THE DEVELOPMENT OF VOCAL COMMUNICATION IN THE LAUGHING GULL (*LARUS ATRICILLA*)

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ABSTRACT OF THE THESIS

The Development of Vocal Communication in
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The development of vocal communication in the Laughing Gull (*Larus atricilla*) is discussed from two perspectives. The physical parameters of vocalizations given by both captive and wild birds from hatching through sexual maturity are described. This analysis demonstrates that there is a continuity in form of the emerging Laughing Gull vocalizations. The early chick calls are either monosyllabic, monofrequency vocalizations or multisyllabic, multifrequency vocalizations. This division is maintained throughout the Laughing Gull's vocal development.

The communication function of both chick and juvenile calls is also described. From observations of Laughing Gull chicks on their nesting grounds, it was found that the chicks' vocalizations meet their age-specific needs. Chick vocalizations give information of the chick's likelihood to interact and feed, and are modified to provide location information. Juveniles were studied in Panama. Results of these observations demonstrate that juveniles primarily give aggressive vocalizations, allowing them to successfully compete with adults for limited resources.

The findings of this study support the contention that the ontogenetic path of a display behavior represents a compromise between an individual's immediate and future communication requirements.

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INTRODUCTION

My thesis will describe the development of vocal communication in the Laughing Gull (*Larus atricilla*). I will trace the acquisition of the adult repertoire along with an analysis of the communication function served by pre-adult calls. The findings of this study will support the contention that the ontogenetic path of a display behavior represents a compromise between an individual's immediate and future communication requirements. Specifically, I will show that although all pre-adult vocalizations of the Laughing Gull can be classified within a progression forming the adult repertoire, each pre-adult vocalization is specially suited to meet the individual's age-specific needs. Underlying this analysis is my belief that natural selection acts on the form and function of displays at all stages of development to ensure an individual's reproductive success.

Early ontogeny studies were initiated during the nature-nurture debates with the hope of describing the roles of inheritance and experience in the expression of behavior patterns. Although some studies focused on the emergence of motor patterns, such as the pecking response in gulls (Tinbergen and Perdeck, 1950; Hailman, 1967) or the development of species-specific recognition (Lorenz, 1935, 1937; Gottlieb, 1971), the majority have examined the emergence of display behavior. The term display, originated by Huxley (1914) to describe the signalling movements of Great-crested Grebes (Podiceps cristatus), has been used by ethologists to designate those behaviors which "in physical form and frequency subserve social signal function" (Moynihan, 1956). Underlying the analysis of displays, has been a recognition since Darwin's The Expression of the Emotions in Man and Animals (1872) that communication behavior is adaptive and results from natural selection. Inherent in the word "adaptive" is the assumption that the form and function of a display must benefit the communicator by increasing his inclusive fitness (Hamilton, 1964). The selective tuning of a display was known to occur both through inherited acquisition of fixed motor patterns and individual learning processes.

Early ethologists were particularly aware of the inherited component of displays. By focusing on detailed comparative studies they attempted to understand the evolutionary history of display patterns as well as the selection pressures responsible for the observed behavior. Work by Whitman (1919) on pigeon behavior and Heinroth (1911; as cited in Brown, 1975) on the Anatidae were the first to demonstrate that behavioral traits were associated with phylogenetic relationships. This idea was later elaborated, and the term "homology," borrowed from comparative anatomy, was used to designate behaviors hypothesized to be similar in form due to a common ancestor. Investigators used homologies to correct and reclassify various groups of birds (Moynihan, 1959; Johnsgard, 1965).

Comparative studies also helped to focus on environmental factors which come to bear on displays. Classic examples now include Crook's analysis of the weaver birds (Ploceidae, 1964), Nelson's examination of the Sulidae (1975) and the numerous studies of the family Laridae (Cullen, 1957; Tinbergen, 1959; Beer, 1966a). From patterns of similarity and difference among closely related species, these investigators were able to hypothesize and then test the adaptive significance of display behavior.

With the awareness that displays must evolve, ethologists attempted to trace the evolutionary path of a display. They hypothesized that displays originated primarily from directly functional acts which provided socially useful information (Smith, 1977:313; Huxley, 1966; Tinbergen, 1952, 1962). The term "ritualization" (Tinbergen, 1952) was developed to name the process by which a display differentiates from its evolutionary precursor. Elaboration or exaggeration of frequency, intensity, or repetition of movement or structure were ways in which ethologists speculated that directly functional motor patterns gained signal function (Tinbergen, 1952; Moynihan, 1955a, b, c; Morris, 1956; Bastock, 1967). Several types of motor patterns were assumed to account for most display precursors, among them thermoregulatory or respiratory behavior such as feather ruffling in birds (Morris, 1956). Incomplete behaviors or "intention movements" (Daanje, 1950) such as preparatory locomotor acts (Meyerrieck, 1960; Baerends and van der Cingel, 1962), "redirected" behaviors onto substitute objects such as the elaboration of a redirected attack to form the swoop-and-soar display of the black-headed gull (Larus ridibundus; Moynihan, 1955a) and "displacement acts" (Tinbergen, 1940; Kortland, 1940 as cited in Hinde, 1970) observed in courtship and agonistic situations such as preening movements in the courtship displays of ducks (McKinney, 1965; Johnsgard, 1960).

Although the evolutionary path of a display can only be a matter for conjecture, ethologists (e.g. Blest, 1961) through comparative studies and analyses of the origin of displays, demonstrated their interest in the phylogenetic history of communication behavior as well as its adaptive value. The concepts of ritualization and homology underline the recognition by ethologists of the inherited basis of communication and the vital role displays serve in social behavior.

Recently, investigators have examined the specific form of a display and its adaptive qualities. In particular, analyses of avian vocal displays have shown that the parameters of a display are finely tuned to its function. Marler (1955) was the first to hypothesize that the structure of bird calls was a result of natural selection. He discovered a convergence in the form of both alarm and mobbing calls which he speculated resulted from an attempt to respectively decrease or increase the locatability of the communicator. Marler found that alarm calls were primarily single frequency calls, that began and ended gradually with no syllabic quality. Mobbing calls, however, were found to have a wide frequency range, syllabic quality and sudden onset and termination. By analyzing the ability of predators to locate different types of sound (Erulkar, 1972; Konishi, 1973; Knudsen and

Konishi, 1979; Knudsen et al., 1979) and the transmission of sound through a variety of habitats (Morton, 1970, 1975; Wiley and Richard, 1978; Marten and Marler, 1977; Marten et al., 1977; Roberts et al., 1979; Roberts et al., 1981; Martin, 1981) exploration into the adaptive features of avian vocalizations has both supported Marler's original contention and related other qualities of bird calls and singing behavior to the ecological constraints of the communicator's environment.

Thus, it has been established that displays are adaptive and can be inherited like other species-specific traits. However, findings such as the necessity for many birds to hear their own species calls for complete vocal development led ethologists to study the role of experience in the manifestation of displays.

Influential work by Lorenz (1935, 1937) on imprinting sparked an interest in examining the acquisition of species-specific preference and behavior (for reviews see Bateson, 1971; Hess, 1959, 1973). Lorenz felt that imprinting represented a special type of learning restricted to a "critical period" in an individual's life.

Unfortunately Lorenz's work established a belief that a dichotomy existed between inheritance and learning in the acquisition of a behavior. Although Lorenz's views were strongly contested (Lehrman, 1955, 1970) his influence remained substantial.

Out of the nature-nurture controversy arose numerous studies on vocal development in birds. The ontogeny of bird vocalizations has been thoroughly studied for several reasons. With the advent of the sound spectrograph or sonagraph, bird vocalizations could be analyzed with greater precision and reliability than other forms of display patterns (Marler, 1969). Also, attractive were the possible parallels between birdsong and human speech development (Marler, 1970; Nottebohm, 1970) including lateralization of neural control (Nottebohm, 1971, 1972a), the overproduction of syllables during early stages of song development (like the babbling of human infants, Marler and Peters, 1981) and similarities to linguistic grammar in bird vocalizations (Beer, 1975, 1976).

Most enticing of all however, were results from early experiments showing striking species differences in the amount of learning needed for vocal development, encouraging scientists to believe that this research would clarify the role of inheritance and acquisition of a motor pattern. Isolation experiments showed that environmental factors have little influence on vocal development in most species of birds (Konishi, 1963; Nottebohm and Nottebohm, 1971) and cross-breeding experiments demonstrated that a bird's genome could determine its vocal pattern (Lade and Thorpe, 1964). However, vocal learning was shown to be important in four groups of birds: the Passeriformes, hummingbirds, parrots and toucanets (Nottebohm, 1970, 1972b). The Passeriformes in particular attracted researchers to explore the roles of inheritance and experience in the acquisition of adult song. By manipulating the acoustic environment of young songbirds, much was discovered concerning birdsong development. The necessity for acoustical stimulation, either from parents or siblings was examined by isolating nestlings in sound-proof chambers (Marler and Tamura, 1964; Nottebohm, 1969a; Rice and Thompson, 1968; Thorpe, 1958). Tapes of normal or altered adult song were presented to determine which components of adult song may be needed for song learning (Dittus and Lemon, 1969; Immelmann, 1969; Lemon, 1975; Marler et al., 1972). Deafening young song birds demonstrated the role of auditory feedback in the control and development of song (Konishi, 1965; Marler and Waser, 1977; Nottebohm, 1968).

From these studies it was found that song birds have "critical periods" in which they learn species-specific calls and that the timing and duration of these critical periods varies between species. Associated with this finding was the development of the "Auditory-Template" theory by Marler (1976) to explain the selective responsiveness of a young bird to particular patterns of acoustical stimulation and the subsequent modification of its vocalization to its model.

Researchers also found that song birds pass through stages of song development representing increasing complexity and completeness of the song (Marler, 1956). Three basic phases of this developmental process were generally recognized: subsong, plastic song and crystallization of the full song (Konishi and Nottebohm, 1969). Although new song components could be added during the early stages of vocal development, it was found that once full song was reached the song pattern could not be altered.

Therefore, the emphasis in these studies was to describe the stages of vocal development in terms of the end product: adult song.

Since adult song plays a major role in crucial social activities including territorial defense, attraction of a mate and maintenance of the pair bond, the acquisition of the components of adult song is relevant to the bird's later reproductive success. For example, the discovery of cultural transmission of dialects, or similarities in the syllabic structure and sequence in songs of birds from a given geographic region (Baptista, 1975; Lemon, 1966; Marler and Tamura, 1962; Nottebohm, 1969b), suggests that bird song could play a role in reproductive isolation. If birds having one dialect remain in the same area to breed, and if females have a preference for a mate with the local dialect, a selective advantage for dialects might be to prevent panmixia between neighboring populations. Bird dialects, acting as markers, could quickly lead to assortative mating and local population adaptations (Nottebohm, 1969b). Recent experiments have shown that song structure can affect an individual's ability to procure a mate and territory as well as influence the choice of a mate (King et al., 1980; Searcy and Marler, 1981; Peters et al., 1980). The timing of the critical period in relation to forming flocks, therefore, could play a significant role in the acquisition of the appropriate dialect.

However, by stressing the importance of the acquisition of the appropriate motor pattern, the social aspects of song development were overlooked. Immelmann's (1969, 1972) studies which demonstrated that estrildid finches preferentially learn the song of a foster parent of another species over a tape of its own species song contradicted earlier findings that acoustic experience is sufficient for developing species-specific vocalizations and showed the importance of social interaction in the ontogeny of birdsong. Price (1979) has also shown the necessity for social bonding in the development of Zebra Finch (Taemopygia guttata) song and similarly Payne (1981) has found that Indigo Buntings (Passerina cyanea) match the song of a visible tutor in preference to one which can only be heard. A series of studies on the Cowbird (Molothrus ater) have demonstrated that a male's social and not acoustic experience determines the effectiveness of its song in eliciting female courtship response and the male's reproductive success (King and West, 1977; West and King, 1980; West et al., 1979, 1981). These studies illustrate the importance of social interaction in the determination of final adult song and highlight the communication function present at all stages of vocal development.

This failure to examine the social aspects of song learning is a reflection of an underlying problem in many ontogeny studies: every stage of development is not viewed as an adaptation necessary for the survival of the individual.

> Ontogeny is often intuitively regarded as having one terminal goal, the adult-stage phenotype, but the real goal of development is the same as that of all adaptations, the continuance of the dependent germ plasm. The visible somatic life cycle is the indispensible machinery by which this goal may be met, and each stage is as rightfully a goal as any other. (Williams, 1966:44)

Only recently have investigators examined the ecological and functional aspects of ontogeny to reveal the adaptive qualities of developing behaviors. For example, both Stamps' (1978) study of developing lizard behavior and Bekoff's (1972) analysis of the emergence of mammalian play, have demonstrated that viewing a juvenile as an incomplete version of an adult prevents the investigator from recognizing the often unique functions of pre-adult behaviors which reflect their age-specific needs. Beaver's (1978) study of the ontogeny of vocalizations in the Greater Rhea(*Rhea americana*) revealed a variety of chick vocalizations used for soliciting food and other forms of care. Unlike pre-adult songbird vocalizations, these calls did not develop into adult vocalizations but rather, call-note production was completely eliminated by seven weeks of age, leading to an adult vocal repertoire that consists of only very occasional vocalizations. Beaver suggests that this dramatic drop in vocal frequency is associated with a change from a dependence on vocal to visual displays and results from heavy predation pressure on chicks which is absent in adults. This example of behavioral regression demonstrates that chick vocalizations cannot be viewed solely as products without purpose or merely incomplete adult calls but also must be analyzed as adaptations serving the requirements of the individual at that time.

In the following chapters I will describe the ontogeny of vocal behavior in the Laughing Gull (*Larus atricilla*) by tracing the acquisition of the adult repertoire as well as examining the communication function served by the pre-adult calls. Through this analysis, I hope to show that each stage of the Laughing Gull's vocal development is an adaptation for immediate survival as well as a necessary precursor for succeeding stages.

The Laughing Gull is a member of the family Laridae (Dwight, 1925) and the sub-genus Xema or "primitive" hooded gulls (Moynihan, 1959a). There are 44 species of gulls in the family Laridae ranging from the Arctic to the tropics (Moynihan, 1959a).

Laughing Gulls are colonial ground nesters. Characteristically they nest on low-lying salt-water marsh islands along the Gulf and Atlantic coasts of North America (Bent, 1921; Klopfer and Hailman, 1965; Bongiorno, 1970). Their eastern breeding range has traditionally run from Maine to North Carolina, however, recent reports have noted colonies as far south as Florida (Southern, 1980; Dinsmore and Schreiber, 1974).

