, and hence are shown in Fig. 11 as being derived from the single note call. The 1-note call in turn appears to be derived from the wit-ou of chicks.

Two and 3-note adult recognition calls were given in essentially the same context as the 1-note recognition call, but despite this similarity in context, do not appear to represent merely repetitions of the single note call. The stable rhythm of the 2-note calls suggests that it is derived from the double note, rather than single note juvenile recognition call (Figs. 8 and 9). The 3-note call differed only in that there was one added component which looked like, and sounded like the other notes typical of the 2-note call.

The ontogeny of the adult incubation and foot-slapping calls is more problematical. As they are single notes of short duration, it might be assumed that they are closely allied with the broody, alarm, and single note recognition call group. However, inspection of sonogram traces indicates that structurally, these short single notes do not

appear to form a single, homogeneous group. Because the incubation and foot-slapping calls resemble one another more closely than they resemble the other short single note calls (Figs. 9 and 10), it seems reasonable that they should be placed, tentatively, in a separate group.

Structural similarities with individual notes of the adult 2-note recognition call (Figs. 9 and 10) raises the possibility that they represent single note variants of the multiple note recognition calls, and hence could be ontogenetically derived from the juvenile 2-note recognition call. As indicated in Fig. 11, the final status of the adult incubation and foot-slapping calls remains open to doubt.

Other adult vocalizations consist of single long notes. These include the perturbation call (including the repeated form), and the growl. Structurally, perturbation notes were identical to juvenile distress calls, suggesting a direct path of development from the latter (Fig. 11). The growl has a 'throaty' quality, probably due to the temporal structure of the call (Fig. 9). The temporal structure of the growl resembles that of recognition, broody, and alarm calls, though its length suggests an affinity to the perturbation call. Its ontogenetic origin thus remains open to doubt (Fig. 11).

Discussion

Results must be discussed in light of the fact that most observations of chicks and juveniles were made of captive birds, while those of adults were made of wild birds. It is unlikely that call characteristics differ between wild and adult birds as studies have shown that environment usually has no effect on development of calls in non-passerine species (Nottebohm 1972). There is a possibility, however, that repertoires of captive birds may be smaller than those of wild birds if the stimuli normally eliciting calls are absent. Thus it is possible that calls normally given by young wild coots have not been given under laboratory conditions.

Changes in vocalizations prior to 1 month of age appear to be related to growth of the birds, and do not correlate with any obvious major changes in call function or chick behaviour. All calls showed changes in pitch during this early period, usually a decrease in frequency level. Changes in call length during this time were restricted to the wit-ou and the distress calls.

Changes in repertoire after about 1 month of age appear to be directly correlated with changes in other behaviour of young coots. The first major change in call use was the dropping of the twitter, and the concurrent use of distress calls during feeding at about 30 days of age. Caswell (1972) describes a similar dropping of twitters in

Mallards (Anas platyrhynchos) at 11 weeks, after which flight intention calls were used. He suggested that such calling may function to attract birds to a common location for flocking. While distress calling in coots may serve a similar function after 8 weeks, when flocks were forming for migration, this function does not explain why calling should occur as early as it does.

An alternative interpretation of the early shift in call use in coots is that it reflects increased independence and mobility of young birds at that time. Use of the louder distress call rather than the twitter during feeding would enable auditory contact to be maintained between far-ranging juveniles and adults as the maturing broods became more mobile. Field observations suggest that this correlation is not exact, however, as distress calling in the presence of adults commonly occurred as early as about 1 month of age, whereas the number of chicks seen feeding alone with no adults present remained low until about 6 weeks of age. Functional interpretation is further complicated by other events, occurring at the time that the distress call was used in the context of feeding and other movements around the territory. At about 6 weeks of age chicks were also being subjected to parental aggression. Whether this aggression was in some way a direct cause of distress calls, or whether it tended to increase distress calling indirectly, by facilitating

the dispersal of the young, remains to be determined.

The dropping of alarm calls represented another major change in vocal repertoire at about 2 months of age. This occurred somewhat later than the dropping of the twitter, and tended to correlate more closely with the break-up of the breeding territories. Prior to disintegration of territories, alarm calls were given in response to parental attacks. Such calls in young chicks may serve to elicit parental aid, or in the case of attacking parents, may act as an appeasement call. Tinbergen (1953) suggests that full grown young may incur hostile behaviour on the part of the parent, and that use of appeasement postures in the presence of parents reduces attacks on juveniles. Once in flocks, where intraspecific aggression should be minimal, and where young are completely independent of parents, alarm calls would perhaps be of less functional value.

Other changes in juvenile coots occurring during August suggest that hormonal changes are occurring at this time. Calls, especially of females, began to take on the adult tonal quality, and sexual dimorphism became apparent. The callus, or fleshy portion of the shield, became orange at this time. Callus growth has been shown to depend on hormone levels (Gullion 1951). It thus appears probable, although not proven, that hormone changes are similarly responsible for at least some of the changes in juvenile vocalizations which occur late in the season, prior to

migration.

Adult calls associated with reproduction, which include calls other than recognition notes, probably do not appear until the breeding season. Marler (1956) states that in the Chaffinch (Fringilla coelebs), male sexual and aggressive calls are confined to the breeding season. Similar observations have been made for other species, and for both males and females (Ellis and Stokes 1966, Lanyon 1960, Stokes 1961 1967, Williams 1969). Hormonal levels at this time are known to affect both shield growth and levels of aggression (Gullion 1951), and can be expected to exert a corresponding influence on changes in adult vocal behaviour (Andrew 1969, Thorpe 1961).

Vocal development in coots, then appears to follow four phases. The initial, chick phase consists of a stable repertoire of four call types, changing only gradually as the chicks mature. The subsequent juvenile stage is one of more abrupt change, where two calls are lost and more striking voice changes occur, including the onset of sexual differences. These changes, moreover, are apparently more under the influence of hormonal changes than during the chick stage. The third phase, from about September to early spring, is probably again relatively stable with several call types being used which sound similar to those typical of adults. The final phase is

that of adulthood, where the breeding season and its hormonal changes induce the full adult vocal repertoire functional under contexts of courtship, aggression, and brood rearing.

Few ontogenetic studies of vocalizations exist with which to compare the development of coots. Moynihan (1959) studied vocal development in Franklin's Gulls (Larus pipixcan) and Ring-billed Gulls (L. delawarensis). He described only two calls in young gulls, but also stated that a number of intermediates occurred between the low and high intensity distress calls. Impekoven (1971), however, studied Black-headed Gulls (L. ridibundus) and described four distinct call types and three intermediates in chicks. In both species studied by Moynihan, most adult calls developed from the high intensity distress call. This differs from coots where most adult calls appear to develop from a call intermediate to twitter and distress calls.

Another difference between young coots and gulls is the apparent lack of an alarm call in the latter (Moynihan 1959), although the 'harsh' call described by Impekoven (1969) may serve this function. According to Moynihan (1959), alarm calls associated with escape responses in gulls do not occur until at least 15 to 20 days of age, at which time it resembles the adult call. This difference in repertoire may reflect a difference in mobility between

the two species. While coots are mobile within a day or two of hatching, gulls are restricted to the vicinity of the nest site (Evans 1970a, Tinbergen 1953). Fear or alarm calls in ducks and gallinaceous birds suggest that such a call occurs in highly mobile young. The 'fear trill' described by Collias and Joos (1953) for young domestic chicks, by Kruijt (1964) for Junglefowl (Gallus gallus spadiceus), and the aerial alarm call described by Starky (1973) for the Mallard appear analagous to the alarm call of young coots. The latter may be a more specialized call if restricted only to aerial predators. Chicks able to locomote after hatching would be more likely to incur dangerous situations, and alarm or fear notes could presumably elicit parental assistance.

Gull vocal development, according to Moynihan's study, occurs at a different rate than in coots. Most juvenile calls in gulls have become clearly differentiated by 35 days, but fully adult calls are apparently delayed until sexual maturity, usually at 2 or 3 years of age. In coots, major changes are just beginning by 35 days, but adult calls are developed by 1 year when breeding begins (Crawford 1975). Mallards seem to resemble coots with an initially slow rate of vocal change. Calls resembling those of adults begin to appear by about the tenth week of age (Caswell 1972). Similarly, in Junglefowl, calls take on an adult quality around 70 days of age (Kruijt 1964).

One would perhaps expect coots to resemble waterfowl and galliforms more closely than gulls, in part because their age at first breeding is similar. In addition, young coots, like truly precocial species, leave the nest shortly after hatching, and though they are fed for several weeks by the adults, they are highly mobile. In this sense Skutch (1976) terms them as being sub-precocial. The coot normally breeds in marshes (Fredrickson 1970, Kiel 1955) where visibility is often restricted by vegetation. Like many other species living where there are similar constraints on visual signalling (Wilson 1975), coots represent a species in which vocalizations play an especially important role in social behaviour (Gullion 1952), presumably at all ages. The repertoire of young coots appears to be typical of truly precocial species (see Kear 1968 for descriptions of calls of young waterfowl). The rate of change in call structure also appears to be similar to galliform and waterfowl species that have been studied. One difference appears to be in the origin of adult calls. In Mallards, adult calls are thought to develop from twitters (Caswell 1972), whereas in coots, adult calls appear to develop from a call intermediate to the twitter and distress call. Whether this is an actual difference or a result of terminology is open to question. Little attention has been paid to intermediate call types, either in terms of function or development. Depending upon

the classification scheme, intermediates may be ignored or lumped with other call types. The results of this study suggest that it may be of some value to look more closely at intermediate call types, to determine what role they play in vocal development.

Part B. Individual and Brood Differences in Distress
Calls of Young American Coots

Introduction

Young of precocial species give distress calls in response to aversive stimuli such as cold and hunger, and in response to social isolation (Kaufman and Hinde 1961). Collias and Collias (1956) observed young Canvasback (Aythya valisineria) giving distress calls when separated from the brood. Presumably in cases of social isolation, distress calls enable lost chicks to regain contact with the family unit. Distress calls may also contain cues that facilitate recognition of lost young by parents or siblings (Evans 1970a, Miller and Emlen 1975, Noseworthy and Lien 1976).

Although progress has been made in identifying relevant cues for recognition in voices of adult birds of various species (Beer 1970, Falls 1969, Emlen 1972, White and White 1970), apparently no attempt has been made to quantify these parameters in the distress calls of young precocial birds. In this study, I therefore compared distress calls between individual American Coots (Fulica americana) to determine whether such cues could be present. In addition, the possibility that distress calls provide potential cues for family recognition was examined.

Although apparently not previously documented in precocial birds, it is possible that cues common to family members would also enable recognition of close relatives as a class, thus providing a physical basis to facilitate selective responses to close kin. Because voice characteristics of young coots change with age (Part A), brood and individual voice characteristics were examined over an age range of 2 to 28 days to determine the possible effects of this variable on the development of potential recognition cues.