The choice of nesting habitat among gulls appears to be strongly influenced by predation pressure (Beer, 1966a; Buckley and Buckley, 1972; Burger, 1974; Cullen, 1960). The salt-marsh island is inaccessible to terrestrial predators (Montevecchi, 1975) and therefore represents a good choice for the ground nesting Laughing Gull.

However, the daily tidal flooding of the salt-marsh has been shown to be a serious threat to the ground nesting species in the salt marsh (Andrews, 1977; Montevecchi, 1975, 1978; Storey, 1978). Particularly during the spring tides, when the gravitational forces of a new or full moon act in consort with the sun, the unusually high tides can flood much of the marsh and threaten the survival of both eggs and young chicks. Montevecchi (1975, 1978) has demonstrated that nest-site selection among Laughing Gulls is determined by the marsh flooding, with areas the least susceptible to the destruction of the rising waters being the preferred nesting areas.

Two breeding colonies were observed for this study; a colony of approximately 2,000 breeding pairs in the Brigantine National Wildlife Refuge, New Jersey and an 11,400 pair colony in Stone Harbor, New Jersey. At both sites, the gulls nested on relatively homogenous salt-marsh islands consisting of meadows of Spartina grasses and irregularly interspersed tidal creeks, brackish pools and mats of hay.

Laughing Gulls are monogamous. Both the male and female help to construct the nest which is an elaborate bowl-shape formed from material collected from Spartina mats. Laughing Gulls lay between one and three eggs. The eggs hatch asynchronously resulting in a feeding hierarchy based on age and size differences among siblings which Hahn (1977, 1981) has found facilitates regular food distribution within the clutch and serves to increase the parent's overall reproductive success.

Preventing aggression towards newly arrived young and establishing a close relationship between parent and offspring has been recognized as a crucial and fundamental problem among many species (Rosenblatt, et al., 1979). The factors controlling the transition between incubation and parental behavior has been of interest in the Laridae. Beer has examined the behavior of adults during the pre-laying (1963a), incubation (1961,1962,1963b), and hatching periods (1966) in the Black-headed Gull(Larus ridibundus) and has found that external stimuli, such as the presence of chicks, primarily goven the timing and facilitate a switch from incubation to brooding. Impekoven (1973, 1976b) has found that Laughing Gull embryos have a preference for the familiar vocalizations of their parents prior to hatching and that this preference along with the responsiveness of adults to the calls of their chicks while still in the egg facilitate parental behavior and suppress aggression once the chicks hatch (1976b). Evans has examined the responsiveness of Ring-billed (Larus delawarensis; 1975a, 1977a, 1980b) and Herring Gull (Larus argentatus, 1975b, 1979) chicks immediately post-hatch to the calls of their parents and has found that the immediate and learned selectivity of the chicks towards adult vocalizations reflects both the environmental constraints of the nesting habitat and the need to facilitate a bond between parent and chick (1973, 1980b).

Laughing Gull chicks have been described as semi-precocial (Nice, 1962). This means that they are fully covered with natal down at hatching and have limited locomotory abilities. However, they restrict their early movements to the nest area and depend upon their parents for food and brooding. As discussed by Evans (1977b, 1980a) a semi-precocial mode of development represents a balance between conditions favoring reduced mobility, such as dependence on parents for vital food resources, and the ability to move quickly away from the nest site when exposed to predators.

Laughing Gull chicks can be described as passing through three developmental stages representing increased mobility from the nest.

Stage I is characterized by the chicks remaining predominately on the nest with at least one adult consistently present. Chicks are often being brooded and adults take turns both brooding and feeding the young. The adults regurgitate food they have collected to feed to their chicks. The parents hold the food in their bill and allow the chicks to peck at it. Hailman (1967) has demonstrated that the chicks' pecking movements stimulate regurgitation. Stage I lasts approximately 10 days post-hatch.

During Stage 2, the chicks are still in the nest area but no longer receive constant attention from the adults. Adults remain at the nest site primarily to feed the chicks. When the adults are away collecting food, the chicks stay hidden in the Spartina marsh grasses surrounding the nest. This period lasts from approximately ten days to three weeks post-hatch.

As has been described by Beer (1979), chicks and a newly arrived parent engage in vocal exchange which resembles an antiphonal duet. When an adult arrives at the nest or feeding area, it gives either a long-call (Noble and Wurm, 1943) or "ke-hah" vocalization (for description see Beer, 1970b). The chicks return with "chiz-ik" (Nice, 1962; Hailman, 1967) or "chirirah" (Beer, 1970a) calls. Both adult and chicks continue to vocalize as they approach each other. Once reaching the parent, the chicks switch to "peer" (Nice, 1962; Hailman, 1967) vocalizations as they solicit food.

Individual recognition of parental vocalizations has been shown in a variety of gulls (Black-billed Larus bulleri, Evans, 1970b; Ring-billed Larus delawarensis, Evans, 1970a) and serves to prevent chicks from approaching foreign adults and risking attack. Through playback experiments, Beer (1969, 1970a, b, c, 1972) has demonstrated that the long call of the adult has individual characteristics which are recognized by the chicks. From analysis of sound spectrograms, Beer discovered that the individually identifying part of the long call is the string of short notes at the beginning of the vocalization. The rate, duration and frequency modulation of each note as well as the number of short notes are constant for each individual but vary greatly between birds. Recognition of the components of the parent's long call appears to develop prior to 6 days post-hatch (Beer, 1972).

Beer (1973) has also found that adults direct their calls towards their chicks and other adults and that chicks can discriminate those long calls which are directed at them. By examining amplitude/time sonagrams of both adult-directed and chick-directed long calls, Beer (1975, 1976) found a consistent difference in the amplitude pattern of the short notes. The first one or two short notes of long calls directed at chicks are higher in amplitude than the rest; the reverse is found in long calls directed at adults.

Thus, Beer has demonstrated that the long call has a "signature" which appears to be learned by the chicks before six days post-hatch, and, in addition, the parameters of the long call can specify an address.

Tinbergen (1953) suggested that Herring Gulls (Larus argentatus) can individually recognize their chicks by five days post-hatch. The necessity for a gull to recognize its own chicks seems important in preventing feeding of unrelated young. However, in a series of experiments, Beer (1979) was unable to show parental recognition of Laughing Gull chicks. Davies and Carrick (1962) suggested that the onset of parent-young recognition should occur when brood mobility allows possible brood mixing. This hypothesis has recently been discussed by Evans (1980) in a review of parent-young recognition among seabirds and adds support that brood mixing and not the prevention of feeding unrelated young may be the determining factor controlling the development of parental recognition of chicks. Since Laughing Gull chicks do not form creches or associate extensively with other chicks until they have fledged, it is perhaps not surprising that parental recognition of chicks has not evolved.

After the chicks are three weeks post-hatch, they are considered Stage 3 chicks. During this period, many are observed congregating in shallow tidal pools with other chicks. Approximately four weeks post-hatch, the chicks fledge; however they often remain in the nesting area and continue to receive food from their parents for as long as 60 days of age (Burger, 1980).

By early fall most of the fledglings and adults leave the nesting grounds and return to their wintering grounds. Their wintering range runs from North Carolina to South America (Southern, 1980). For this study, juveniles were observed in Panama City, Panama. From November through March, both adults and juveniles can be found in large numbers around Panama City (Ridgely, 1976). The gulls are generally observed feeding in flocks on the schools of fish sporadically found in the bay during the dry season's upwelling. Flocking by Laughing Gulls is likely to be an adaptation to increase the efficiency of harvesting a clumped and unpredictable food resource (Cody, 1974; Hamilton and Watt, 1970; Murton, 1971; Rand, 1954; Ward and Zahavi, 1973; Zahavi, 1971).

During March and April, adult birds acquire their breeding plumage and begin courtship behavior. By the end of April most adults have left for their northern breeding grounds. Juveniles remain in their southern habitat for two years, not reaching breeding maturity until their third year post-hatch (Bent, 1921; Dwight, 1925). Delay in maturation has been speculated to be important in a variety of species to prevent young, inexperienced individuals from breeding until they can sufficiently feed their offspring without jeopardizing later clutches thus maximizing their eventual reproductive success (Ashmole, 1966; Case, 1978; Goodman, 1974; Lack, 1966).

Several aspects of the developing Laughing Gull's ecology are particularly relevant to their vocal ontogeny. First, the chicks' relatively long period of dependence on their parents for food and protection creates a situation in which vocal exchange is important. The chicks must rely on vocalizations to provide location information to their parents and for soliciting food and brooding. To achieve these goals, a close interaction must develop between parent and chicks which allows for efficient vocal communication. The "signature" and "chick-directed" version of the adult long call exemplify the necessity for an effective and responsive vocal system between chicks and their parnts. Also, as discussed by Beer (1973a, b, 1979) the dynamic quality of vocal communication between parent and chicks provides experience leading to competence in signal use at maturity. The function served by the chicks' vocalizations as a reflection of their unique needs and the chicks' developing vocal relationship with their parents will be described in Chapter 2.

The long pro-adult period during which juveniles must interact with others in competitive situations also necessitates development of effective vocal displays. As described in Chapter 3, the abundant use of vocalizations allows the juveniles to successfully compete for limited resources with more experienced adult gulls.

Chapters 2 and 3 will illustrate that the form and use of the pre-adult vocalizations are specially adapted to the needs they serve. However, the adult vocal repertoire is complex and the developing Laughing Gull must gain competence in both creating the adult vocalizations and using them appropriately. The structure of the emerging vocalizations will be described in Chapter 1 along with a discussion of message acquisition and signalling ability.

Finally, in Chapter 4, Laughing Gull chick vocalizations will be compared to those of Herring Gulls and Black-backed Gulls in order to test the functions speculated to be served by gull chick calls.

Through this analysis it should become evident that the ontogeny of vocalizations in the Laughing Gull is an adaptation for immediate survival as well as the necessary path to a complete adult vocal repertoire.

CHAPTER 1 - DESCRIPTION OF LAUGHING GULL VOCALIZATIONS FROM HATCHING THROUGH SEXUAL MATURITY.

Vocal ontogeny, though well-studied in songbirds (e.g. Thorpe, 1958; Mulligan, 1966; Lemon and Scott, 1966; Immelmann, 1969; Marler and Peters, 1977) has received little attention in the Family Laridae. Although Nice (1962) has described the development of motor patterns in a variety of gull chicks, Moynihan (1959b) has provided the only detailed description of the emergence of display patterns in gulls. Moynihan developed an "ontogenetic tree" to describe the development of both vocal and postural displays in the Ring-billed Gull (Larus delawarensis) and the Franklin's Gull (Larus pipixcan). In this study, Moynihan emphasized the concept of "ontogenetic ritualization", the process by which the chicks' display patterns become standardized both in form and signal function.

Unfortunately, Moynihan was able to examine in detail just those vocalizations given from hatching through fledging. He could only speculate on the stability of the juvenile vocalizations and on the important transition between juvenile and adult vocal patterns.

In this chapter the development of vocalizations in the Laughing Gull will be described from hatching through sexual maturation. Not only will I emphasize the physical parameters of the emerging vocalizations but also I will discuss the timing of their emergence as a possible method of evaluating their function.

The majority of the chick and juvenile vocal analysis is from field recordings of chicks hatched in two breeding colonies in southern

NewJersey, and of juveniles wintering in Panama. Observations of captive birds will be relied upon to describe the transition between juvenile and adult calls.

Part 1 - Vocalizations from Hatching Through Fledging

Methods

Observations were conducted during the 1977 and 1978 breeding season at the Brigantine National Wildlife Refuge and at Stone Harbor, New Jersey. I sampled three time periods.

(a) Stage 1 - Chicks and at least one of the adults were consitently on the nest. Chicks were often being brooded. This period lasted approximately ten days post hatch. Recordings were made at the Brigantine colony.

(b) Stage 2 - Chicks were still in the nest area but no longer received constant attention from the adults. Adults remained at the site primarily to feed the chicks. When the adults were away collecting food, the chicks stayed hidden in the *Spartina* marsh grasses surrounding the nests. This sample period was approximately ten days to three weeks post-hatch. These recordings were collected both at the Brigantine and Stone Harbor colonies.

(c) Stage 3 - Chicks in the Stone Harbor colony were observed after they had moved off their nest sites to a shallow tidal pool. As many as 30 chicks could be seen congregating at the pool at any one time. Chicks were making no attempt to hide when their parents were not present. Although most could fly, they still received food from adults. In addition to on-colony recordings this period also includes recordings of fledglings that were attempting to scavenge food from fishermen at the Stone Harbor Marina. This period was sampled for two weeks in August, 1978.

All Stage 1 and Stage 2 recordings were gathered from blinds constructed in the breeding colonies. Recordings were made at 7 ½ IPS on a Uher 4200 series tape recorder. The vocalizations were obtained using a Uher M516 microphone hidden in the Spartina grasses surrounding active nests or feeding areas. Stage 3 recordings made at the tidal pools were gathered in a similar manner from blinds located beside the pools. No attempt was made to avoid detection while recording fledglings scavenging for food at the Stone Harbor Marina. This appeared to have little effect on the birds' behavior.

Recordings were analyzed on a Kay elemetrics 6061B Sona-Graph using the wide-band filter on the .8 - 8 Khz. scale.

Over 800 sonagrams representing chicks from more than 30 nests were examined to determine the categories of vocalizations used by the chicks during each of the three stages. Once the categories of vocalizations had been determined one call per chick, or if individual identities were not known from a nest, one call per nest, were randomly chosen for each type of vocalization. Several parameters of the vocalizations were analyzed from these sonagrams. These included:

(1) Duration of Total Call - From beginning to end of continuous tracing in single note calls. All notes and intervals between notes included in multi-note vocalizations.

(2) Number of Syllables - A syllable was defined as a continuous trace on the sonagram with no abrupt changes and could be repeated in one call (Marler and Isaac, 1961; Marler and Tamura, 1962)

(3) Duration of Syllables

(4) Number of Distinct Frequencies in Each Syllable - Included three classifications:

(a) Presence of Harmonics - frequency bands at regular intervals

(b) Presence of Overtones - indistinct or irregular frequency bands

(c) Principal Frequencies - energy concentrated in one to three distinct frequency bands

(5) Frequency Modulation of Distinct Frequencies in Each Syllable - (adapted from whistle patterns of Atlantic Pilot Whales, Globicephala melaena - Taruski, 1979)

(a) Level - Any frequency inflections less than .5 Khz.

(b) Rising - frequency change upward of at least .5 Khz.

(c) Falling - frequency change downward of at least .5 Khz.

(d) Rise-Fall - frequency change upward then downward of at least .5 Khz. in both directions.

(e) Fall-Rise - frequency change downward then upward of at least .5 Khz. in both directions.

(f) Waver - at least two symmetrical frequency inflections around a mean frequency.

(g) Multiple Hump - at least two irregular frequency inflections.

(6) Distinct Frequency Range - Measured from lowest to highest point of distinct frequencies or range of harmonics and overtones.

(7) Rate of Repetition of Call - Where applicable - the number of calls per second.

Results

Stage 1 Vocalizations

During this period four types of calls are given by the

Laughing Gull chicks: "peer" (Nice, 1962; Hailman, 1967), "Chiz-ik (nice, 1962; Hailman, 1967)-chirirah" (Beer, 1970a), "cheeps" and "vireo". The two primary calls used by the chicks are the "peers" and "chiz-ik-chirirah" ("chz-chr") calls.

1. "Peers"

"Peers" are given by chicks even before they emerge from the egg (Impekoven, 1973). As discussed in Chapter 2, these calls are given by the chicks when they are attempting to solicit care, either in the form of food or brooding from their parents. "Peers" can be given singly, or more commonly, in bouts as the chicks peck at their parents bil or try to get under their parents' feathers. As the chicks grow older, bill-pecking develops into a "head-pumping" movement which is given in a horizontal posture and is not necessarily directed at the parent's bill.

Table I-1 summarizes the vocal parameters of the early "peer" calls. They are all monosyllabic, with a dominant frequency that usually shows a Rise-Fall pattern and ranges from a low of 2.0 Khz. (±14 S.E.M.-Standard Error of Mean) to 4.64 Khz. (±.15 S.E.M.). One-half of these "peers" had some overtones although they were of low intensity and added only slight harshness to the tone of the vocalizations.

Figure I-1-A shows several examples of "peer" calls during Stage I. As can be seen from these examples there is little variation between individuals in the form of the "peer" call.

The interval between "peers" and the duration of a "peer" bout seems to depend on the likelihood that a chick will accept food or

TABLE 1-1 - Analysis of Stage 1 "Peers"

Call Number	Total Duration (sec.)	Number of Syllables	Overtones-Harmonics	Frequency Range (Khz.) Low	High	Number of Distinct Frequencies	Pattern of Distinct Frequencies	Frequency Range Distinct Frequencies Low	High
1	.3	1	NP	-	-	1	d	1.5	4.5
2	.3	1	ov-sl	2.0	4.0	1	d	2.0	4.0
3	.35	1	ov-sl	1.0	3.5	1	f	1.0	3.6
4	.35	1	NP	-	-	1	d	1.5	4.5
5	.3	1	ov-sl	1.5	3.5	1	a	3.5	3.5
6	.3	1	NP	-	-	1	d	1.5	5.0
7	.35	1	ov-sl	1.0	3.5	1	d	2.0	4.5
8	.3	1	ov-sl	2.0	4.0	1	d	2.0	4.7
9	.25	1	NP	-	-	1	d	1.5	4.5
10	.32	1	NP	-	-	1	d	3.0	6.5
11	.3	1	ov-sl	2.5	4.0	1	d	3.0	5.0
12	.25	1	NP	-	-	1	d	2.0	4.0
13	.25	1	ov	2.0	8.0	1	d	1.5	4.8
14	.38	1	NP	-	-	1	d	2.5	5.0
15	.35	1	NP	-	-	1	d	2.0	5.3
16	.25	1	NP	-	-	1	d	2.0	5.0
17	.38	1	ov-sl	1.5	3.5	1	d	2.0	4.5
18	.35	1	ov-sl	1.5	3.5	1	d	2.0	4.5
19	.38	1	NP	-	-	1	d	1.0	4.5
20	.30	1	ov-sl	1.0	4.0	1	g	1.5	5.0

Key for Tables in Chapter 1

A. Overtones = ov

faint overtones = ov-sl

B. Harmonics = h

C. No Harmonics or Overtones = NP

D. Frequency Range - noted for:

1. overtones or harmonics
2. distinct frequencies in each syllable

E. Pattern of Distinct Frequencies in each Syllable

a. level
b. rising
c. falling
d. rise-fall
e. fall-rise
f. waver
g. multiple hump

numbers denote syllables which exhibit specific frequency pattern

For Table 8 - Juvenile Long Calls

A. each type of note is analyzed separately

B. Frequency Pattern

syllable number - harmonics - h - frequency shape
(1,2,3) overtones - o a.
b.
c.
d. (as designated
e. above)
f.
g.

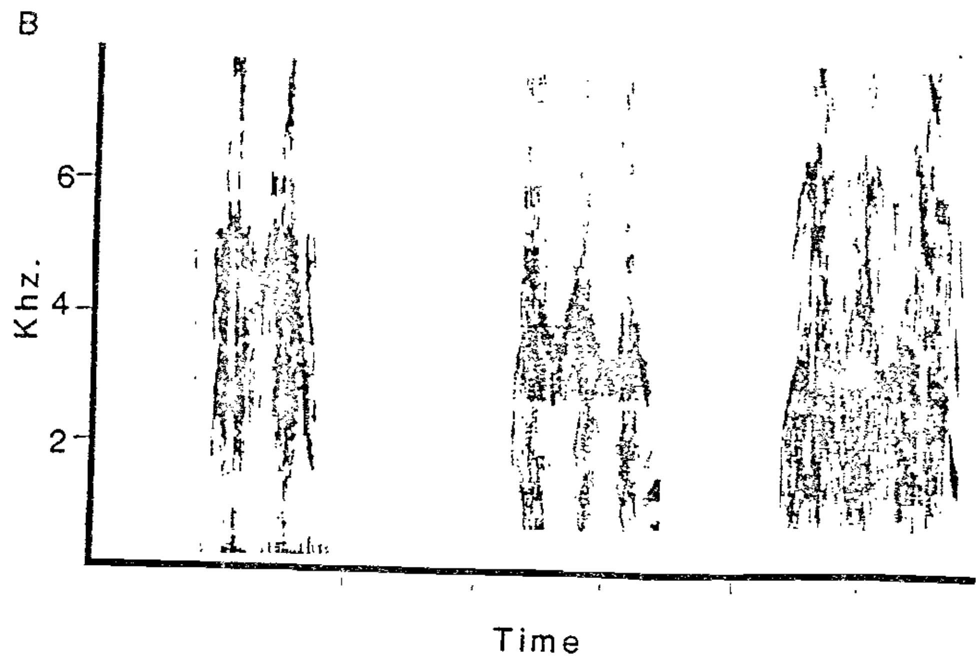
Figure I-1 - Sonagrams of Stage 1 Chick Vocalizations - I

A. "Peers"

B. "Chz-Chr"

note: time markings = .2 sec.


A
6
4
2
Khz.
Time


B
6
4
2
Khz.
Time

brooding. Chicks were often observed giving rapid "peers" ($>$ 3/sec.) just prior to accepting food, the rate dropping dramatically ($<$ 1/5 sec.) when the chick became sated.

As discussed in Chapter 2, characteristics of the "peer" call reduce the locatability of the call to a binaural animal. Specifically these include a single frequency that begins and ends gradually with no syllabic qualities (Marler, 1955; Konishi, 1973; Knudsen and Konishi, 1979; Knudsen et al., 1979). The relationship between these characteristics and the function of the peer call is described in Chapter 2.

2. "Chiz-ik-Chirirah"

"Chiz-ik-Chirirah" ("Chz-Chr") calls are given by the chicks soon after hatching during Stage 1. They are not given as frequently as "peer" calls, possibly reflecting their function of providing location information to their parents, vital, later in the breeding season (see Chapter 2 for elaboration on this point).

As can be seen from Table I-2 and Figure I-1-B "chz-chr" calls always have a syllabic quality. Syllables range from two to five but during Stage 1 "chz-chr" calls with two or three syllables are most commonly observed. The distinction between "chiz-ik" and "chirirah" calls depends solely on the number of syllables; "chiz-ik" calls have two syllables and "chirirah" calls anywhere from three to five during this stage.

A common feature found in the "chz-chr" call is a dominant frequency present in all syllables. Generally, this frequency is either Level or shows one inflection (either Rise-Fall or Fall-Rise). The

TABLE I-2 - Analysis of Stage 1 "Chz-Chr" Vocalizations

Call Number	Total Duration (sec.)	Number of Syllables	Overtones-Harmonics	Frequency Range(Khz.) Low	Frequency Range(Khz.) High	Number of Distinct Frequencies/Syllable 1	2	3	4	5
1	.25	3	ov	1.0	8.0	1+ov	1+ov	1+ov	1+ov	-
2	.2	2	ov	1.0	8.0	1+ov	1+ov	-	-	-
3	.3	3	ov	1.0	8.0	1+ov	1+ov	1+ov	-	-
4	.23	3	ov	1.5	8.0	ov	ov	ov	-	-
5	.2	2	ov	1.0	8.0	1+ov	1+ov	-	-	-
6	.15	2	ov	1.5	8.0	1+ov	1+ov	-	-	-
7	.25	3	ov	1.5	8.0	1+ov	1+ov	1+ov	-	-
8	.33	5	ov	1.5	8.0	1+ov	1+ov	1+ov	1+ov	1+ov
9	.25	4	ov	1.5	8.0	1+ov	1+ov	1+ov	1+ov	-
10	.23	3	ov	2.0	8.0	1+ov	1+ov	1+ov	-	-

TABLE I-2 - continued

Call Number	Frequency Range/Syllable 1		2		3		4		5		Primary Frequency Pattern (numbers=syllables with pattern)							Duration of Each Syllable			
	Low	High	Low	High	Low	High	Low	High	Low	High	a	b	c	d	e	f	g	1	2	3	4
1	4.0	4.5	4.0	4.5	3.5	4.0	3.0	4.0	-	-	-	-	-	-	1,2,3	-	-	.09	.06	.05	.05
2	2.0	2.5	2.0	2.5	-	-	-	-	-	-	2	-	-	1	-	-	-	.1	.1	-	-
3	2.5	3.3	3.0	3.0	1.5	2.5	-	-	-	-	2	-	-	1,3	-	-	-	.05	[illegible]	.05	-
4	no main frequency				-	-	-	-	-	-	-	-	-	-	-	-	-	.1	.03	.05	-
5	3.5	5.0	2.0	5.0	-	-	-	-	-	-	-	-	-	-	-	-	1,2	.1	.1	-	-
6	4.0	5.0	1.5	5.0	-	-	-	-	-	-	-	-	-	-	1	-	2	.08	.07	-	-
7	3.5	3.5	3.5	3.5	2.5	3.5	-	-	-	-	1,2	-	3	-	-	-	-	.11	.09	.05	-
8	3.5	5.0	3.5	4.5	4.7	4.7	4.7	4.7	4.7	2.0	3,4	-	5	1,2	-	-	-	approx. .07			
9	4.5	4.5	4.0	4.5	4.0	4.5	3.5	3.5	-	-	1,4	-	-	-	2,3	-	-	.07	.07	.06	.05
10	3.0	3.0	2.5	3.7	2.0	3.0	-	-	-	-	-	-	-	2,3	-	-	-	.1	.06	.07	-

mean frequency range is fairly constant throughout the call with no significant changes between syllables. (low- $p=0.503$; high- $p=0.911$).

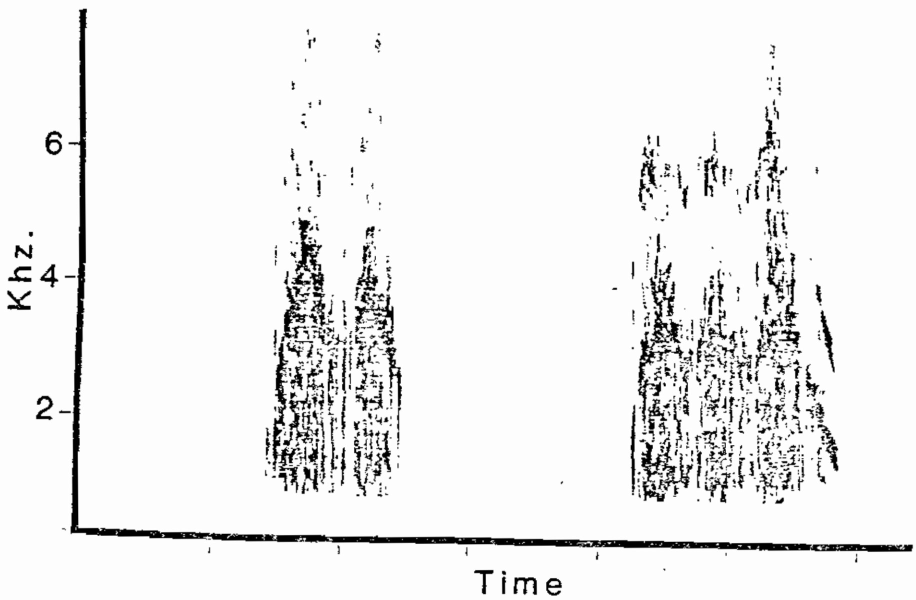
All the "chz-chr" vocalizations had overtones with a mean range from 1.35 Khz. (±.11 S.E.M.) to 8.0 Khz. (±0.0 S.E.M.) superimposed over the dominant frequencies. The overtones along with the syllabic nature of these calls, give the "chz-chr" vocalization a much harsher quality than the whistle-like "peer" vocalization. As discussed in Chapter 2, the wide frequency range, syllabic quality and sudden on-set and termination, increase the locatability of the "chz-chr" calls which may subserve their function.

Although the number of syllables in the "chz-chr" calls can vary, total duration shows little variability ($\overline{X}$ = .24 sec. ±.02 S.E.M.). Physiological constraints in the respiratory system very likely impose an upper limit on the length of a single vocalization. Calder(1970) has demonstrated by measuring respiration rate that the length of song in canaries (*Serinus canaria*) reflects these birds' respiratory needs. Similarly Nottebohm (1975) has shown that the song of *Zonotrichia capensis* is influenced by respiratory constraints by demonstrating an inverse relationship between song length and increasing altitude.