Methods

While studying vocal development in coots (Part A), recordings were obtained of early distress calls from laboratory-reared birds placed in social isolation during three age periods: 2 days, 8 to 15 days, and 21 to 28 days. Calls were measured from sonagrams produced by a Kaye Electric Company Model 675 Missilyzer. For the present study, a sample of 8 calls per bird per age period was randomly chosen from the tapes. A total of 14 birds from 3 family groups was used in the analysis of brood and age differences. Data from 9 of the birds (3 birds selected at random from each of 3 broods) were then examined to determine if individual differences in distress calls were present at each age period.

Calls were compared on the basis of several charac-

teristics including length, minimum frequency, maximum frequency, frequency range, presence of nonharmonic tones, and the number of notes per call. Call length, and the three frequency characteristics were tested for brood differences at three ages using a two way repeated measures analysis of variance (Hays 1973). These characteristics were analyzed for individual differences using a one way repeated measures analysis of variance (Hays 1973).

Results

Brood Differences

Length and Frequency. Call length and minimum frequency differed significantly between broods, whereas maximum frequency and frequency range did not (Table 1). All length and frequency characteristics changed significantly with age (Table 1). Both length and frequency range increased as birds aged, while minimum frequency and maximum frequency decreased (Fig. 1). Significant brood by age interactions occurred for call length, maximum frequency, and frequency range.

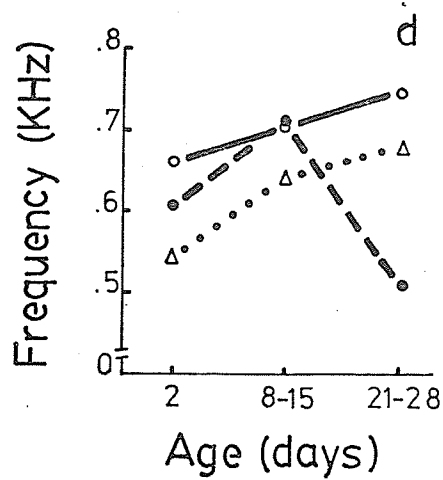
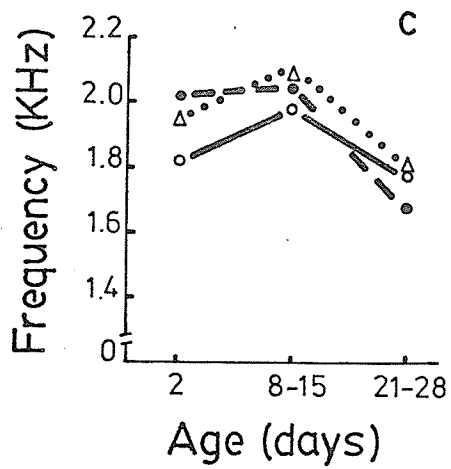
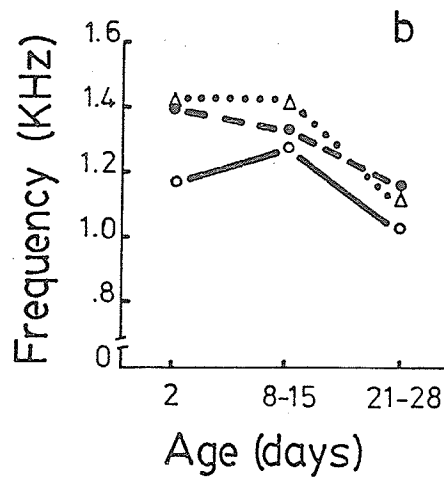
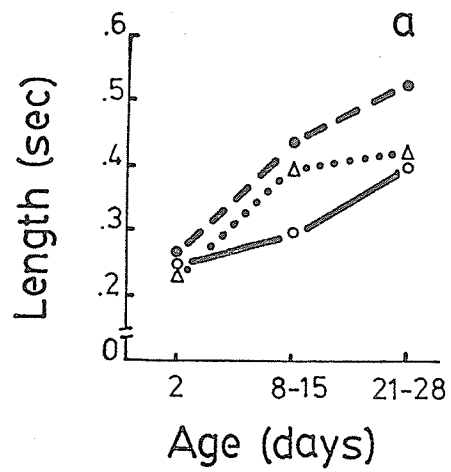
For each call characteristic measured, significant brood by age interactions appeared to be due primarily to one brood, number 2 (Fig. 1). For characteristics other than minimum frequency, this brood showed unusual age-

Table 1. Results of analysis for brood differences and age-related changes of distress calls.

Characteristic	Brood			Age			Interaction		
	df	F	p	df	F	p	df	F	p
Length	2,109	74	0.001	2,218	428	0.001	4,218	27	0.001
Minimum Frequency	2,109	14	0.001	2,218	31	0.001	4,218	2	0.10*
Maximum Frequency	2,109	2	0.10*	2,218	48	0.001	4,218	5	0.05
Frequency Range	2,109	3	0.06*	2,218	3	0.05	4,218	4	0.05

*Not significant.

Figure 1. Age-related changes in distress calls for three broods (Brood 1= $\circ$, Brood 2= $\bullet$, Brood 3= Δ) showing brood by age interactions. a) length, b) minimum frequency, c) maximum frequency, d) frequency range.



related changes relative to other broods studied. The greatest difference in age-related change between brood 2 and the others was in frequency range, where brood 2 showed a sharp drop during the last week. This difference was not due to sex, as all broods contained approximately equal numbers of males and females.

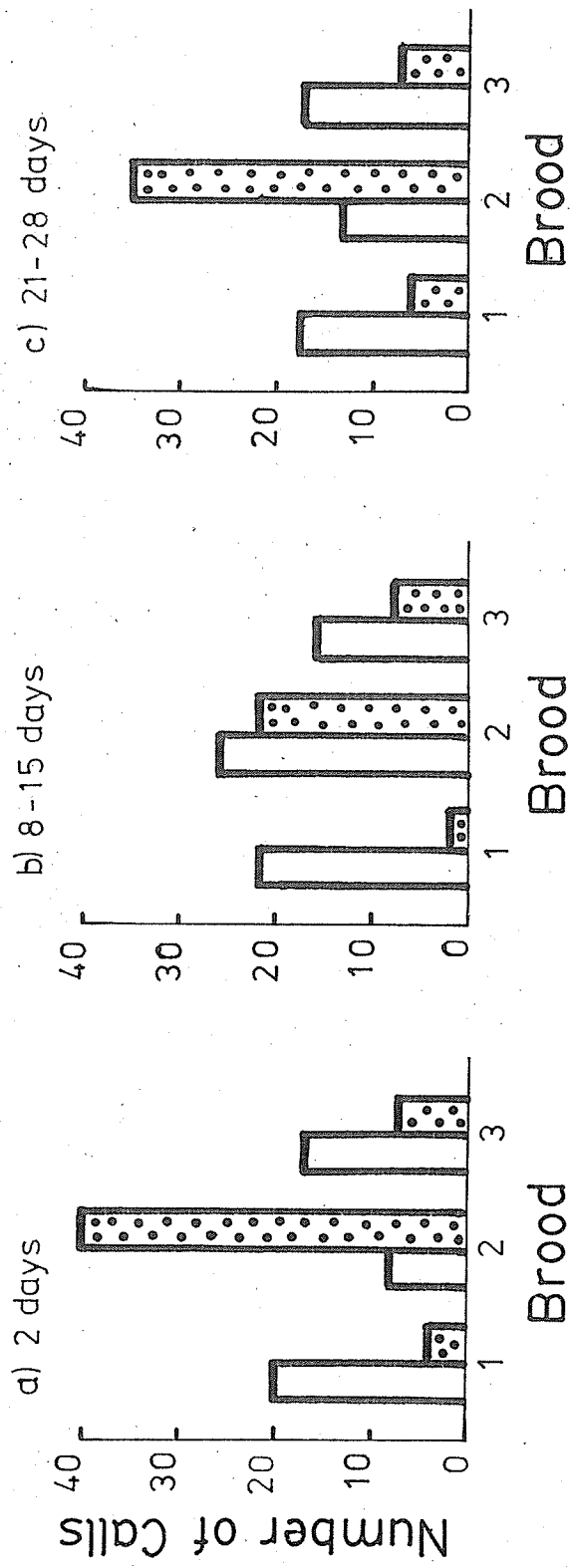
Nonharmonic Tones. All distress calls contained at least one harmonic which was double the frequency of the fundamental note, the latter being defined as the component of lowest frequency in a complex tone (Davis 1964). In addition, some calls contained tones which did not show this mathematical relationship with the fundamental (Fig. 2). This has been described as the two-voice phenomenon (Miller 1977, Miller and Gottlieb 1976) where two independent sound sources are involved in producing vocalizations. Broods were compared to see whether variation in this characteristic could provide cues for recognition. Fig. 3 shows the number of calls of either single or double voice origin at each of the three ages.

At 2 days of age broods 1 and 3 used largely single voice calls while brood 2 used a high proportion of double voice calls. Similar results were obtained for other ages. While these data indicate that variation occurred between broods, the similarity between two of the broods suggests that the presence of single or double voice is not always a distinguishing characteristic.

Figure 2. Distress calls of 15 day old coots showing double voice (a), and single voice (b) origin of sound.



Figure 3. Number of distress calls of young coots showing the presence of single ($\square$), or double ($\boxplus$) voice origin.



Number of Notes. Calls were also variable in terms of the number of notes used. Broods were compared for variation in this characteristic (Fig. 4). Again some differences occurred, as brood 1 used largely single note calls while broods 2 and 3 used a high proportion of double note calls at 2 days of age. At 8 to 15 days of age broods 2 and 3 retained a high proportion of 2-note calls, while brood 1 showed an increase in this call type. At 21 to 28 days all broods commonly used single note calls, and two of the broods also commonly used double note calls. The number of notes emitted per call appears not to constitute a reliable cue for brood identification.

Individual Differences

Length. Mean call length was significantly different between individuals at all ages tested (Table 2). Differences between birds became more pronounced with age, as between bird variability was greatest at 21 to 28 days (Fig. 5). At this time similarities between birds were primarily confined to siblings.

Minimum Frequency. Though individual variation in minimum frequency was large at all ages, analysis indicated that significant differences were present between birds (Table 2). While mean values tended to differ between individuals, the high individual variation resulted in

Figure 4. Number of distress calls containing 1 note () ,
2 notes () , or 3 notes () .