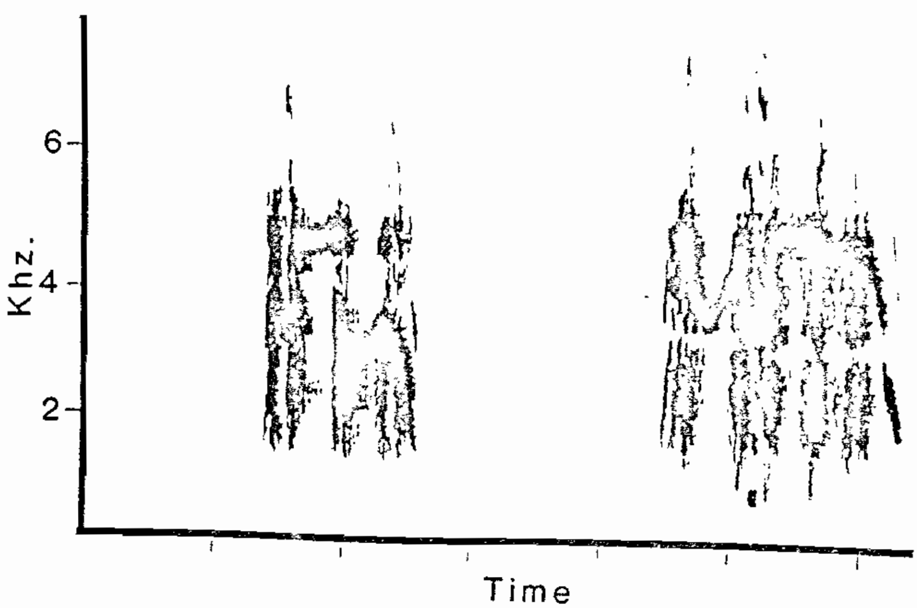
Individual chicks vary the number of syllables in their own calls (see Figure I-2). This can occur in the same vocal sequency with no obvious pattern. If providing location information is the primary function of "chz-chr" calls one would hypothesize that chicks should give calls with as many syllables as possible thus providing maximum location information. However, the number may be limited by the chick's

Figure I-2 - Sonagrams of "Chz-Chr" Vocalizations by Two Chicks

A



B



activity and physical capabilities, thus not representing a functional change in the call.

3. "Cheeps" and "Vireos"

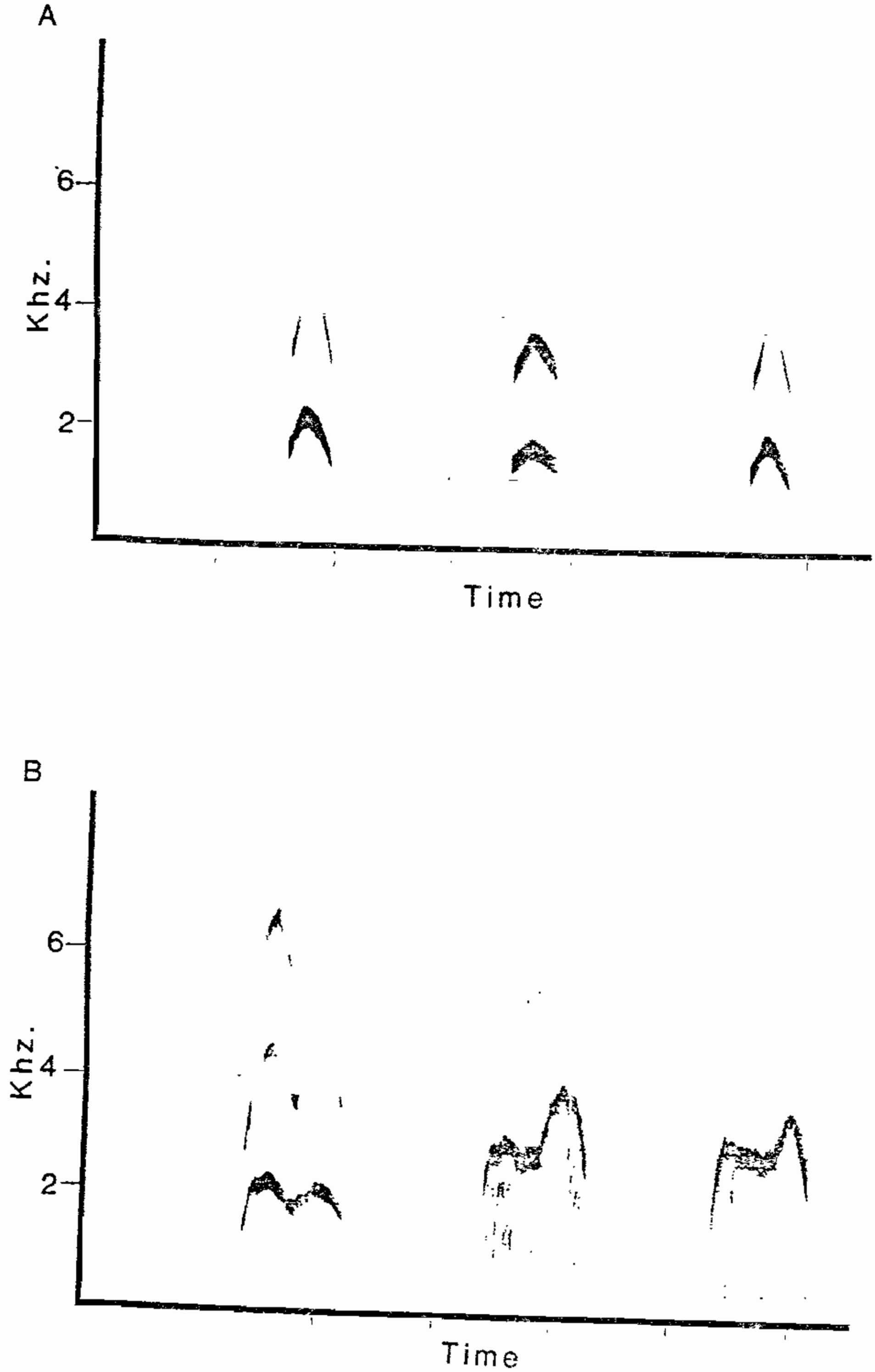
During Stage 1 two other types of vocalizations are given by chicks,"cheeps" and "vireos". Both calls are rarely heard after the first few days post-hatch. Examples of "cheeps" can be seen in Figure I-3-A. "Cheeps" look and sound very much like abbreviated "peers". The Rise-Fall pattern, characteristic of Stage 1 "peers",is contracted, giving the "cheeps" an abrupt quality(duration$\sim$.25 sec). Two primary frequencies are commonly observed in "cheeps" usually falling between 2-6 Khz. "Cheeps" are given in short, rapid bouts lasting only a few seconds and often precede or an intermingled with a bout of "peers". Their function is apparently similar to that of "peers", although this was difficult to determine as they were observed infrequently.

"Vireo" calls given during the first few days post-hatch have a Waver frequency pattern with two inflections (see Figure I-3-B). Energy is usually concentrated in one frequency in "vireos" with a low intensity second frequency that matches the primary's inflection pattern. The principal frequency falls around 3-5 Khz. with inflections up to 1.5 Khz. "Vireos" have a duration of approximately .2-.3 sec. The Waver pattern of the "vireo" gives this call a syllabic quality similar to the Stage 1 "chiz-ik" calls. For this reason, it seems likely that "vireos" are an early form of the "chz" vocalization in which the harshness and abrupt syllabic qualities are missing. Few chicks were observed giving the "vireo" leaving its function a mystery. It is possible

Figure I-3 - Sonagrams of Stage 1 Chick Vocalizations - II

A. "Cheeps"

B. "Vireo"


A
6
4
2
Khz.
Time
B
6
4
2
Khz.
Time

that it is just a poorly controlled "chiz-ik" call.

Stage 2 Vocalizations

1. "Peers"

Stage 2 "peers" though similar in many ways show some distinct differences from Stage 1 "peers". Head-pumping very commonly accompanies the Stage 2 "peers". Although Stage 2 "peers" are usually monosyllabic they can have two and occasionally three syllables (see Table I-3). The additional syllables are short introductory or concluding syllables (mean duration- .05 sec.=.01 S.E.M. for introduction). The introductory syllable usually has harmonics or overtones present (86%). The presence of overtones sometimes gave the "peer" call a harsh quality. In the field, these calls were often labelled "harsh peers" distinguishing them from "peers" but highlighting their similarity.

Although the Rise-Fall pattern is observed in a large percentage (40%) of the Stage 2 "peers", the Level pattern has become as common (44%) (see Fig. I-4-A). Also the duration of the Stage 2 "peers" (.38 sec = .02 S.E.M.) is significantly longer (p=.004) than that observed for Stage 1 "peers".

In general, Stage 2 "peers" closely resemble extended Stage 1 "peers" resulting in a longer duration with a reduction of the frequency modulation. Since the Stage 2 and Stage 1 "peers" are used in a similar manner (see Chapter 2), these alterations are probably a result of physiological changes within the growing chick which enable it to overcome physiological barriers in the length of the call, and do

TABLE I-3 - Analysis of Stage 2 "Peers"

Call Number	Total Duration (sec.)	Number of Syllables	Overtones-Harmonics	Frequency Range(Khz.) Low	High	Number of Distinct Frequencies/Syllable 1	2	3
1	.3	3	ov+h	2.5	8.0	1	1	1
2	.4	2	NP	-	-	1	1	-
3	.45	1	NP	-	-	1	-	-
4	.32	1	Ov	1.0	8.0	1	-	-
5	.35	1	ov	1.0	8.0	1	-	-
6	.3	1	NP	-	-	1	-	-
7	.35	1	ov	1.0	8.0	1	-	-
8	.32	1	NP	-	-	1	-	-
9	.32	1	NP	-	-	1	-	-
10	.5	2	ov	1.0	6.0	1	1	-
11	.4	1	NP	-	-	1	-	-
12	.3	2	h-(1)	1.0	7.0	H	1	-
13	.6	1	NP	-	-	1	-	-
14	.25	2	h-(1)	1.5	8.0	H	1	-
15	.35	1	ov	2.5	4.0	1	-	-
16	.35	2	h-(1)	1.5	4.5	H	1	-
17	.3	1	NP	-	-	1	-	-
18	.45	1	NP	-	-	1	-	-
19	.42	1	NP	-	-	1	-	-
20	.35	1	NP	-	-	1	-	-
21	.40	1	NP	-	-	1	-	-
22	.42	1	NP	-	-	1	-	-
23	.32	1	NP	-	-	1	-	-
24	.45	1	NP	-	-	1	-	-
25	.40	2	ov-(1)	1.0	8.0	ov	1	-

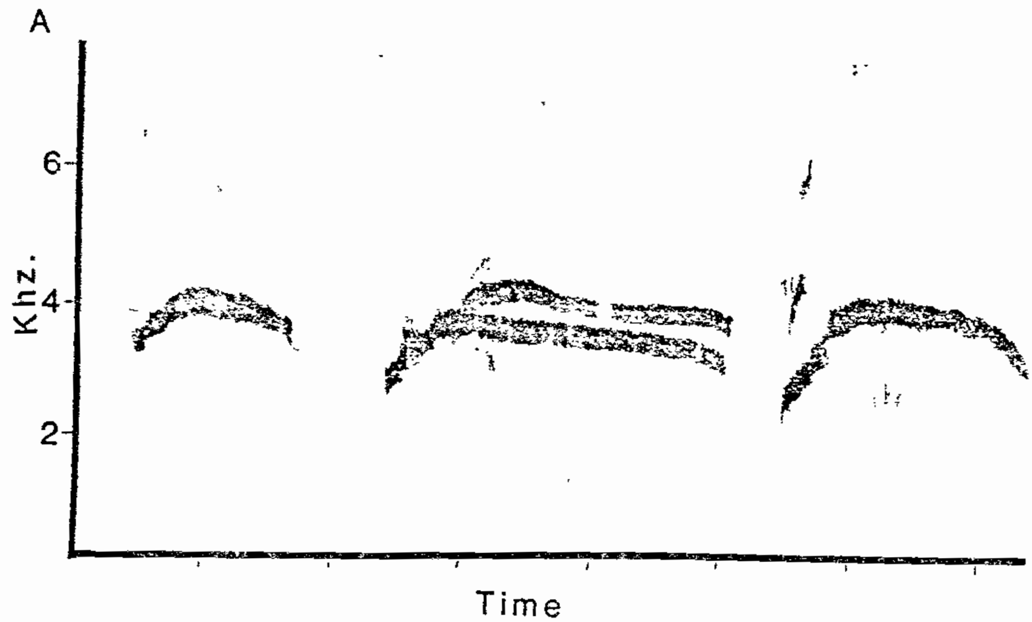
TABLE I-3 - continued

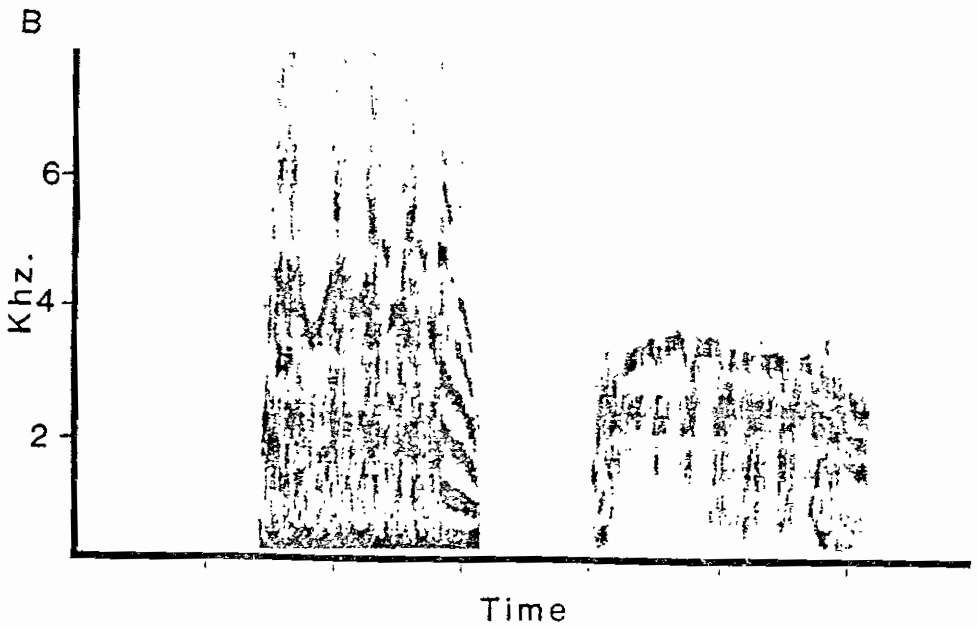
Call Number	Frequency Range/Syllable 1 Low	1 High	2 Low	2 High	3 Low	3 High	Primary Frequency Pattern a	b	c	d	e	f	g	Duration of Each Syllable 1	2	3
1	2.5	3.0	3.5	3.5	2.5	3.5	2	3	1	-	-	-	-	.07	.20	.03
2	3.0	4.2	3.5	4.2	-	-	-	2	1	-	-	-	-	.03	.38	-
3	4.0	4.0	-	-	-	-	1	-	-	-	-	-	-	.43	-	-
4	2.5	4.0	-	-	-	-	-	-	-	1	-	-	-	.32	-	-
5	2.5	4.0	-	-	-	-	-	-	-	1	-	-	-	.35	-	-
6	4.2	4.2	-	-	-	-	1	-	-	-	-	-	-	.30	-	-
7	3.5	3.5	-	-	-	-	1	-	-	-	-	-	-	.35	-	-
8	4.5	5.0	-	-	-	-	-	-	-	1	-	-	-	.32	-	-
9	2.5	4.5	-	-	-	-	-	-	-	-	-	1	-	.32	-	-
10	3.0	3.7	3.7	3.7	-	-	2	-	1	-	-	-	-	.05	.45	-
11	4.0	4.5	-	-	-	-	1	-	-	-	-	-	-	.4	-	-
12	H		3.0	4.0	-	-	-	-	-	2	-	-	-	.02	.28	-
13	4.0	4.0	-	-	-	-	1	-	-	-	-	-	-	.6	-	-
14	H	8.0	3.0	4.5	-	-	-	-	-	2	-	-	-	.05	.2	-
15	2.5	3.7	-	-	-	-	-	-	1	-	-	-	-	.35	-	-
16	3.0	3.0	3.5	4.0	-	-	1	-	-	2	-	-	-	.07	.28	-
17	3.0	4.0	-	-	-	-	-	-	-	1	-	-	-	.3	-	-
18	3.0	4.0	-	-	-	-	-	-	1	-	-	-	-	.43	-	-
19	3.5	4.0	-	-	-	-	-	-	-	1	-	-	-	.42	-	-
20	4.0	4.0	-	-	-	-	1	-	-	-	-	-	-	.35	-	-
21	3.5	3.5	-	-	-	-	1	-	-	-	-	-	-	.40	-	-
22	4.0	4.0	-	-	-	-	1	-	-	-	-	-	-	.42	-	-
23	3.0	3.7	-	-	-	-	-	-	-	1	-	-	-	.32	-	-
24	4.0	4.0	-	-	-	-	1	-	-	-	-	-	-	.45	-	-
25	ov		3.0	4.5	-	-	-	2	-	-	-	-	-	.05	.35	-

Figure I-4 - Sonagrams of Stage 2 Chick Vocalizations

A. "Peers"

B. "Chz-Chr"


A
6
4
2
Khz.
Time


B
6
4
2
Khz.
Time

not reflect functional changes of the call.

2. "Chiz-ik-Chirirah"

The basic pattern of Stage 2 "chz-chr" calls closely resembles that of Stage 1 "chz-chr" vocalizations. However there are important differences.

The mean total duration of "chz-chr" calls during Stage 2 (.38± sec. .03 S.E.M.) is significantly longer than Stage 1 "chz-chr" vocalizations ($p=.002$). (See Table I-4 and Figure I-4-B). Also, the variability of syllable number has increased in Stage 2, and ranges from 2-8. Since most of the syllables have a short duration ($<$ .07 sec.) similar to that observed in Stage 1 "chz-chr" calls, this increase in the overall duration of Stage 2 "chz-chr" calls is due to an increase in the number of syllables rather than extending the duration of individual syllables.

All of the Stage 2 "chz-chr" calls have either harmonics or overtones which usually range from 1-8 Khz. The mean dominant frequency range for Stage 2 "chz-chr" vocalizations is similar to that found in Stage 1. Level or Waver is the most common pattern of the principal frequencies in Stage 2 "chz-chr" calls like that found in Stage 1.

Overall, the Stage 2 "chz-chr" vocalizations resemble Stage 1 "chz-chr" calls with additional syllables. The lengthening of the "chz-chr" calls as the chicks grow older, like the lengthening of the "peer" vocalization, probably represents a physical change in the chicks' respiratory system and not a functional change of the call. As discussed in Chapter 2, the characteristics of these calls make them highly locatable which is a reflection of their use.

TABLE I-4 - Analysis of Stage 2 "Chz-Chr" Vocalizations

Call Number	Total Duration (sec.)	Number of Syllables	Overtones-Harmonics	Frequency Range(Khz.) Low	High	Number of Distinct Frequencies/Syllable 1	2	3	4	5+
1	.25	4	ov	1.5	8.0	1	-	-	-	-
2	.42	7	Ov	1.0	4.5	3	-	-	-	-
3	.55	8	ov	3.0	8.0	-	1	1	1	1 to end
4	.23	4	ov	1.o	8.0	1	1	1	1	-
5	.40	85	h(1+8) ov(2-7)	1.0	8.0	h	2	2	2	2 to last syllable=h
6	.25	7	h(1+7) ov(2-6)	1.0	8.0	h	1	1	1	1 to last syllable=h
7	.42	3	ov	1.0	5.0	-	1	1	-	-
8	.48	10	h=1 ov=2-10	h	1	1	1	1	1	1 to end
9	.35	7	ov	1.0	5.0	1	1	1	1	1 to end
10	.45	8	h=1	1.0	8.0	h	2	2	2	2 to end

TABLE I-4 - continued

Call Number	Frequency Range/Syllable 1 Low	1 High	2 Low	2 High	3 Low	3 High	4 Low	4 High	5 Low	5 High	Primary Frequency Pattern a	b	c	d	e	f	g	Duration of Each Syllable 1	2	3	4	5
1	3.5	4.0	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	.07	.06	.06	.06	-
2	2.5	4.0	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	.15 rest about .06				
3			4.0	4.0	4.0	4.0	4.0	4.0	-	-	2-8	-	-	-	-	-	-	all between .05-.1				
4	4.0	4.0	3.5	4.0	3.5	4.0	2.5	4.0	-	-	1	-	-	-	2,3	4	-	.03	.07	.05	.08	
5	h		2.0 3.5	6.0 6.5	2.0 3.5	6.0 6.5	2.0 3.5	6.0 6.5	same to end last=h		-	-	-	-	-	2-7	-	less than .08				
6	h		2.5	3.0	2.5	3.0	2.5	3.0	same to end last=h		2-6	-	-	-	-	-	-	less than .05				
7	h		3.5	4.0	3.0	4.0	-	-	-	-	-	-	-	-	-	2,3	-	.05	.07	.3	-	-
8	h		3.5	4.0	3.5	4.0	3.5	4.0	same to end last=h		-	-	-	-	-	2-10-		less than .05				
9	2.5	2.5	2.5	2.5	2.5	2.5	2.5	2.5	same to end		1	-	-	-	-	2-7		approx. .03				
10	h		3.5 3.5	6.5 6.5	3.5 3.5	6.5 6.5	3.5 3.5	6.5 6.5	same to end		2-8	-	-	-	-	-	-	approx. .03				

3. "Cheehah" (Beer, personal communication)

The "cheehah" vocalization is given only occasionally by Stage 2 chicks. Generally these vocalizations are heard when Laughing Gull chicks are acting aggressively toward an unrelated chick or adult. Characteristically when giving the "cheehah", chicks lift their carpels and raise their neck so the head is held high and the neck is vertical similar to an adult "upright" or the neck may be bent, bill pointing downward, in a position resembling that of choking in the adult (Beer, 1975).

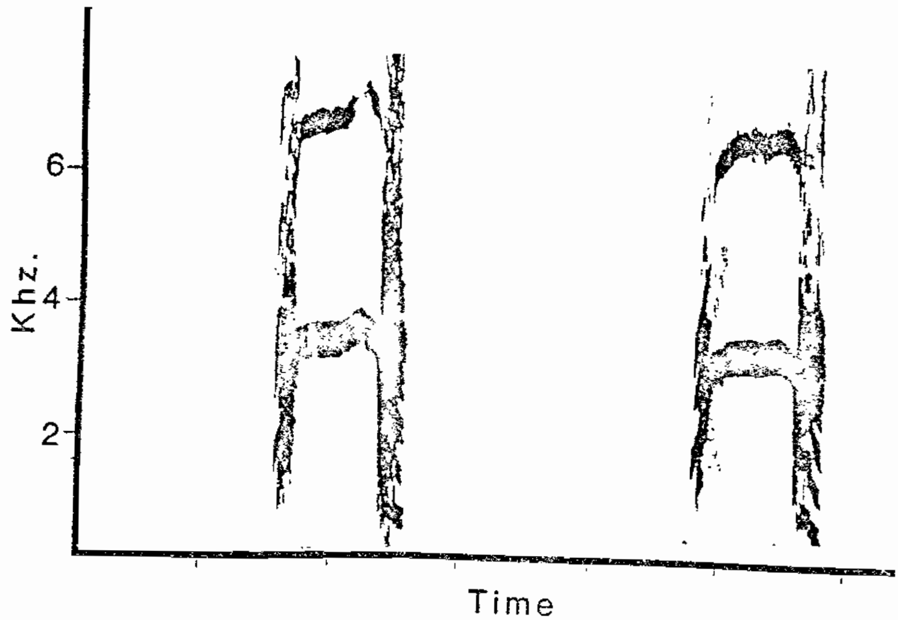
The "cheehah" is a three syllable harsh vocalization with a sharp onset and termination syllable and an extended middle syllable. As can be seen from Figure I-5, the introductory and concluding syllables have overtones ranging from 1 to 8 Khz. The middle syllable has one or two frequencies (approx. 3-4 and 5-6 Khz.) which are Level or slightly modulated. "Cheehahs" are usually given in abrupt, loud bouts approx. 2/sec.

The "Cheehah" somewhat resembles a "chz-chr" vocalization with an extended extended middle syllable. These vocalizations are not heard past fledging and thus appear to be restricted to aggressive encounters during the early stages of Laughing Gull vocal development.

Stage 3 Vocalizations

Stage 3 is a period of transition between chick and juvenile vocalizations. During this period, fledglings were regularly observed giving "peers" and "chz-chr" calls that did not differ from those described for Stage 2. However, Stage 3 Laughing Gulls were also

Figure I-5 - Sonagrams of the "Cheehah" vocalization


6
4
2
Khz.
Time

observed using vocalizations characteristic of older juveniles including "whines", "extended-awks" and the "juvenile long call".

Figure I-6 shows examples of chick vocalizations ("peers" and "chz-chr") given by Stage 3 fledglings. As can be seen, these vocalizations are very similar to those described for Stage 2 chicks. The variability in number of syllables and total duration of "chz-chr" calls is similar to that found in Stage 2. Also, the "peer" vocalization is extended and often has an introductory syllable with overtones ranging from 1-8 Khz. During this stage, these vocalizations seem to serve the same function as that described earlier for Stage 2. Chapter 2 discusses in greater detail the function of these calls.

Juvenile vocalizations are also given during this stage. As will be discussed in the following section the "extended awk" appears to be a derivative of the syllabic "chz-chr" vocalizations. The "whine" given by Stage 3 chicks is in form quite similar to the "peer" of Stage 1 and 2 but with a slightly altered frequency pattern.

The "juvenile long call", which will be discussed in the following section, has a rhythmic pattern which strongly resembles the adult long call (for description of adult see Beer, 1970a, but it lacks the highly structured harmonic pattern characteristic of the adult call. To the human ear, the "juvenile long call" sounds like a hoarse, squeaky adult "long call".

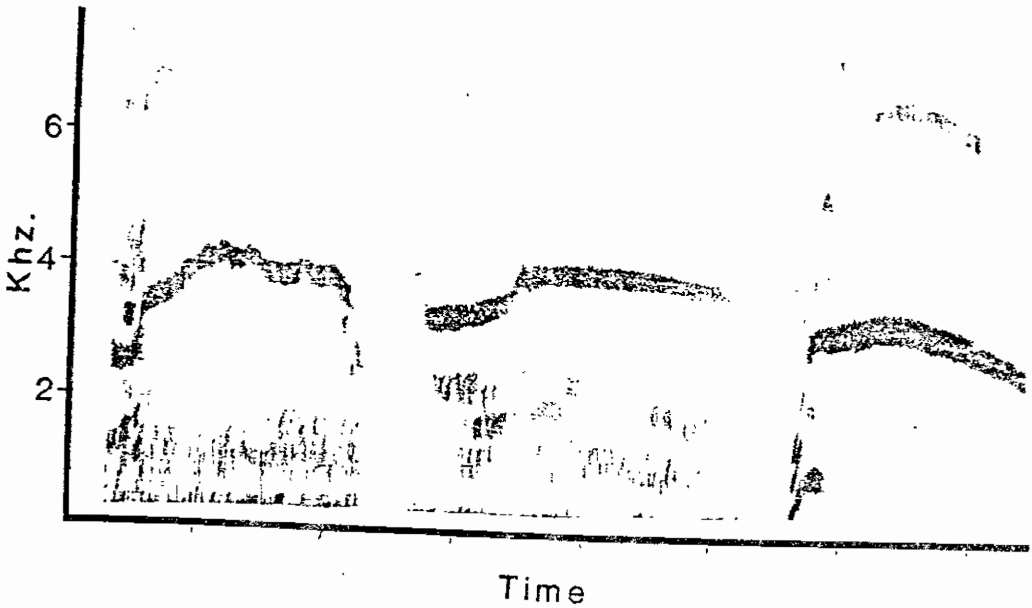
It is interesting to note when the juvenile vocalizations begin to appear in the Laughing Gull repertoire. As discussed in Chapter 3, the juvenile vocalizations are primarily aggressive vocalizations which