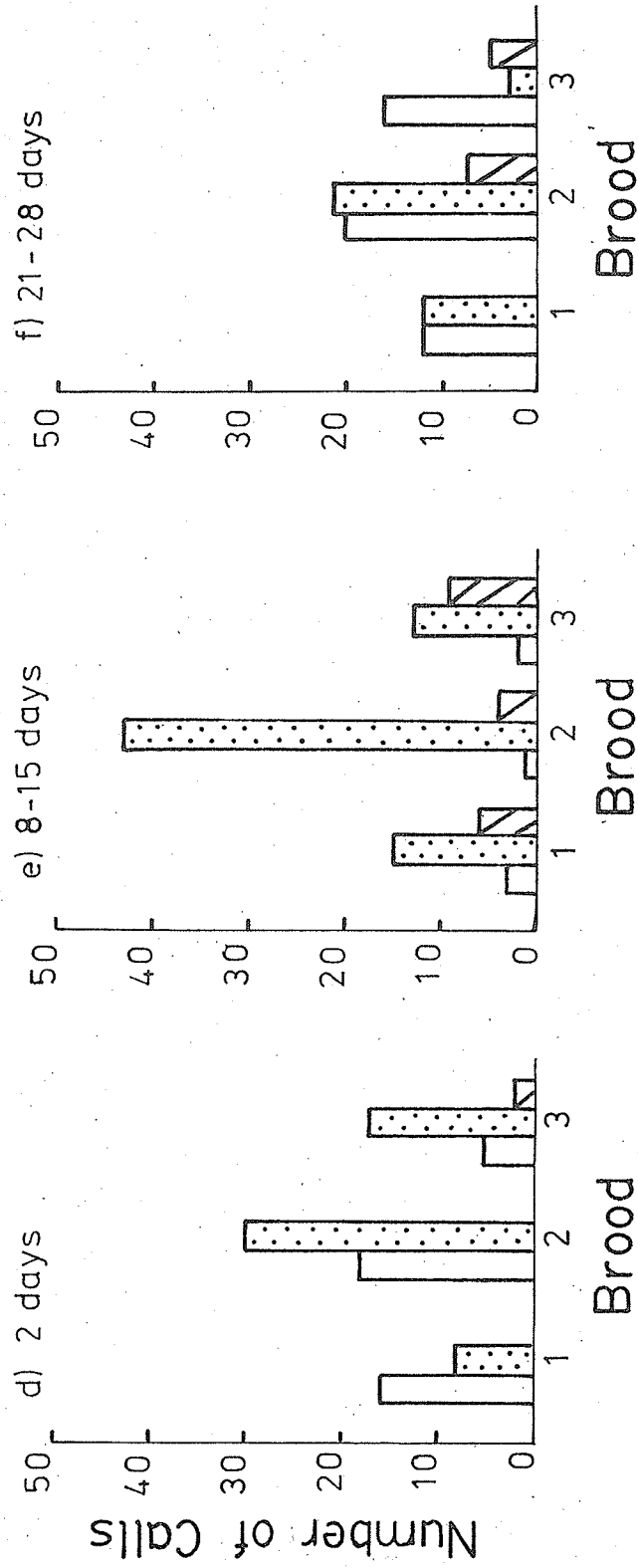
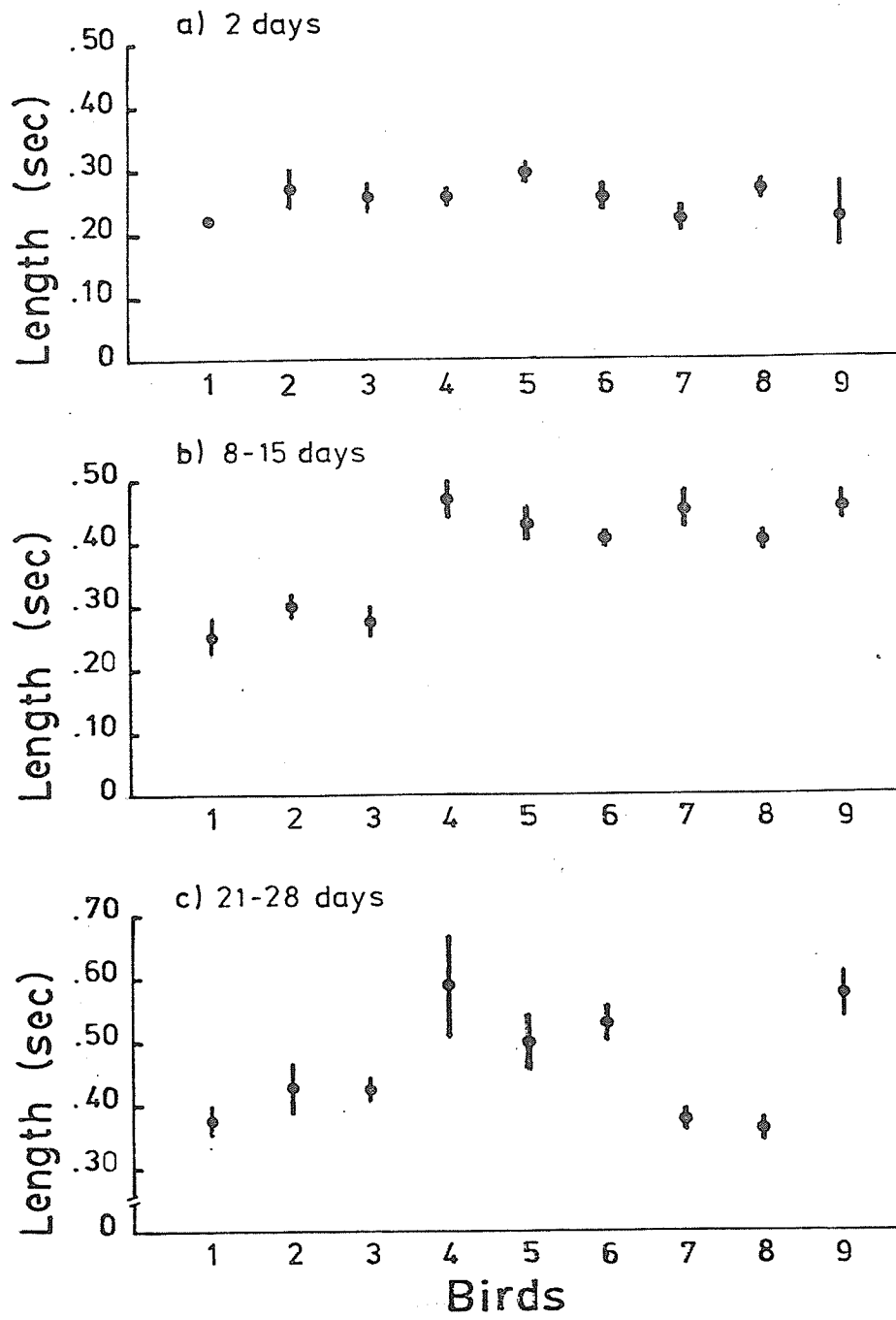


Table 2. Individual differences in distress calls.

Characteristic	Age	df	F	p
Length	2	8,63	8	0.001
	8 to 15		81	0.001
	21 to 28		37	0.001
Minimum Frequency	2	8,63	8	0.001
	8 to 15		8	0.001
	21 to 28		6	0.001
Maximum Frequency	2	8,63	16	0.001
	8 to 15		7	0.001
	21 to 28		8	0.001
Frequency Range	2	8,63	9	0.001
	8 to 15		6	0.001
	21 to 28		10	0.001

Figure 5. Mean length of distress calls at 3 ages. Circles represent mean values, vertical lines represent standard derviations. Birds 1 to 3= Brood 1, Birds 4 to 6= Brood 2, Birds 7 to 9= Brood 3.



extensive overlap between individuals (Fig. 6).

Maximum Frequency. Individuals were again significantly different at all ages for this characteristic (Table 2). As was found for call length, between bird variation for maximum frequency tended to increase with age (Fig. 7), however similarities between birds did occur both within and between broods.

Frequency Range. Individual differences were significant at all ages (Table 2). Between bird variation increased with age (Fig. 8), older birds tending to become more distinct.

Nonharmonic Tones. Some individual differences in the presence of a single or double voice in calls were apparent at 2 days of age, as some chicks used only single voice, while others used only double voice calls. Most birds, however, emitted both types of calls (Fig. 9a). At 8 to 15 days birds maintained similar proportions of the two call types (Fig. 9b). At 21 to 28 days, individuals tended to become more variable in the type of call used (Fig. 9c). Six birds used calls of both types, thus the presence of single or double voice origin in calls does not appear to be a consistent cue enabling recognition. No sex differences were apparent for this characteristic.

Number of Notes. At 2 days of age, two birds gave strictly single note calls, while two birds gave only double note calls (Fig. 10a). Most birds gave both types of calls.

Figure 6. Minimum frequency of distress calls at 3 ages. Circles represent mean values, vertical lines represent standard deviations. Birds 1 to 3= Brood 1, Birds 4 to 6= Brood 2, Birds 7 to 9= Brood 3.