Figure I-6 - Sonagrams of Stage 3 Chick Vocalizations

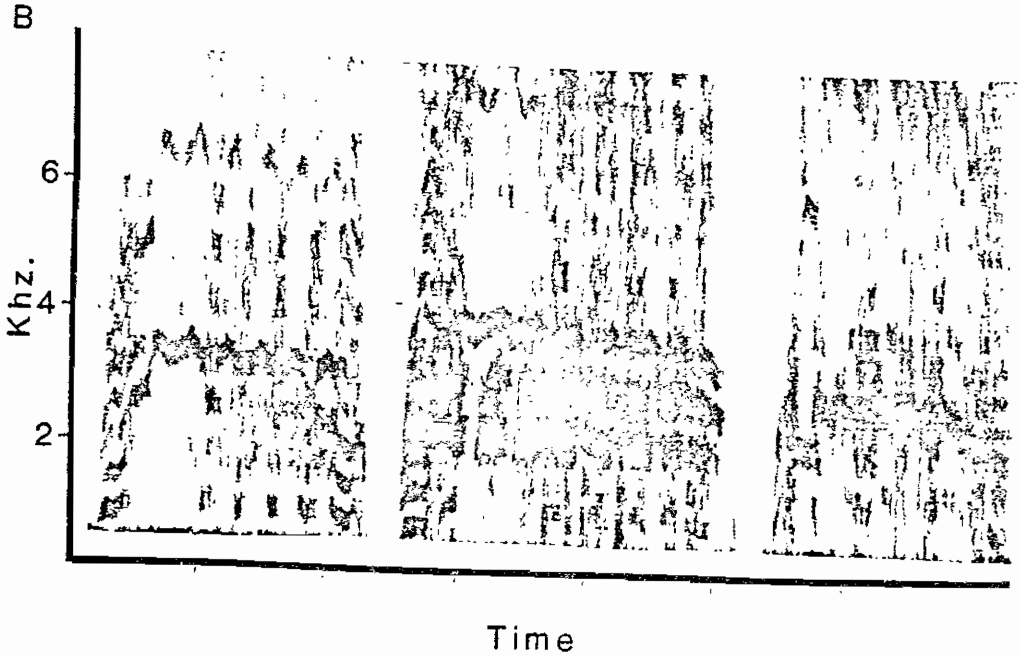
A. "Peers"

B. "Chz-Chr"

A



B



help the communicator compete for limited resources. During Stage 3, the fledglings were often observed in aggressive encounters, primarily with other fledglings. On numerous occasions fledglings were observed in the tidal pools defending either a small circular area around themselves or an object. Their behavior was quite similar to that later observed in juveniles feeding in the sewer streams (see Chapter 3). Like the juveniles, the fledglings gave gape-jabs with "extended awks" at other juveniles, who usually retreated. The "juvenile long call" was seen on a few occasions and seemed to be related to the retaining of a site.

Therefore, it appears that fledglings are capable of giving both chick and juvenile vocalizations. The use of these two classes of vocalizations by the fledglings is similar to that observed during the time when the vocalizations either originate or are most common. Thus, the fledglings' vocalizations represent a transition between chicks and juveniles both in form and function.

Part 2 - Juvenile Vocalizations - Field Observations

Methods

Field recordings of juvenile Laughing Gulls were restricted to first-year (1Y) juveniles whose plumage is distinctive from second-year and third-year or older, adult Laughing Gulls (Dwight, 1925). Vocalizations were collected from January through April 1979 in Panama. In this study, 1Y birds had hatched during the 1978 breeding season and were spending their first winter in Panama. Most of the recordings were from 1Y birds feeding in three sewer streams that emptied into the bay of Panama City.

Vocalizations were gathered by connecting a Uher M516 microphone to a stake alongside a stream and recording ten to fifteen meters away on a Uher 4200 series tape recorder. The birds habituated to the microphone and observer within a few minutes.

Individual birds were observed for several minutes at a time. The observer spoke into a separate microphone noting the type of call given by the vocalizing 1Y bird. An attempt was made to record each bird only once during a daily recording session.

Recordings were analyzed using a Kay Elemetrics 6061B Sona-Graph by the method previously described for chick vocalizations.

One call per bird, per day was used in the statistical analysis of the sonagrams. Since the 1Y birds were not color-marked, there can be no assurance that the same bird was not recorded twice. However, since recordings were made from three sites and the recording location was rotated daily, the likelihood and effect of recording the same bird do not seem too great.

The vocal parameters that were examined are the same as those used in the analysis of the chick calls. As the 1Y vocalizations showed no apparent change during the four-month sampling period, the sonagrams were analyzed as one group.

Results

Four major types of vocalizations are given by juveile 1Y Laughing Gulls. These are: 1. "Squeak-Whines"=Squeak- Head-Toss"

2. "Extended Awks"

3. "Uks"

4. "Juvenile Long Call"

1. "Squeak-Whines" and "Squeak- Head-Toss"

"Squeak-Whines" were characteristically given by 1Y birds in a hunched posture. Often a "head-toss" would accompany a "squeak".

"Squeaks" are distinguished from "whines" only by total call duration. As can be seen from Table I-5, the duration of "juvenile squak-whines" can range from .07 sec. to .7 seconds ($\overline{X}$=.3 ±.02 S.E.M.). Vocalizations identified as "whines" have longer durations with slightly fewer overtones and reduced frequency modulation.

The majority of "squeak-whines" have two syllables (60%) usually, a short introductory note ($\overline{X}$= .05 sec. ±.01 S.E.M.) followed by a longer syllable ($\overline{X}$= .25 sec. ±.03 S.E.M.). Harmonics or overtones were observed in 74% of the introductory notes. One or two frequencies were most commonly seen in single syllable "squeak-whines" and the longer syllable of multi-syllable "squeak-whines". There is no significant difference between syllables' frequency range (low p= .33; high p= .89). As can be seen from Table I-5 and Figure I-7-A, the dominant frequency pattern in the majority of syllables is Level.

"Squeak-Whines" have a whistle-like quality similar to that described for chick "peer" vocalizations. With the exception of the short

TABLE I-5 - Analysis of Juvenile "Squeak" Vocalizations

Call Number	Total Duration (sec.)	Number of Syllables	Overtones-Harmonics	Frequency Range (khz.) Low	High	Number of Distinct Frequencies/Syllable 1	2	3
1	.2	2	h(1)	2.0	5.0	h	2	-
2	.3	1	-	-	-	2	-	-
3	.3	2	ov(1)	4.0	6.0	ov	3	-
4	.1	1	-	-	-	1	-	-
5	.25	1	-	-	-	1	-	-
6	.25	1	-	-	-	3	-	-
7	.07	1	-	-	-	1	-	-
8	.27	1	-	-	-	1	-	-
9	.25	2	-	-	-	2	2	-
10	.30	2	ov(1)	1.5	4.5	ov	1	-
11	.28	1	-	-	-	1	-	-
12	.25	2	-	-	-	1	2	-
13	.4	2	h(1)	1.0	5.0	h	2	-
14	.5	2	h(1)	1.5	5.5	h	2	-
15	.3	2	h(1)	1.5	5.0	h	2	-
16	.32	2	ov(1)	1.5	7.5	ov	4	-
17	.35	2	h(1)	2.5	5.5	h	1	-
18	.32	3	ov(1)	1.5	7.0	ov	4	2
19	.3	2	-	-	-	3	3	-
20	.42	1	-	-	-	3	-	-
21	.3	2	ov(1)	1,5	8.0	ov	3	-
22	.2	2	-	-	-	1	1	-
23	.2	2	ov(1)	2.0	7.0	ov	1	-
24	.18	2	-	-	-	2	2	-
25	.25	1	-	-	-	2	-	-
26	.17	2	ov(1)	2.0	5.0	ov	1	-
27	.5	2	ov(1)	1.0	6.5	ov	4	-
28	.7	1	-	-	-	2	-	-
29	.5	2	h(1)	1.5	6.0	h	3	-
30	.35	1	-	-	-	2	-	-

TABLE I-5 - continued

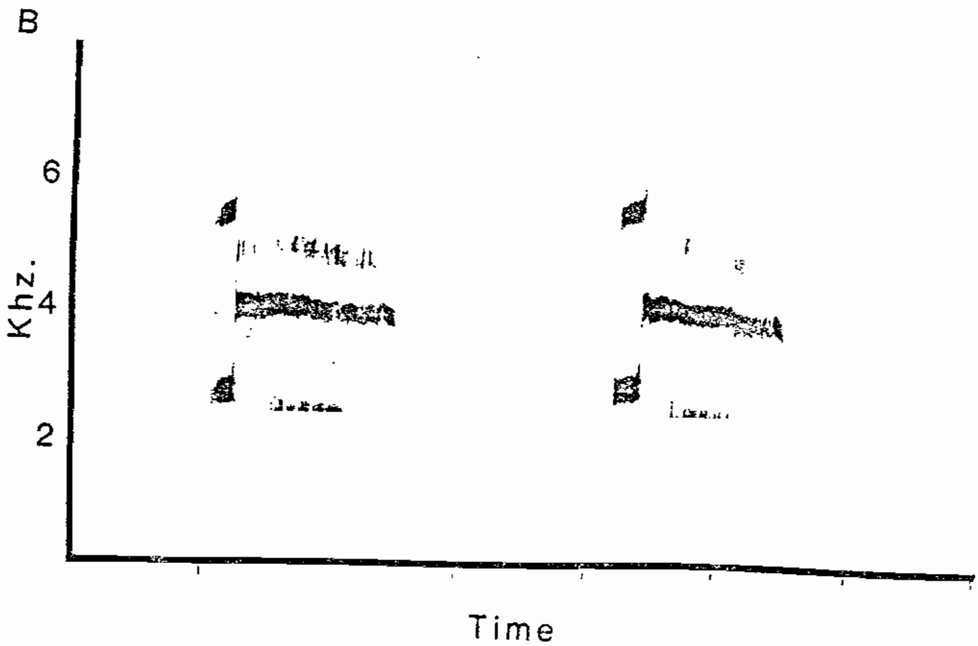
Call Number	Frequency Range/Syllable 1 Low	1 High	2 Low	2 High	3 Low	3 High	Primary Frequency Pattern a	b	c	d	e	f	g	Duration of Each Syllable 1	2	3
1	h		2.2	3.8	-	-	1	-	-	2	-	-	-	.05	.15	-
2	2.7	7.5	-	-	-	-	1	-	-	-	-	-	-	.3	-	-
3	ov		2.0	6.7	-	-	1	-	-	2	-	-	-	.05	.25	-
4	3.3	3.3	-	-	-	-	1	-	-	-	-	-	-	.1	-	-
5	3.8	3.8	-	-	-	-	1	-	-	-	-	-	-	.25	-	-
6	3.0	5.0	-	-	-	-	1	-	-	-	-	-	-	.25	-	-
7	4.0	4.0	-	-	-	-	1	-	-	-	-	-	-	.07	-	-
8	3.7	3.7	-	-	-	-	1	-	-	-	-	-	-	.27	-	-
9	2.4	3.8	2.2	4.8	-	-	2	1	-	-	-	-	-	.05	.20	-
10	ov		3.5	3.5	-	-	2	1	-	-	-	-	-	.05	.25	-
11	2.2	2.2	-	-	-	-	1	-	-	-	-	-	-	.28	-	-
12	5.0	5.0	2.5	5.2	-	-	2	1	-	-	-	-	-	.03	.22	-
13	h		3.0	6.0	-	-	2	-	-	-	-	-	1	.07	.33	-
14	h		2.0	4.5	-	-	2	-	-	-	-	-	1	.05	.45	-
15	h		2.0	4.5	-	-	2	-	-	-	-	-	1	.05	.25	-
16	ov		1.5	7.0	-	-	1	-	-	-	-	2	-	.02	.3	-
17	ov		4.0	4.0	-	-	2	1	-	-	-	-	-	.05	.3	-
18	h		1.5	7.0	2.5	5.0	3	1	-	-	-	-	2	.02	.12	.18
19	2.5	7.7	1.5	7.0	-	-	1	-	2	-	-	-	-	.07	.23	-
20	2.0	7.0	-	-	-	-	-	-	-	-	-	-	1	.42	-	-
21	ov		1.5	7.0	-	-	1,2	-	-	-	-	-	-	.05	.25	-
22	4.0	4.0	3.7	4.7	-	-	1	-	2	-	-	-	-	.13	.07	-
23	ov	-	4.0	4.0	-	-	1	2	-	-	-	-	-	.05	.15	-
24	2.5	7.7	3.5	6.8	-	-	1,2	-	-	-	-	-	-	.07	.11	-
25	3.5	7.5	-	-	-	-	1	-	-	-	-	-	-	.25	-	-
26	ov	-	4.0	4.0	-	-	1	-	-	2	-	-	-	.03	.14	-
27	ov		1.5	6.5	-	-	1,2	-	-	-	-	-	-	.02	.48	-
28	3.5	7.5	-	-	-	-	1	-	-	-	-	-	-	.7	-	-
29	h		1.5	4.5	-	-	2	1	-	-	-	-	-	.08	.42	-
30	3.5	7.5	-	-	-	-	1	-	-	-	-	-	-	.2	-	-

Figure 7 - Sonagrams of Juvenile Vocalizations - Wild - I

A. "Squeak-Whine"

B. "Squeak- Head-toss"


A
6
4
2
Khz.
Time


B
6
4
2
Khz.
Time

introductory note and a slightly higher frequency range, the "squeak-whines" in particular closely resemble the Stage 2 and Stage 3 chick "peer" vocalizations. However, as described in Chapter 3, the function of "squeak-whines" is not to solicit food or caregiving; instead they appear to be low-intensity aggressive calls. This change in function is not surprising since it was observed that the begging of Stage 2 and Stage 3 chicks was so incessant that the adults were forced to leave. Thus the chicks' begging call seems to have an aggressive component which later becomes the predominant message in the "squeak-whines".

"Squeak- Head Toss" vocalizations are quite similar to "Squeak-whines", excepting the end of the vocalizations, which is always accompanied with a "Head Toss." "Squeak- Head Toss" calls have a slightly shorter duration than "Squeak-whines" (.25 sec. ±.01 S.E.M.; $p= .026$). (See Table I-6 and Figure I-7-B). They are usually two syllable calls (63%) with a short introductory syllable (.07 sec. ±.01 S.E.M.). 12% of the "squeak-head toss" calls have a third syllable which has a short duration (.08 sec. ±.03 S.E.M.). Overtones or harmonics are visible in 40% of the introductory notes. The second and third syllables have one or two primary frequencies with a range similar to that of "squeak-whines." They usually have a Level form.