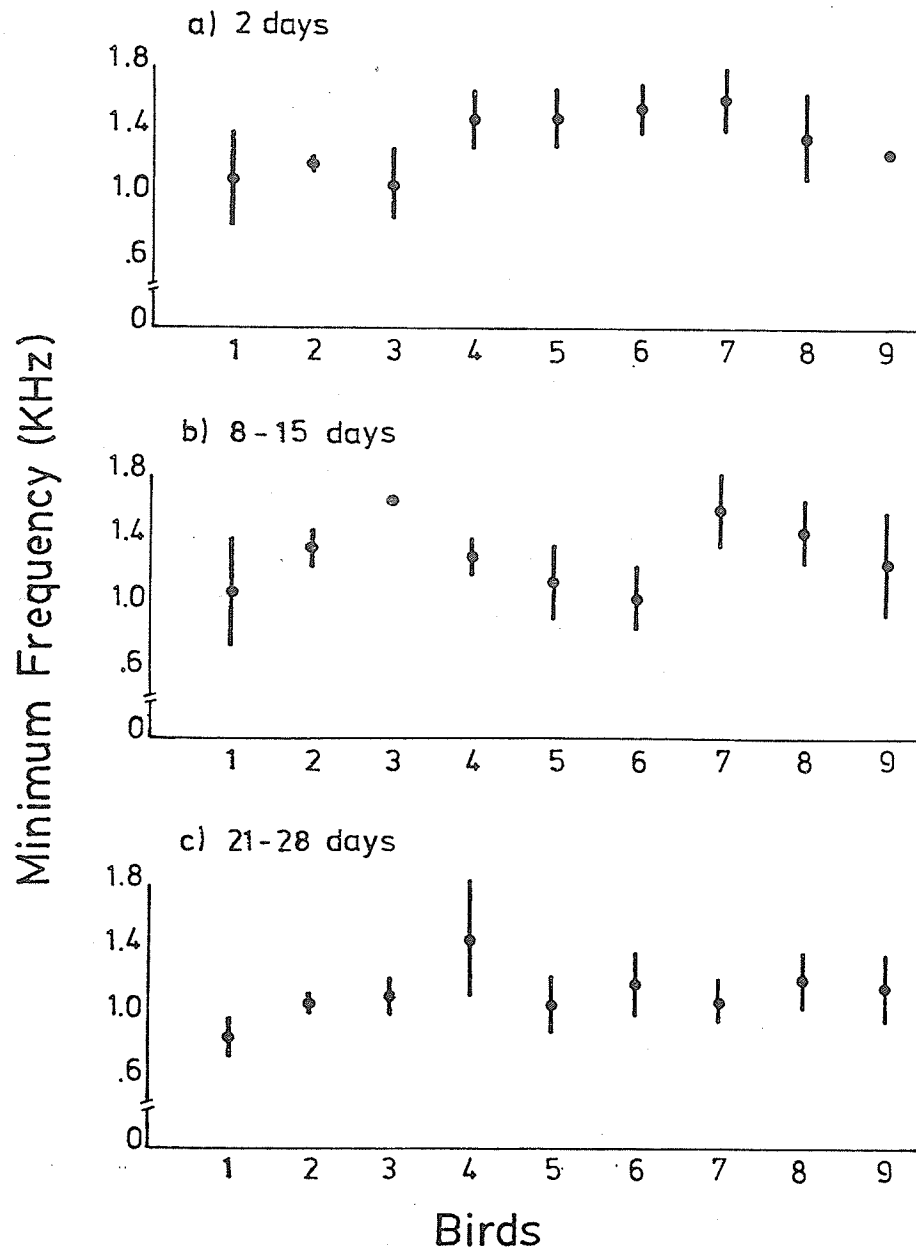


Figure 7. Maximum frequency of distress calls at 3 ages. Circles represent mean values, vertical lines represent standard deviations. Birds 1 to 3= Brood 1, Birds 4 to 6= Brood 2, Birds 7 to 9= Brood 3.

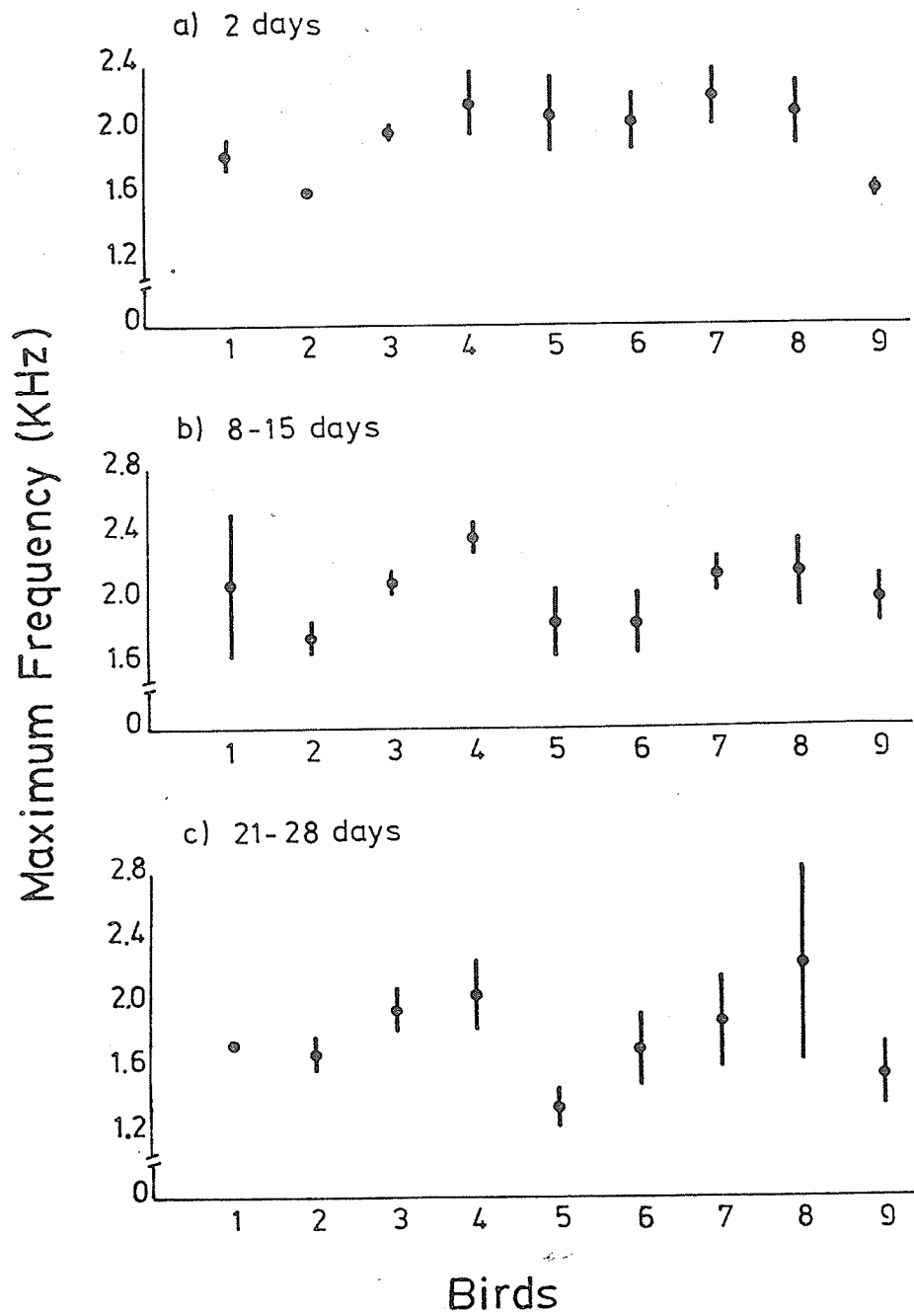


Figure 8. Frequency range of distress calls at 3 ages. Circles represent mean values, vertical lines represent standard deviations. Birds 1 to 3= Brood 1, Birds 4 to 6= Brood 2, Birds 7 to 9= Brood 3.

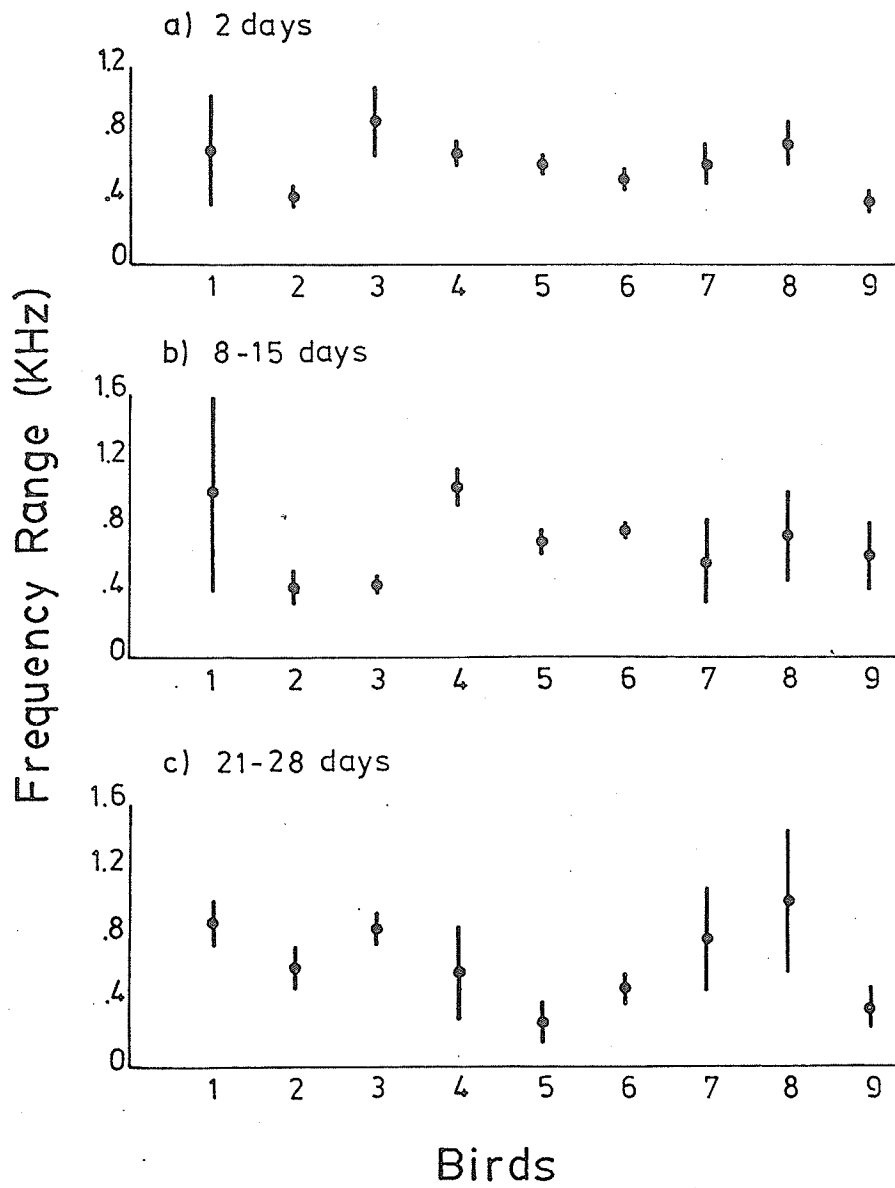


Figure 9. Individual differences in the presence of a single () , or double () voice in distress calls. Birds 1 to 3= Brood 1, Birds 4 to 6= Brood 2, Birds 7 to 9= Brood 3.