The function of the "squeak-head-toss" appears to be similar to "squeak-whines." The function of the "Head-toss" remains obscure, as it is in adults (Beer, 1973a), although it often seems to occur when a juvenile is turning away from another bird, and may represent a slightly

TABLE I-6 - Analysis of "Squeak-head-toss" Vocalizations

Call Number	Total Duration (sec.)	Number of Syllables	Overtones-Harmonics	Frequency Range(Khz.) Low	High	Number of Distinct Frequencies/Syllable 1	2	3
1	.25	2	NP	-	-	2	3	-
2	.35	2	ov-(1)	2.0	5.5	ov	3	-
3	.25	1	NP	-	-	2	-	-
4	.25	2	ov-(1)	2.0	6.0	Ov	3	-
5	.25	2	NP	-	-	1	2	-
6	.28	2	NP	-	-	2	2	-
7	.3	2	NP	-	-	2	1	-
8	.25	3	ov(1)	1.5	7.0	ov	4	2
9	.27	3	NP	-	-	2	2	2
10	.25	2	NP	-	-	2	1	-
11	.2	1	NP	-	-	3	-	-
12	.27	2	h-(1)	2.5	4.0	h	2	-
13	.30	1	NP	-	-	2	-	-
14	.30	2	h(1)	2.5	5.7	h	2	-
15	.16	2	NP	-	-	3	2	-
16	.3	2	h(1)	2.5	5.5	h	2	-
17	.2	2	NP	-	-	3	2	-
18	.3	2	h(1)	1.5	6.5	h	2	-
19	.32	2	h(1)	2.0	4.5	h	1	-
20	.32	2	NP	-	-	3	2	-
21	.25	1	NP	-	-	2	-	-
22	.3	2	NP	-	-	2	2	-
23	.35	2	ov(1)	2.5	8.0	ov	2	-
24	.3	1	NP	-	-	2	-	-
25	.2	1	NP	-	-	2	-	-
26	.2	1	NP	-	-	4	-	-
27	.2	2	ov(1)	3.5	8.0	ov	1	-
28	.2	2	NP	-	-	3	2	-
29	.2	2	NP	-	-	2	2	-
30	.18	3	NP	-	-	2	2	1
31	.3	2	ov(1)	3.0	8.0	ov	1	-
32	.26	1	NP	-	-	1	-	-
33	.20	2	NP	-	-	3	2	-
34	.25	2	NP	-	-	3	2	-
35	.22	3	NP	-	-	3	1	3
36	.22	3	NP	-	-	3	2	1
37	.16	2	ov-(1)	2.5	5.0	ov	2	-
38	.19	2	NP	-	-	2	3	-
39	.28	1	NP	-	-	2	-	-
40	.25	1	NP	-	-	2	-	-

TABLE I-6 - continued

Call Number	Frequency Range/Syllable 1		2		3		Primary Frequency Pattern							Duration of Each Syllable		
	Low	High	Low	High	Low	High	a	b	c	d	e	f	g	1	2	3
1	3.5	7.0	2.0	6.0	-	-	1,2	-	-	-	-	-	-	.1	.15	-
2	ov		3.0	6.0	-	-	1	-	-	2	-	-	-	.05	.3	-
3	3.3	7.3	-	-	-	-	1	-	-	-	-	-	-	.25	--	-
4	ov		2.0	6.2	-	-	1,2	-	-	-	-	-	-	.05	.2	-
5	3.8	3.3	4.7	5.0	-	-	1	-	-	2	-	-	-	.05	.2	-
6	2.8	5.6	4.0	4.0	-	-	1,2	-	-	-	-	-	-	.05	.23	-
7	3.5	5.2	4.0	4.0	-	-	2	-	1	-	-	-	-	.05	.25	-
8	ov		1.5	7.0	2.0	6.0	1,2,3		-	-	-	-	-	.03	.2	.02
9	2.5	4.0	2.5	4.8	4.0	4.8	2,3	-	-	1	-	-	-	.07	.1	.1
10	2.5	7.2	4.5	4.5	-	-	1,2	-	-	-	-	-	-	.05	.2	-
11	2.5	7.0	-	-	-	-	-	1	-	-	-	-	-	.2	-	-
12	h		6.5	7.0	-	-	1,2	-	-	-	-	-	-	.07	.2	-
13	3.5	4.3	-	-	-	-	1	-	-	-	-	-	-	.3	-	-
14	h		3.5	6.8	-	-	1,2	-	-	-	-	-	-	.05	.25	-
15	2.2	6.7	2.9	6.7	-	-	1	2	-	-	-	-	-	.12	.04	-
16	h		3.0	6.0	-	-	2	-	1	-	-	-	-	.12	.18	-
17	2.5	7.5	3.7	7.5	-	-	2	-	1	-	-	-	-	.05	.15	-
18	h		3.0	6.2	-	-	1	-	-	2	-	-	-	.12	.18	-
19	h		3.2	3.2	-	-	2	-	-	-	-	1	-	.12	.20	-
20	2.0	7.5	3.0	3.5	-	-	-	1,2	-	-	-	-	-	.15	.17	-
21	2.0	4.5	-	-	-	-	1	-	-	-	-	-	-	.25	-	-
22	2.0	7.0	2.0	3.7	-	-	1,2	-	-	-	-	-	-	.2	.1	-
23	ov		2.0	4.0	-	-	1,2	-	-	-	-	-	-	.15	.2	-
24	3.5	7.0	-	-	-	-	1	-	-	-	-	-	-	.3	-	-
25	3.5	7.5	-	-	-	-	1	-	-	-	-	-	-	.2	-	-
26	2.0	7.6	-	-	-	-	1	-	-	-	-	-	-	.2	-	-
27	ov		4.0	4.0	-	-	-	2	1	-	-	-	-	.1	.1	-
28	2.5	4.7	2.2	4.5	-	-	1	2	-	-	-	-	-	.1	.1	-
29	4.0	4.5	2.2	4.5	-	-	-	-	1	2	-	-	-	.07	.13	-
30	2.5	5.0	4.0	5.7	4.5	4.5	1,2,3		-	-	-	-	-	.05	.1	.03
31	ov		4.0	4.0	-	-	1,2	-	-	-	-	-	-	.02	.28	-
32	4.0	4.0	-	-	-	-	1	-	-	-	-	-	-	.26	-	-
33	1.5	3.5	2.5	3.5	-	-	1,2	-	-	-	-	-	-	.04	.19	-
34	3.0	6.0	4.0	5.0	-	-	1,2	-	-	-	-	-	-	.05	.2	-
35	1.5	4.5	4.2	4.2	2.2	4.5	1,2,3		-	-	-	-	-	.02	.04	.16
36	2.5	4.0	2.0	4.5	3.5	3.5	1	2,3	-	-	-	-	-	.07	.07	.08
37	ov		2.5	5.0	-	-	-	-	1	2	-	-	-	.03	.13	-
38	3.5	6.7	2.0	4.5	-	-	2	-	1	-	-	-	-	.05	.14	-
39	3.5	7.5	-	-	-	-	1	-	-	-	-	-	-	.28	-	-
40	3.5	7.5	-	-	-	-	1	-	-	-	-	-	-	.25	-	-

reduced level of aggressiveness.

2. "Extended- Awks"

"Extended awks" are harsh vocalizations which have a multiple frequency Waver pattern (Table I-7 and Figure I-8-A). The total duration is not different from "squeak-whines" (.31 sec. ±.01 S.E.M.; p= .832). Single syllable "extended awks" are unusual (17%) with two syllable "awks" being most common (63%). The introductory syllable and the last syllable of four syllable "awks" are short (.08 sec. ±.01 S.E.M.). The remaining syllables are longer and do not differ from each other (p=.18).

Unlike "squeak-whines" and "squeak-head-toss" vocalizations, overtones and harmonics are not restricted to the first syllable but are found throughout the "awk" vocalization. Although the principal frequencies are often Level, the Waver pattern is quite common. The frequency range of the "awk" does not differ from the juvenile "squeak-whine".

The form of the "extended awk" resembles a less syllabic Stage 3 "chz-chr" vocalization, with a clearer frequency pattern. The "extended awk" has a richer quality than the "chz-chr" call because of the reduction in syllables and increase in distinct frequency bands. The function of the "extended awk", however, does not resemble that described for the "chz-chr" vocalizations. As discussed in Chapter 3, the "extended awk" is given in aggressive situations, and is used by juveniles to secure needed food and roosting sites quite different from the localizing function of the chick "chz-chr" calls. Also, unlike the "chz-chr"

TABLE 1-7 - Analysis of Juvenile Extended Awks

Call Number	Total Duration (sec.)	Number of Syllables	Overtones-Harmonics	Frequency Range(Khz.) Low	High	Number of Distinct Frequencies/Syllable 1	2	3
1	.2	2	h(1)	1.5	5.5	h	3	-
2	.5	2	h(1)	1.2	4.7	h	5	-
3	.3	2	h(1,2)	2.0	8.0	h	h	-
4	.37	2	h(1)	2.2	6.2	h	5	-
5	.30	3	h(1,3)	2.0	7.0	h	2	h
6	.3	1	ov(1)	1.0	8.0	ov	-	-
7	.3	1	ov(1)	1.0	6.0	ov	-	-
8	.35	2	h(1)	1.2	3.2	h	4	-
9	.3	1	h(1)	1.0	6.0	h	-	-
10	.3	1	h(1)	1.5	6.0	h	-	-
11	.3	2	h(1,2)	1.0	6.5	h	h	-
12	.3	2	h(1,2)	1.5	5.0	h	h	-
13	.35	3	ov(1,3)	1.0	5.7	ov	2	Ov
14	.35	2	ov(1)	1.5	6.5	ov	3	-
15	.3	2	ov(1)	1.0	8.0	ov	4	-
16	.2	2	h(1,2)	1.5	5.0	h	h	-
17	.2	2	h(1)	1.5	4.5	h	2	-
18	.22	3	h(1)	1.5	5.5	h	2	2
19	.25	3	h(1)	1.0	5.0	h	2	2
20	.3	2	h(1)	1.0	3.0	h	3	-
21	.32	2	h(1)	1.0	4.5	h	2	-
22	.45	2	h(1)	1.0	3.5	h	2	-
23	.3	2	h(1,2)	1.7	3.0	h	h	-
24	.28	2	h(1,2)	1.4	4.5	h	h	-
25	.35	1	h(1)	1.5	4.5	h	-	-
26	.3	2	ov(1)	1.5	7.0	ov	4	-
27	.22	2	h(1)	1.5	5.5	h	2	-
28	.32	2	ov(1)	1.5	7.0	ov	4	-