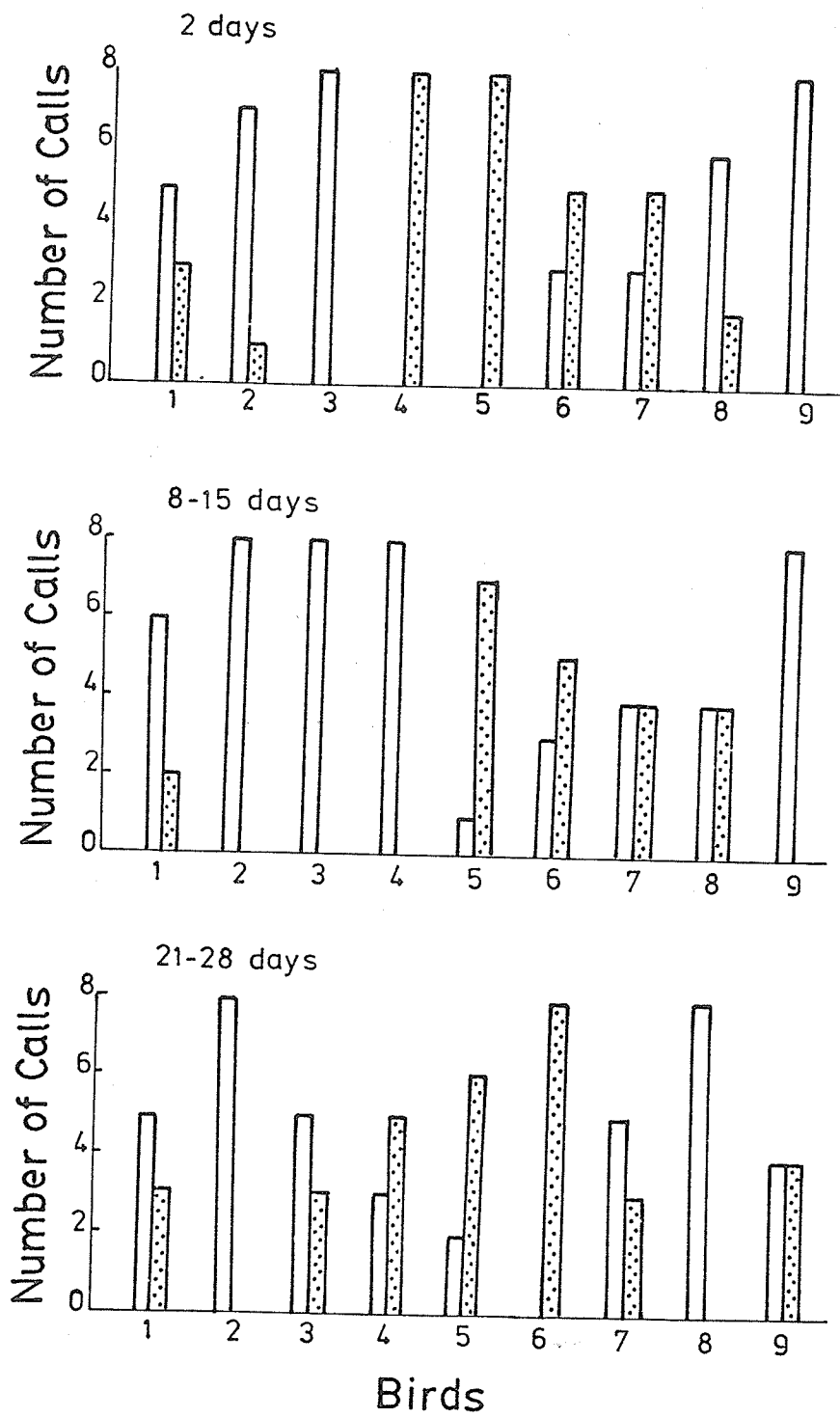
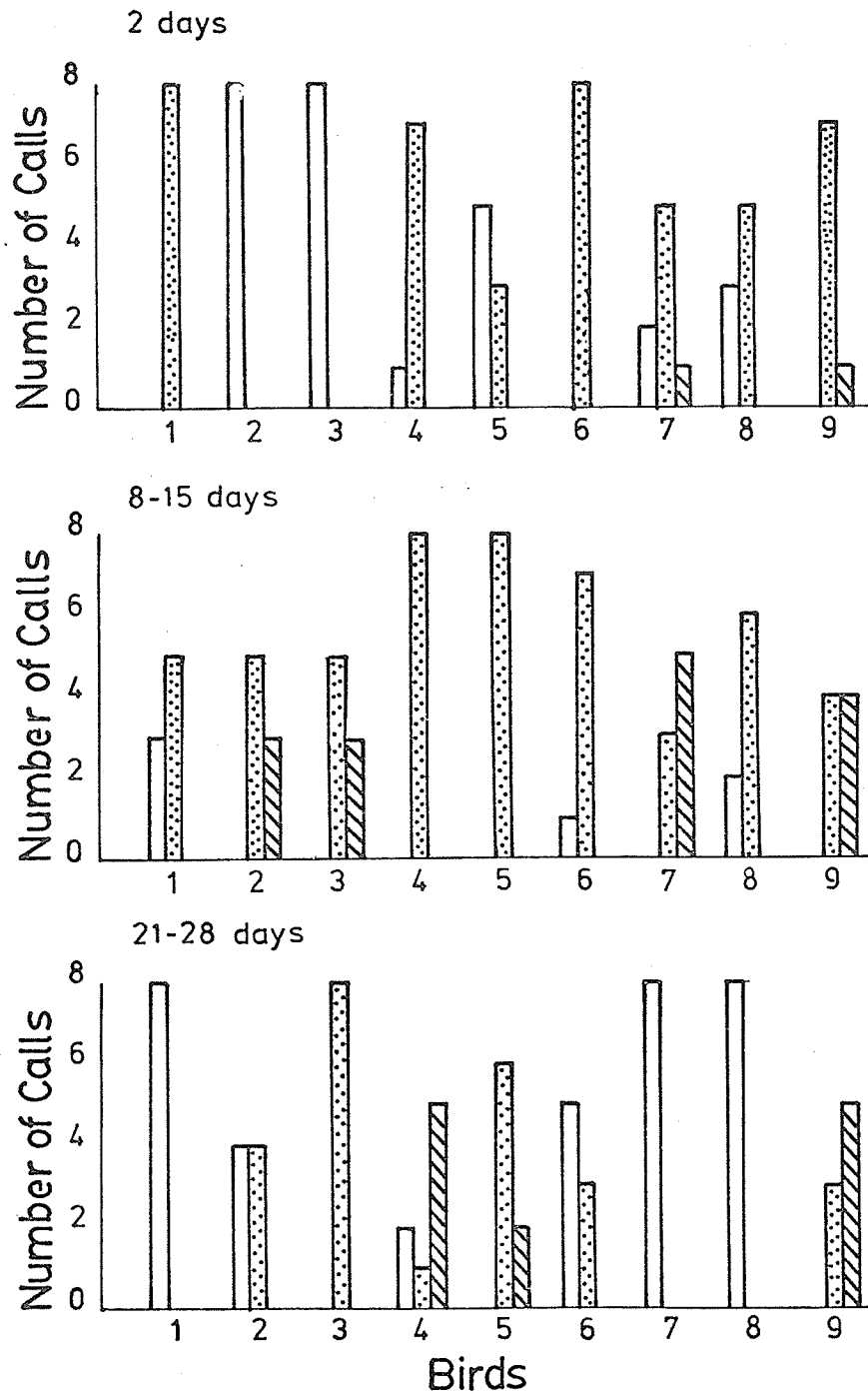


Figure 10. Individual differences in the presence of 1 note () , 2 notes () , or 3 notes () in distress calls. Birds 1 to 3= Brood 1, Birds 4 to 6= Brood 2, Birds 7 to 9= Brood 3.



At 8 to 15 days all birds gave double note calls (Fig. 10b). At 21 to 28 days three birds gave only single note calls, while a fourth chick gave only double note note calls (Fig. 10c). Others emitted calls of at least two types, thus note structure appears to be a poor cue for differentiating individuals.

Multiple Cues. It is apparent that it may not be possible to identify individuals from this sample of nine on the basis of any single call characteristic. Combinations of cues, however, do appear to provide sufficient information for recognition. To illustrate this point, individuals of 21 to 28 days were first ranked by call length. As is shown in Table 3, they fall into 4 categories, birds within each being fairly similar. Addition of one more cue, minimum frequency, results in virtually no birds being identical. The most similar birds are 2 and 3 which are siblings. If maximum frequency is now considered, these birds become readily separable. Thus, if multiple cues are used, no two birds within the sample of nine are the same.

While not shown, the same procedure can be used for birds at earlier ages. Again, combining call characteristics results in individual distinctiveness of distress calls.

Coefficients of variation (standard deviation divided by the mean) have been used (Miller and Gottlieb 1976) to determine whether cues are sufficiently variable between

Table 3. Individual differences in distress calls
at 21 to 28 days when birds are ranked
according to call length.

Bird	Length (sec)	Frequency (Hz)		
		Minimum	Maximum	Range
8	.360	1228	2225	997
1	.375	836	1740	876
7	.375	1094	1873	779
3	.426	1124	1964	893
2	.433	1082	1691	609
5	.497	1079	1343	264
6	.529	1219	1710	491
9	.575	1188	1549	360
4	.591	1470	2046	576

individuals to enable recognition. When this procedure is used for characteristics at 21 to 28 days of age (Table 4), the most likely single cue for recognition is call length, as coefficients for individuals were usually much smaller than the overall coefficient of variation for this characteristic. Results for birds at 2 days and 8 to 15 days (not shown) were similar to those for 21 to 28 days. Discrimination by frequency range is less likely as coefficients for individual birds were often large relative to the overall coefficient. The relatively small overall coefficient obtained for all variables, except frequency range, further suggest that single cues may not provide sufficient discrimination between birds to enable recognition of individuals.

Discussion

The results of this study provide evidence that both individual and brood differences occur in distress calls of young coots. While it has not yet been shown that recognition by auditory cues exists in coots, the potential is clearly present. My data indicate that individual differences become more marked during the first four weeks, thus presumably increasing the ease with which discriminations could be made among the older, more mobile chicks.

Data further suggest that if recognition does occur,

Table 4. Coefficients of variation for distress
call characteristics at 21 to 28 days.

Bird	Call Characteristics			
	Length	Minimum Frequency	Maximum Frequency	Frequency Range
1	.06	.15	.04	.16
2	.08	.06	.08	.20
3	.04	.09	.08	.14
4	.13	.24	.10	.50
5	.11	.16	.10	.53
6	.05	.15	.13	.18
7	.06	.12	.14	.27
8	.06	.14	.27	.45
9	.07	.17	.13	.36
Overall	.20	.20	.20	.48

it is not likely to be based on only a single cue. The use of even one additional cue, however, should provide enough information to reliably differentiate between most individuals within group sizes likely to be encountered by young coots in their natural habitat. Espmark (1975) similarly concluded that recognition of distress calls of Reindeer (Rangifer tarandus) calves by mothers is probably not based on single cues.

Alley and Boyd (1950) showed that European Coots (Fulica atra) recognized and attacked strange young by the time their own young were about 2 weeks old. They did not discern whether auditory or visual cues were being used to differentiate between chicks. Beer (1970) suggested that individual recognition is likely to be shown by species living in dense vegetation. The tendency for American Coots to forage in emergent vegetation (Gullion 1954) is thus consistent with the hypothesis that individual recognition using auditory cues is likely to occur in this species. Evidence for recognition of young by voice in another marsh-nesting species, the Red-winged Blackbird (Agelaius phoeniceus), has been presented by Peek, Franks, and Case (1972).

Differences in call characteristics between coot broods, shown for call length and minimum frequency, suggest two hypotheses on the possible functional significance of these cues. They may reflect genetic similarity between siblings

which has no particular function in behavioural interactions. Secondly, similarities between siblings at these ages could facilitate recognition of broods either by parents, or by other broodmates, and hence could be relevant to kin selection processes within family groups (Wilson 1975). This could no doubt be accomplished through individual recognition, but it seems reasonable to expect that cues common to family units would facilitate recognition of kin.

Several questions are raised by the potential to recognize broods or individuals as found in this study. Firstly, do the same cues identifying families and individuals extend beyond the age range studied? If so, how does the onset of sexual dimorphism (Part A) affect the cues, especially those which have been shown to differ between sibling groups? Are they maintained in both sexes, in one sex, or do they disappear? With respect to possible kin recognition and selection, the discussion may be extended to ask whether assistance by relatives occurs in the coot. According to Skutch (1976) assistance by older siblings to feed and preen younger family members occurs in the Common Gallinule (Gallinula chloropus), as does allopreening by sibling coots. Other members of the rail family have also been observed to aid family members (Skutch 1976). Further study is clearly required to clarify these issues for coots.

Part C. Habitat Acoustics and Call Structure
of Young American Coots

Introduction

According to Chapuis (1971) and Morton (1975), avian song structure has evolved at least in part as a result of selective pressures by habitat on sound transmission. Both found that tropical forest birds used tonelike songs of frequencies which showed low attenuation within dense forest vegetation. Grassland birds, in contrast, used songs which incorporated higher frequencies and tended to be of a wider frequency range. Species within a given habitat type have shown convergence in song structure as a result of selection for optimum transmission (Morton 1975).

Selection for optimum transmission should act on any call type including song, which functions over relatively long distances. Alternatively, some calls are close contact vocalizations which need function over only short distances. Selection in the latter case may act to minimize transmission distance. If within a habitat, frequencies do not carry equally well, then long distance and close contact calls may be of a different pitch. Moynihan (1967) suggests that pitch differences in primate calls may reflect different transmission distances.

While studying vocalizations of the coot (Parts A and B), it became apparent that calls of young chicks formed a dichotomy both in pitch and function. The low intensity, high pitched twitters are close contact calls, while other higher intensity calls such as the wit-ou, distress, and alarm calls are lower pitched and function over longer distances. A series of tests was therefore devised to determine whether or not call pitch is related to attenuation within coot habitat. It was hypothesized that high pitched twitters would attenuate more rapidly than the lower pitched call types.

Methods

To determine how sound attenuates in the marsh, pure tones were broadcast through emergent stands of vegetation in habitats used by breeding coots. Experiments were carried out during 1976 and 1977 at Delta Marsh, Manitoba. To determine whether or not call attenuation followed that of tones, calls of young coots were broadcast during 1977 at the same site as pure tones.

Pure Tones

Tones from 200 to 1000 Hz at 100 Hz intervals, and from 1000 to 7000 Hz at 1000 Hz intervals were produced

using an RCA Model 1421 Audio Generator and recorded on a Uher 4000 Report L tape recorder. Tones were amplified using a Fanon Model 3527 mobile amplifier powered by a 12 Volt battery, and broadcast through an Electro Voice 8 ohm loudspeaker. A small boat anchored at the test site held the broadcasting equipment.

Sound levels (dB) were measured at 0 (arbitrarily set as 30 cm from the speaker), 5, 10, and 20 m from the speaker using a hand-held General Radio Model 1565-A Sound Level Meter (C slow scale). Each series of tones was measured at 0 m, and then again at each of the other test distances. At each test distance, 20 measurements were taken of each tone. Both the sound source and sound level meter were placed at 44 cm (1.5 ft) above the water level for all dB measurements.

For each completed test with a given pure tone, I calculated the attenuation over one doubling of distance by subtracting the dB reading at 10 m from the reading at 5 m. A second value for attenuation over one doubling of distance was then calculated by subtracting the dB reading at 20 m from that at 10 m. The mean attenuation rate per doubling of distance (dd) was obtained by averaging these two values for the entire 20 readings from each tone. Theoretically, sound attenuates at a rate of 6 dB per doubling of distance from the sound source. To find the difference between the actual and theoretical rate, the

value of 6 dB/dd was subtracted from the observed attenuation rate. This value is termed Excess Attenuation (EA) (Morton 1975). If actual attenuation is higher than the theoretical value, then EA is positive, and if attenuation is lower than the theoretical value then EA is negative.

Vocalizations

The twitter, wit-ou, distress, and alarm calls of young coots were tested in the same way as pure tones. One call of each type, obtained from laboratory-reared coots was recorded on a tape loop using a Sony TC 800 tape recorder. In the case of alarm calls where several notes were given in a series, one note from a series was used. Calls were broadcast using the Sony recorder and other audio equipment. The sound level meter was set on the C fast scale, as calls were brief bursts of sound. EA for calls was determined in the same way as for pure tones.

As well as measuring dB levels, I recorded the calls at 0 m from the loudspeaker using the Uher 4000 Report L tape recorder and Uher M539 microphone. Lab analysis was then undertaken to determine the relative amplitude of different frequency bands present within the calls. A General Radio Model 1952 Universal Filter, set in the 'band pass' mode, was used to isolate bands of sound from the fundamental note of each recorded call. A maximum to

minimum frequency ratio of 1.3:1.0 was used to determine band width. Calls were played from the tape recorder through the filter to a Beckman R511A Dynograph. The dynograph provided a record of the relative amplitudes of the signals passed by the filter. The filter setting was progressively increased by increments of 50 Hz, as measured at the lower setting of the band pass filter, to obtain amplitude recordings for the entire frequency range of the calls. Frequency-amplitude plots indicated where peak amplitudes occurred, and what the frequency ranges of the calls were.

Analysis

EA values for pure tones were analyzed using a two way analysis of variance. Tones were grouped into 3 classes: low (200 to 600 Hz), middle (700 to 2000 Hz), and high (3000 to 7000 Hz) frequencies. These intervals were chosen as they corresponded to frequency levels of the vocalizations tested. Twitters contained frequencies corresponding to the high frequency interval while other call types contained frequencies corresponding to the middle frequency interval. The low frequency group contained no frequencies associated with the vocalizations.

EA values for vocalizations were analyzed using one way analysis of variance.

Effect of Vegetation

Plant density was measured within 10 randomly chosen quadrats between the sound source and the last test distance of 20 m. The transect method (Kershaw 1973) was chosen, as sound levels were measured in a direct line from the loudspeaker. Within each quadrat, 10 plants were sampled for height, and number of leaves per plant. If fewer than 10 plants were present in the quadrat, all plants were measured. Plants were sampled by taking a point every 20 cm along 2 sides of the quadrat, measuring in 10 cm and choosing the nearest plant.

To determine how plant growth might affect sound transmission, the first series of attenuation readings in 1976 was taken in May when vegetation growth was minimal. Subsequent readings were taken at the end of June, and again at the end of July, by which time vegetation growth was essentially complete. The same test site, which consisted of emergent stands of Scirpus acutus Muhl. interspersed with Scirpus paludosus Nels. and Scolochloa festuacea (Willd.) Link. was used all summer.

The 1977 site consisted of a dense stand of emergent Typha (T. latifolia L. x T. angustifolia hybrid). This site was used to test pure tone attenuation during mid-June, when hatching normally occurs. Vegetation was again sampled, as described above, thus enabling a comparison to

be made between the Scirpus and Typha sites for attenuation of pure tones. This site was also used to test attenuation of calls of young coot.

Experimental Conditions

To standardize conditions and minimize the effect of wind on sound transmission, experiments during 1976 were done between 6:00 and 9:00 a.m. on days when wind speed was below 10 km/hr. Due to poor weather conditions during 1977, testing occurred in either mid-morning or mid-afternoon whenever wind speed was negligible.

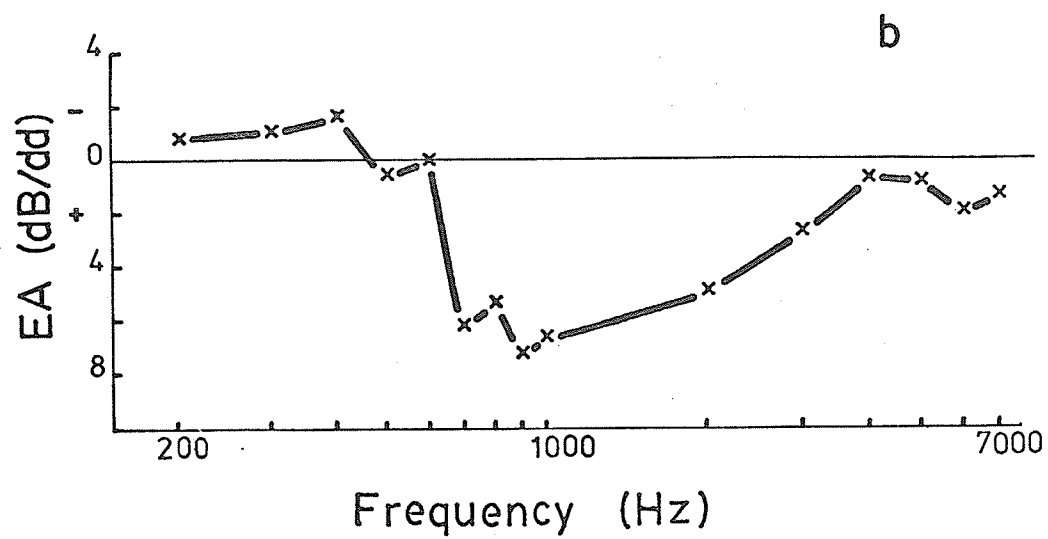
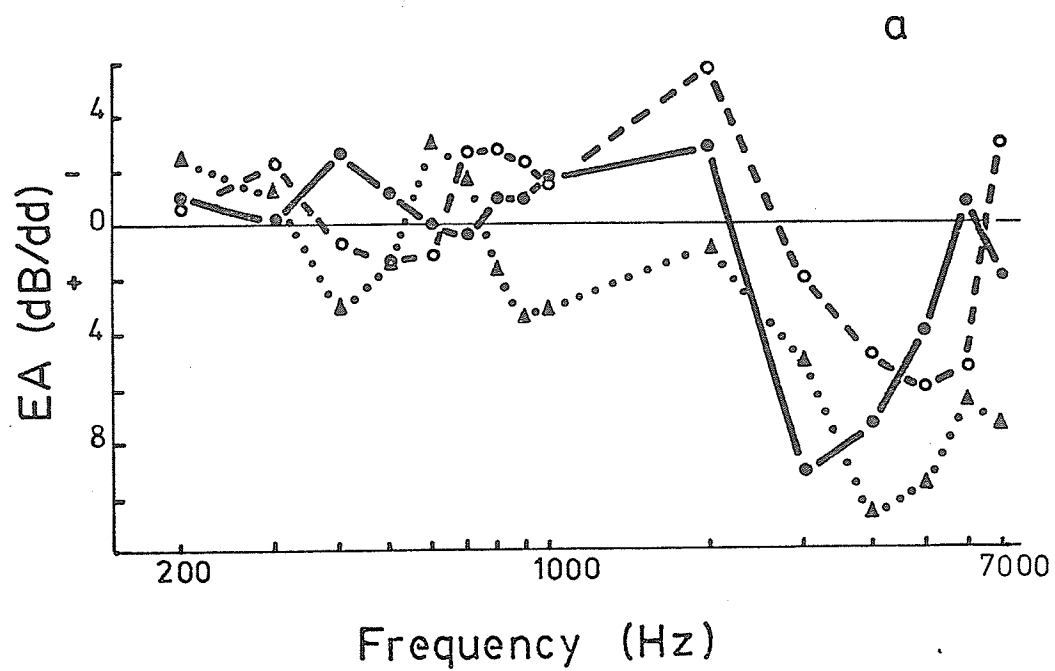
Water conditions varied between test series, especially during 1976. May and June readings for pure tones were taken over water. Due to lack of precipitation, the Scirpus site dried and readings from July were taken over a mud surface. Results obtained under the different conditions are treated separately. The 1977 site had a water level comparable to that of May and June 1976.

Results

Pure Tones

Mean Excess Attenuation (EA) from each test with pure tones is shown in Fig. 1a for May and June 1976, and June

- Figure 1. a) Mean Excess Attenuation of pure tones in Scirpus during May 1976 (○), June 1976 (●), and in Typha during June 1977 (▲) at Delta Marsh.
- b) Mean Excess Attenuation of pure tones in the Scirpus site during July 1976, after the area had dried.



1977. Results for July 1976 are shown separately in Fig. 1b. The theoretical attenuation rate of 6 dB/dd is represented by the line indicating 0 dB/dd. EA is negative if attenuation was less than 6 dB/dd and positive if greater than this value. Values for dB/dd in the upper portion of the graphs thus indicate a relatively strong transmission while values in the lower portion of the graphs indicate relatively poor transmission through the marsh.

Analysis indicated significant effects of test date and frequency on attenuation of pure tones (Table 1). The frequency by date interaction was also significant.

In 1976, the lowest overall mean attenuation averaged for all frequencies (Hz), was 0.00 dB/dd during May at the Scirpus site. By the end of June, it had increased to 0.76 dB/dd, but the frequency response remained similar. Least attenuation occurred at 700 to 2000 Hz and peak attenuation occurred at or above 3000 Hz (Fig. 1a). Results for the Scirpus site in July, after the area had dried, showed not only a higher mean attenuation of 2.34 dB/dd, but also a different frequency response (Fig. 1b). Peak attenuation occurred at frequencies of 700 to 2000 Hz. This appears to be the source of the significant interaction (Table 1).

Results from the June, 1977, Typha site indicated a higher EA (2.79) than was obtained from the May and June Scirpus site. As seen in Fig. 1a, however, peak attenuation again occurred above 3000 Hz. The main difference

Table 1. Two way ANOVA results for pure tone attenuation at the four dates (May, June, July 1976 in Scirpus, and June 1977 in Typha).

Source of Variation	Sum of Squares	df	Mean Square	¹ F
Frequency	4895	2	2447	529
Date	1554	3	518	112
Frequency x Date	5459	6	910	197
Error	5497	1188	5	

1. All results are significant ($p < 0.001$).

between the readings in Scirpus and Typha was the higher EA for middle frequencies in the latter vegetation type.

Low frequencies of 200 to 600 Hz showed similar EA values at all sites, ranging from 0.09 (Scirpus during May) to -1.08 dB/dd (Typha during June). Attenuation rates were usually close to the theoretical rate of 6 dB/dd.

Effect of Vegetation

The variation of EA by date of testing appears to be related to plant characteristics. Plant height, density, and mean number of leaves in relation to EA are shown in Fig. 2. Only the emergent stands, where water was present were used. For all characteristics there tends to be an increase in attenuation with plant growth. The strongest trend was shown between plant height and EA (Fig. 2). Although the number of sites tested was too few to permit statistical testing of the trends, the data are consistent with the view that attenuation increases as plants mature during the early summer.

Vocalizations

Analysis showed a significant difference in EA between calls ($F_{3,76} = 194, p < 0.001$). Attenuation of twitters was double that of any other call type (Fig. 3). It appears

Figure 2. Plant characteristics and corresponding values for mean Excess Attenuation averaged for all tones. Values for EA were determined for May and June, 1976, and June, 1977.

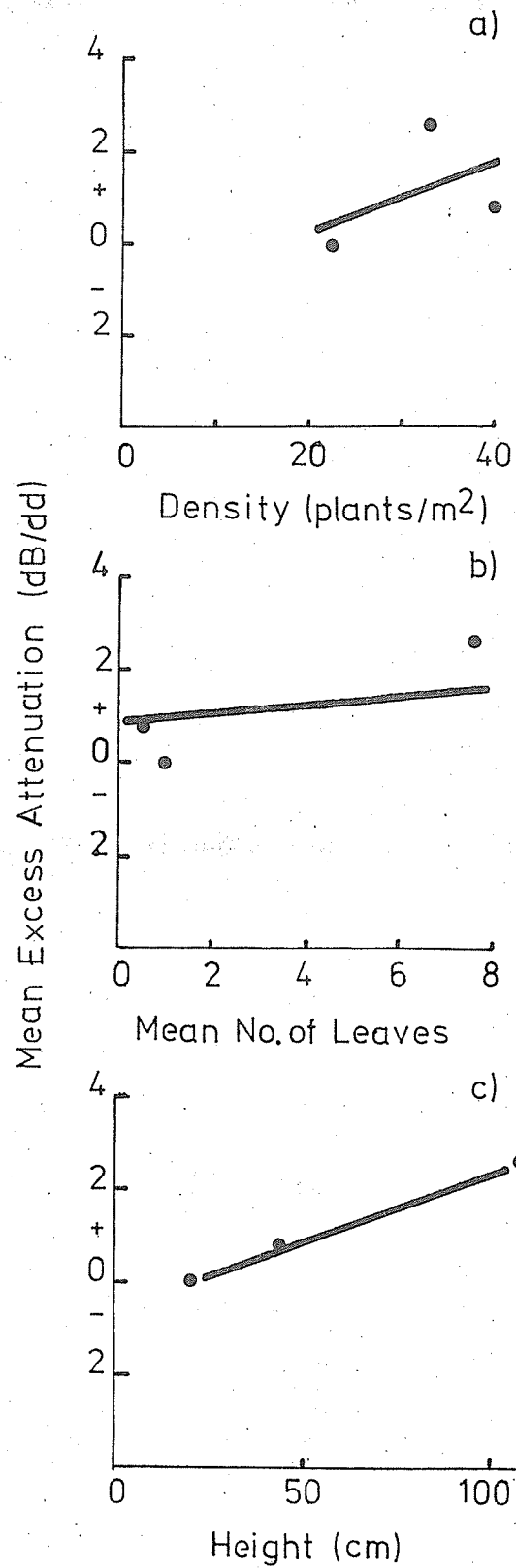
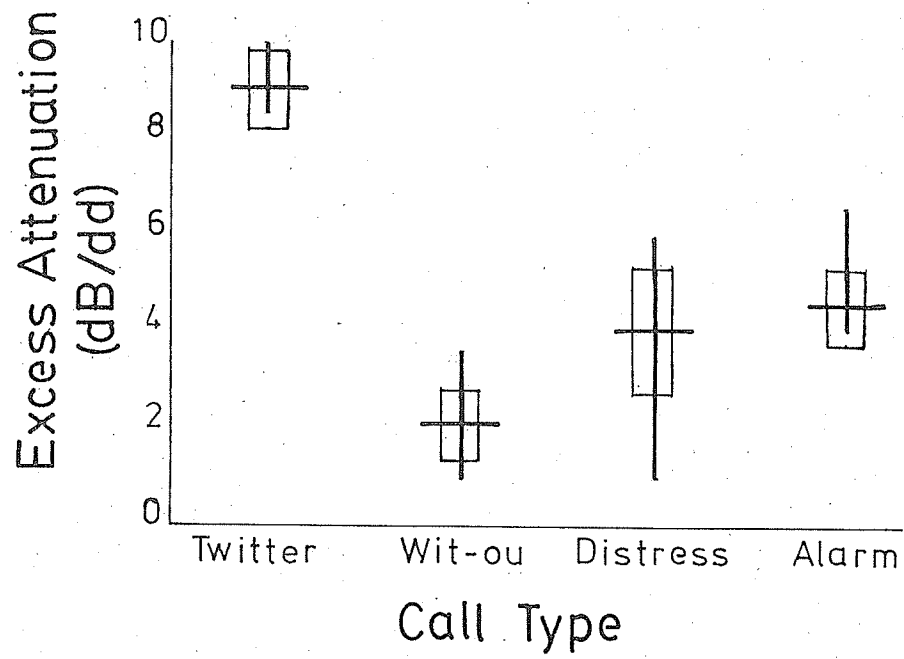


Figure 3. Mean Excess Attenuation of four major call types of young coots when broadcast through Typha at Delta Marsh in June, 1977. Horizontal lines are means, vertical lines are ranges, and boxes are standard deviations.



that twitters carry less well through Typha than do the distress, wit-ou, and alarm calls of young coots.

Since measurement of calls was done at the same time as pure tones in the Typha site, the two groups of data are comparable. Table 2 shows the mean frequencies associated with call types tested. Fig. 4 shows the frequency levels of calls recorded at the test site. Comparison of EA values in Fig. 1 with frequency levels listed in Table 2 and shown in Fig. 4 indicates that call attenuation followed the same frequency dependence as tones. Higher frequencies as in the twitter, attenuated more rapidly than lower frequencies as are present in distress, wit-ou, and alarm calls.

Discussion

Calls differing in pitch show a corresponding difference in attenuation. Attenuation of calls follows the same pattern as that of pure tones of similar frequency.

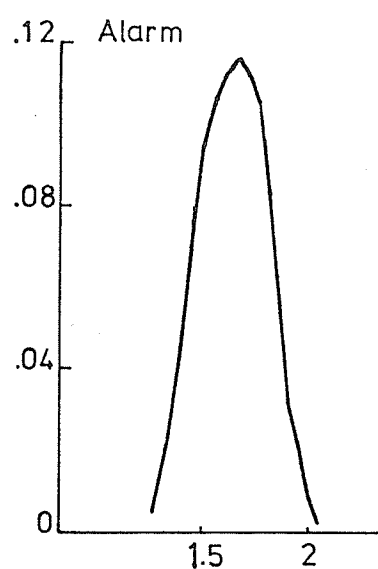
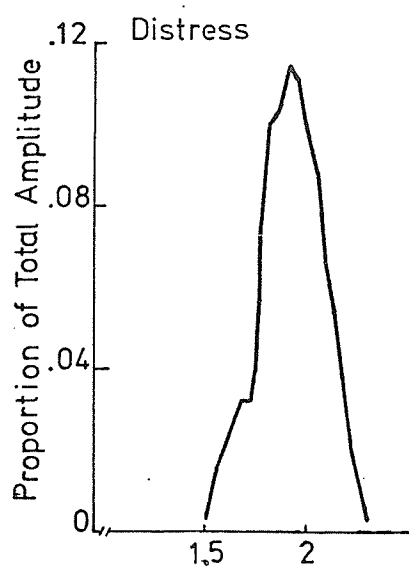
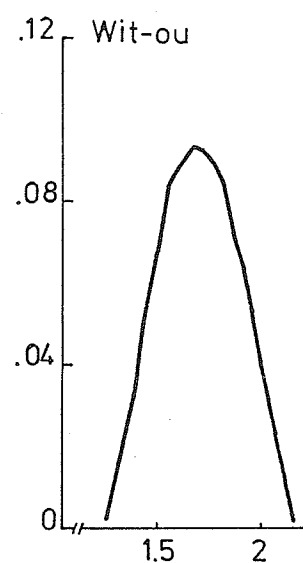
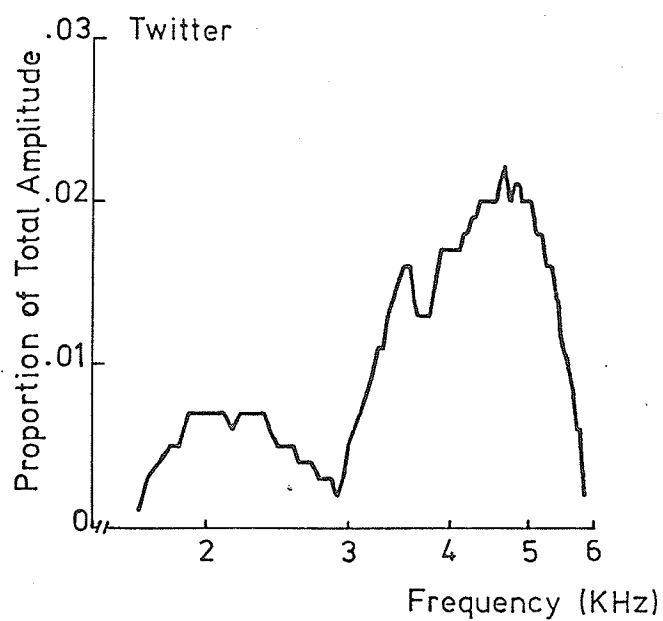
Contrasting transmissibility of calls appears to be related to their function and therefore to their required broadcast distance. The functional significance of twitter and distress calls has been discussed by several authors. Kaufman and Hinde (1961) state that distress calls are evoked by aversive stimuli and by social isolation. Kruijt (1964) suggests that twitters are associated with no overt

Table 2. Frequencies of major call types
of young coot (All calls were
measured from sonagrams).

Call Type	N	Mean Frequency (Hz)	
		Upper	Lower
Twitter	40	5473(1147) ¹	1870(490)
Wit-ou	20	2777(713)	989(216)
Distress	28	1953(203)	1347(223)
Alarm	45	1796(133)	1038(260)

1. Values in parantheses are standard
deviations.

Figure 4. Relative amplitudes of frequency bands within the four call types of young coots recorded at 30 cm from the loudspeaker at the Typha site.



Frequency (KHz)

signs of escape behaviour while distress calls are associated with hunger, cold, escape, and isolation. Collias and Joos (1953) describe twitters as 'contentment notes'. Observations of coot chicks indicated that twitters are given when broods are together, undisturbed, and that distress calls are evoked by social isolation. Twitters are of low intensity, while distress calls are of high intensity.

The context of the wit-ou call is not completely clear. While it may be given when with broodmates, it is often given in isolation and grades into the distress call (Part A), indicating that it may have a contact function. Alarm notes are associated with escape and defense responses when birds are held in the hand. Like distress calls, they are given with high intensity, and appear to function to elicit parental aid.

Wilson (1975) states that volume and frequency of calls seem designed to reach individuals of concern and no others, and that broadcasting beyond this provides an unnecessary homing beacon for predators. This seems to be the case for twitter calls of young coots. Short broadcast distance for twitters would reduce the chance of predators localizing broods. Predators to be avoided would most likely be mammalian, as avian predators would most likely use visual rather than auditory cues (Shalter and Schleidt 1977). While actual data on predation of

coots are limited, studies suggest that mammalian predation is higher than avian predation. Stout and Cornwell (1976) reported that the occurrence of mammalian predation of waterfowl is 3 to 4 times higher than avian predation. Sowls (1955) found that predation of young coot by mink (Mustela vison) was widespread. Since the use of auditory cues by predators would enable localization of broods, reduction of these cues would have survival value.

The distance of transmission of the other three call types is greater than that of the twitter. The distress and alarm calls seem especially important for either regaining auditory contact or eliciting parental aid. In each case, calls would have to carry some distance for parents to hear the signals. Thus the structure of the twitter call appears to reflect selection for short broadcast distance, while structure of other calls appears to reflect selection for distance transmission.

Marsh habitat appears conducive to transmission of sound frequencies below 2000 Hz as EA was usually near zero or negative in that frequency range. Low attenuation may be due to water acting as a reflective surface. Aylor (1971) found that smooth crusted soil produced less attenuation than porous soil, and that attenuation occurred at higher frequencies (600 to 800 Hz) for crusted soil. This effect of substrate appears to explain results obtained for July, 1977 at the dried Scirpus site. Peak attenuation

occurred at lower frequencies than when water was present during May and June, and the mean EA for all frequencies was higher when the site was dry.

In discussing the effect of vegetation on sound transmission, it must be pointed out that results represent attenuation patterns from only 2 sites in the marsh. A more accurate study would involve testing in several more sites where breeding coots occur. However, since results from the 2 sites which were used tend to agree, it seems reasonable to predict that further replications would produce similar data.

In emergent stands of vegetation the frequency dependence of sound attenuation remained similar over time. In all cases peak attenuation apparently increased in response to plant growth. Frequencies below 700 Hz were most stable, showing near zero attenuation for all tests even in the absence of water as a substrate. They were least affected by environmental conditions such as plant growth and water level.

The relationship between density of vegetation and EA can be attributed in part to an effect of plant species. Density values in Fig. 2a of 22.7 and 39.9 plants/m² are for the Scirpus site. Here an increase in density corresponds to a small increase in mean EA. The intermediate density value of 32.6 plants/m² is for the Typha site. The relatively high mean EA value for this site indicates

that plant characteristics other than density affect sound transmission. Mean number of leaves per plant may be a major factor as Fig. 2b indicates that the greater value for Typha (7.6 leaves/plant) corresponds to a high mean EA.

Any correlation between plant density or number of leaves per plant with mean EA would be affected by a third factor, plant height. Plants below the level at which readings were taken (44 cm) would presumably have a minimal effect on sound transmission, as was the case for May, 1976. As a result, the effect of density and leaves would be minimal, at least on direct sound waves. A better measure would have been to take plant density and number of leaves at or above 44 cm as correlates with EA.

Plant characteristics, other than the ones measured, probably affect attenuation of sound in the marsh. Embleton (1966), in a study of attenuation by cylinders, noted that attenuation was directly proportional to the size of the cylinders. He also noted that surface hardness affected attenuation rates, with hard cylinders attenuating high frequencies, and soft cylinders attenuating low frequencies. In a marsh habitat, stems could be classed as hard surfaces which tend to scatter high frequencies. The effect of stem size would in itself be minimal, but increasing the density of plants results in increasing the number of scattering surfaces. Attenuation should then increase as a function of frequency (Embleton 1966). Results agree

with this hypothesis, in that peak attenuation occurred at 2000 to 5000 Hz. The reduced attenuation of the highest frequencies tested may have resulted from the effect of water as a reflecting surface.

Data did indicate that plant growth affected sound transmission, in that as plants increased in density, height, and number of leaves, sound attenuation increased. All sites containing emergent vegetation showed similar frequency responses with high frequencies attenuating more rapidly than low or middle frequencies.

Summary

To trace vocal development in American Coots, from hatching to adulthood, calls of both laboratory-reared and wild birds were recorded and analyzed. Four main calls were used by chicks after hatching. These included the twitter, wit-ou, distress, and alarm calls. Major changes in the vocal repertoire began at about 1 month of age. These changes involved a dropping of the twitter and alarm calls from the repertoire, an increased use of distress calls, and the onset of sexual dimorphism in voice. At the juvenile stage, laboratory-reared coots used three call types. The 1- and 2-note recognition calls were apparently derived from the wit-ou, and the juvenile distress call was apparently derived from the distress call of chicks. Analysis of recorded calls of wild, breeding adults indicated that most adult calls are derived from the recognition notes of juveniles. Only two call types appear to be derived from the distress call. When compared with results from studies done on other species, both altricial and precocial, coots appear to follow a pattern of vocal development similar to typical precocial species.

In Part B, distress calls of laboratory-reared coots were recorded at 2 days, 8 to 15 days, and 21 to 28 days of age. Calls were then analyzed to determine whether call characteristics provided potential cues for both individual

and brood recognition. Brood differences were found for call length and minimum frequency. Individual differences were found for call length, minimum frequency, maximum frequency, and frequency range. Individual variation, however, resulted in similarities between some of the birds for all characteristics analyzed. It was concluded that no single call characteristic is sufficient to distinguish individuals, but that combinations of cues could result in complete differentiation of birds.

Evidence from song birds indicates that the frequency of song may be adapted to the species habitat such that transmission of sound is maximized. Some calls of young coots (wit-ou, distress, and alarm) normally function over greater distances than the twitter. The hypothesis that high pitched twitters would attenuate more rapidly than other lower pitched calls was tested. Attenuation of pure tones was measured in coot breeding habitat during May, June, and July 1976, and during June 1977. Pure tones, measured over water, showed highest attenuation for frequencies above 2000 Hz, which corresponds to the main frequency range of the twitter call. Attenuation of actual vocalizations varied with call type. High pitched twitters attenuated more rapidly than other lower pitched calls, probably reflecting differences in call function and required transmission distance. Measurements of plant characteristics indicated that attenuation increased with plant growth.

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