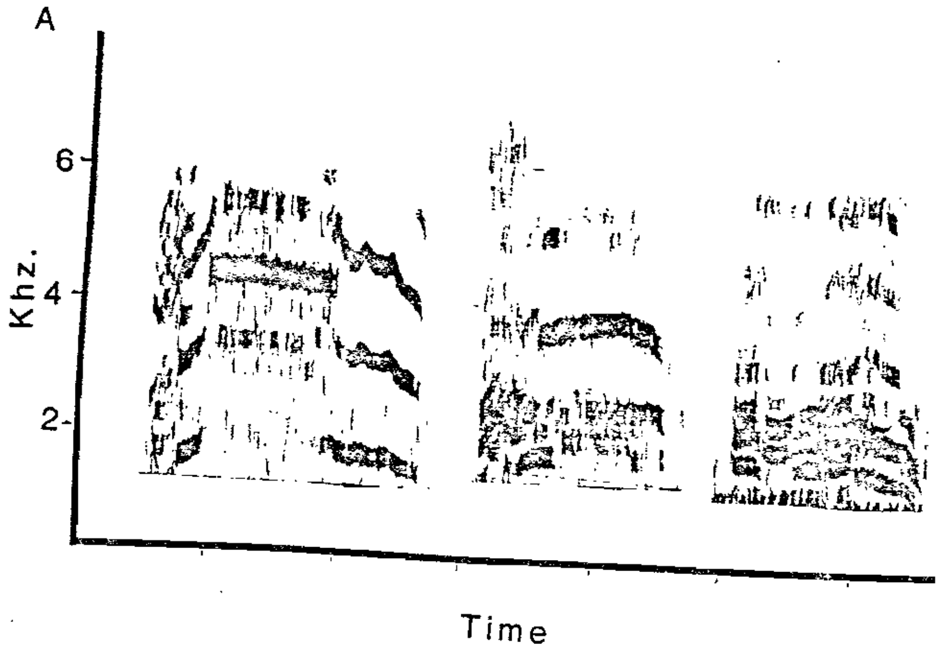
TABLE I-7 - continued

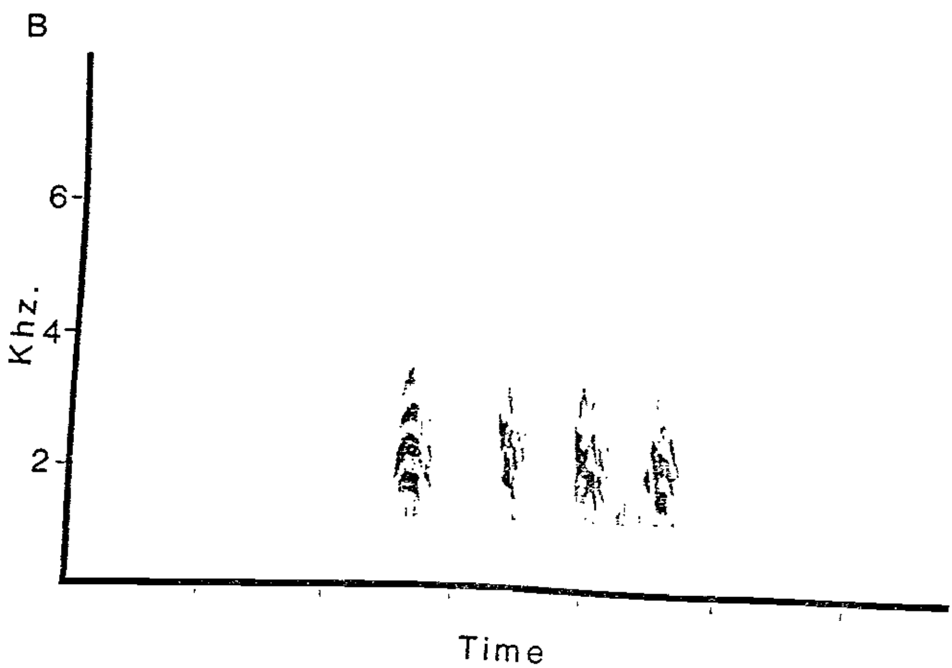
Call Number	Frequency Range/Syllable 1		2		3		Primary Frequency Pattern							Duration of Each Syllable		
	Low	High	Low	High	Low	High	a	b	c	d	e	f	g	1	2	3
1	h	-	2.0	6.0	-	-	2	-	-	-	-	-	1	.1	.1	-
2	h	-	1.2	4.7	-	-	1,2	-	-	-	-	-	-	.2	.3	-
3	h	-	h	-	-	-	1,2	-	-	-	-	-	-	.05	.25	-
4	h	-	3.2	6.7	-	-	2	1	-	-	-	-	-	.07	.3	-
5	h	-	3.5	7.0	-	-	1,2	-	3	-	-	-	-	.1	.1	.1
6	ov	-	-	-	-	-	-	-	-	-	-	-	1	.3	-	-
7	ov	-	-	-	-	-	-	-	-	-	-	-	1	.3	-	-
8	h	-	1.2	3.5	-	-	2	-	-	-	-	-	1	.19	.16	-
9	h	-	-	-	-	-	-	-	-	-	-	-	1	.3	-	-
10	h	-	-	-	-	-	-	-	-	1	-	-	-	.3	-	-
11	h	-	-	-	-	-	-	-	-	1	-	-	2	.05	.25	-
12	h	-	h	-	-	-	2	-	-	-	-	-	1	.12	.17	-
13	h	-	3.2	6.5	h	-	1,2,3		-	-	-	-	-	.05	.2	.1
14	ov	-	2.0	4.6	-	-	-	1	-	-	-	2	-	.05	.3	-
15	ov	-	1.5	7.0	-	-	2	1	-	-	-	-	-	.05	.25	-
16	h	-	h	-	-	-	1,2	-	-	-	-	-	-	.07	.10	-
17	h	-	3.0	6.0	-	-	-	-	-	-	-	-	1,2	.07	.13	-
18	h	-	1.0	2.4	1.5	5.0	1,2,3		-	-	-	-	-	.08	.06	.08
19	h	-	1.0	2.5	1.5	5.0	3	2	-	-	-	-	1	.05	.03	.17
20	h	-	1.0	3.0	-	-	2	-	1	-	-	-	-	.03	.27	-
21	h	-	1.5	3.0	-	-	2	-	-	-	-	-	1	.08	.24	-
22	h	-	1.5	4.5	-	-	2	1	-	-	-	-	-	.03	.42	-
23	h	-	h	-	-	-	2	-	-	-	-	-	1	.2	.1	-
24	h	-	h	-	-	-	1,2	-	-	-	-	-	-	.05	.23	-
25	h	-	-	-	-	-	-	-	-	-	-	-	1	.35	-	-
26	h	-	3.5	7.5	-	-	1,2	-	-	-	-	-	-	.1	.2	-
27	h	-	3.5	6.5	-	-	-	-	2	-	-	-	1	.05	.17	-
28	ov	-	1.5	6.5	-	-	2	1	-	-	-	-	-	.05	.27	-

Figure I-8 - Sonagrams of Juvenile Vocalizations - Wild - II

A. "Extended Awks"

B. "Uks"


A
Khz.
6
4
2
Time


B
Khz.
6
4
2
Time

calls the "extended awk" is not usually given in response to another bird's call. Thus, the use of the "extended awk" seems to be quite different from the "chz-chr" vocalizations although their form is similar. It is possible that the scenario described for the message progression from "peer" to "squeak-whines" has occurred for the "extended awk" emerging from the "chz-chr" vocalizations. Vocalizing Stage 2 and Stage 3 chicks were often avoided by adults. Also this time was marked by an increase in vocal initiation by chicks thus reducing the dependence on the adult vocalizing in determining the timing of giving "chz-chr" vocalizations. A gradual increase in vocal independence associated with aggressively searching for food might explain the change in messages associated with the "extended awk" and its precursor "chz-chr" calls.

3. "Uks"

"Uks" are low intensity vocalizations which may be alarm vocalizations. They were often given by 1Y birds that were standing in a group and were approached by a vulture. As the 1Y birds walked away from the intruder they would collapse into a tighter group and "uk". It was difficult to record this call in the field due to its low volume but Figure 8-B has a few examples. As can be seen, "uks" are short, monosyllabic calls with a Rise-Fall pattern. "Uks" are given in short, quick bouts.

4. "Juvenile Long Call"

Table I-8 and Figure I-9 show some of the major characterisitics of the "juvenile long call". The basic pattern of the "juvenile long call"

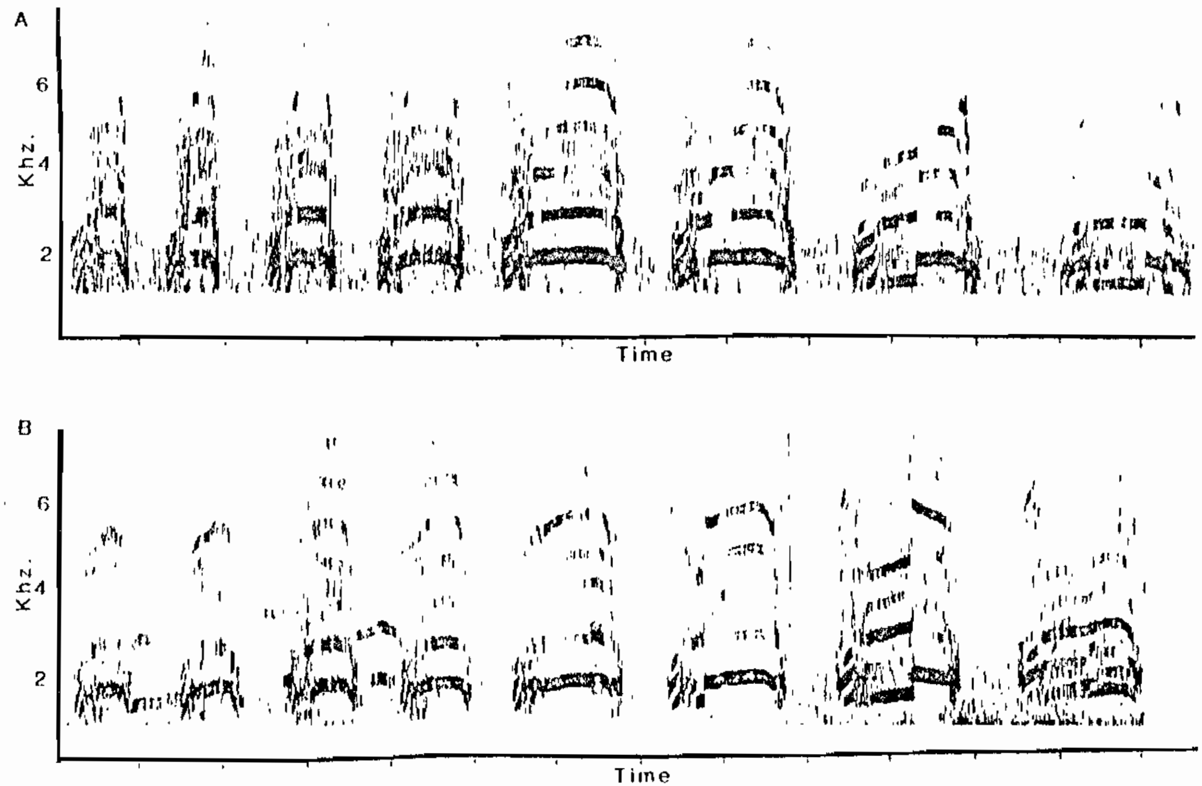
TABLE I-8 - Analysis of Juvenile Long Calls

Call Number	Number of Short Notes	SHORT NOTES General Duration	Number of Syllables	Frequency Pattern	Frequency Range Low	High	Duration Between	LONG NOTES Number of Long Notes	General Duration
1	3	.17	3	1-ho-b 2-ho-a 3-ho-b	1.0	5.5	.12	4	.3
2	3	.1	3	1-ho-c 2-ho-a 3-ho-a	1.2	4.5	.1	3	.2
3	3	.12	3	1-ho-c 2-ho-a 3-ho-a	1.5	5.6	.08	3	.35
4	4	.07	3	1-ho-b 2-ho-d 3-ho-c	1.0	4.5	.1	5	.3
5	6	.1	3	1-ho-b 2-h-a 3-ho-c	1.0	5.0	.12	4	.32
6	4	.12	3	1-ho-b 2-h-a 3-ho-b	1.5	7.0	.09	4	.25
7	5	.08	3	1-ho-b 2-ho-a 3-c	1.5	6.0	.12	3	.3
8	4	.13	3	1-a 2-a 3-a	1.5	7.5	.1	4	.27
9	3	.15	3	1-a 2-ho-a 3-a	1.5	6.0	.1	3	.3
10	3	.15	3	1-a 2-ho-a 3-a	1.5	5.0	.1	4	.25
11	4	.12	3	1-a 2-a 3-ho-c	1.5	5.0	.1	5	.25
12	4	.2	3	1-ho-b 2-ho-a 3-c	1.5	5.0	.12	5	.35

TABLE I-8 - continued

	LONG NOTES					HEAD TOSS NOTE				
Call Number	Number of Syllables	Frequency Pattern	Frequency Range Low	High	Duration Between	Number of Syllables	General Duration	Frequency Pattern	Frequency Range Low	High
1	3	1-ho-b 2-h-a 3-ho-d	1.5	5.2	.2	3	1.3	1-ho-b 2-ho-a 3-ho-b	1.5	4.0
2	3	1-ho-c 2-h-a 3-ho-c	1.5	5.5	.22	3	.32	1-h-b 2-h-a 3-h-a	1.5	5.5
3	4	1-ho-a 1-ho-a 1-ho-a	1.5	5.5	-	-	-	-	-	-
4	3	1-ho-b 2-ho-a 3-ho-f	2.2	4.5	-	-	-	-	-	-
5	3	1-ho-c 2-h-a 3-h-a	1.5	6.0	-	-	-	-	-	-
6	3	1-ho-c 2-h-g 3-h-g	1.5	8.0	-	-	-	-	-	-
7	3	1-a 2-a 3-a	1.5	8.0	-	-	-	-	-	-
8	3	1-b 2-a 3-c	1.5	7.0	-	-	-	-	-	-
9	3	1-b 2-a 3-a	1.5	7.0	-	-	-	-	-	-
10	3	1-a 2-ho-a 3-a	1.5	6.0	-	-	-	-	-	-
11	3	1-b 2-a 3-a	1.5	5.5	-	-	-	-	-	-
12	3	1-ho-b 2-ho-a 3-ho-c	1.5	7.0	.65	1	.32	ho-f	2.5	5.5

Figure I-9 - Sonagrams of two Juvenile Long Calls


A
6
Khz. 4
2
Time
B
6
Khz. 4
2
Time

is similar to the adult "long call" (Beer, 1970a, b). A "juvenile long call" can have three distinct parts: several short notes, long notes and head toss note, although all are not generally present in each call. The postures associated with the parts are also similar to those described by Beer in the adult: the short notes are accompanied by an oblique posture with the neck extended about 45^{o} from the horizontal, a similar posture is adopted in the long note phase but with the head often lowered so it is in line with the axis of the body, and the head toss note is given as the head is thrown backwards.

As discussed in Chapter 3 the function of the "extended awk" and long call is quite similar at this age so it is likely that "extended awks" may be a part of the "juvenile long call."

The number of short notes varies between three and 6 in a "juvenile long call". They usually are three syllable notes with a harmonic pattern that is clouded by overtones. Similarly, the number of long notes can vary between 3 and 5 and also are three syllable notes. As implied by their name, the duration of a long note is greater than a short note ($p < 0.001$). The middle syllable in a long note can be much longer than the other two syllables and may have a clearer harmonic pattern with less overtones. Long notes are often given by the juveniles without any of the other parts of the "juvenile long call" and sound much like a string of "extended awks".

The head-toss note appears to resemble a "squeak-whine" with an emphasis on fewer frequencies.

Overall, the "juvenile long call" is similar to the adult long call but lacks the highly structured harmonic pattern characteristic of the adult call. As stated previously, to the human ear, the "juvenile long call" counds like a hoarse, squeaky adult long call.

Part 3 - Captive Birds' Vocalizations

Laughing Gulls do not reach sexual maturity until their third-year post-hatch (Bent, 1921). The previous discussion of juvenile vocalizations were restricted to 1Y birds since it is difficult to reliably distinguish second-year (2Y) juveniles from third-year (3Y) and older Laughing Gulls. Therefore, the discussion of vocalizations given by 2Y Laughing Gulls and during the transition between immaturity and sexual maturity is based on captive birds of determinate age.

Methods

During the 1977 breeding season, fourteen Laughing Gull chicks were taken from their nests and hand-raised on Little Beach Island in Brigantine National Wildlife Refuge. In August, 1977 the birds were transported to the Institute of Animal Behavior, Newark, New Jersey where they were kept in flight cages. During the winter months, the birds were maintained in indoor, heated flight rooms under a controlled light cycle (12:12). Food was available ad libitum and consisted of Purina Cat Chow and fresh-frozen fish. Water was continuously available both for drinking and bathing.

The birds were observed and recorded at regular intervals during their development. All vocalizations were collected on a Uher 4200 series tape recorder using a Uher M516 microphone.

The recordings were analyzed using a Kay Elemetrics 6061B sonagraph as previously described.

Results

Through the first-year post-hatch the captive birds' vocalizations follow a similar developmental path as that described for their counterparts in the wild. Figure I-10-A shows examples of the captive birds early "peer" vocalizations. As can be seen, the Rise-Fall monosyllabic pattern, characteristic of the Stage 1 "peer" vocalizations of the wild birds, was present in this vocalization during the first weeks post-hatch. Stage 2 "peers", like those of the wild birds, appear to be extended Stage 1 "peers" with reduced frequency modulation.

The captive birds' early "chz-chr" calls also resemble those described for the wild chicks (Figure I-10-B). The Stage 1 "chz-chr" calls generally have two or three syllables with a dominant frequency which is either Level or has a single inflection. Overtones give the call a harsh quality. Like the Stage 2 "chz-chr" vocalizations of the wild chicks, the captives' Stage 2 "chz-chr" calls have an increased number of syllables but otherwise greatly resemble the Stage 1 "chz-chr" vocalizations.

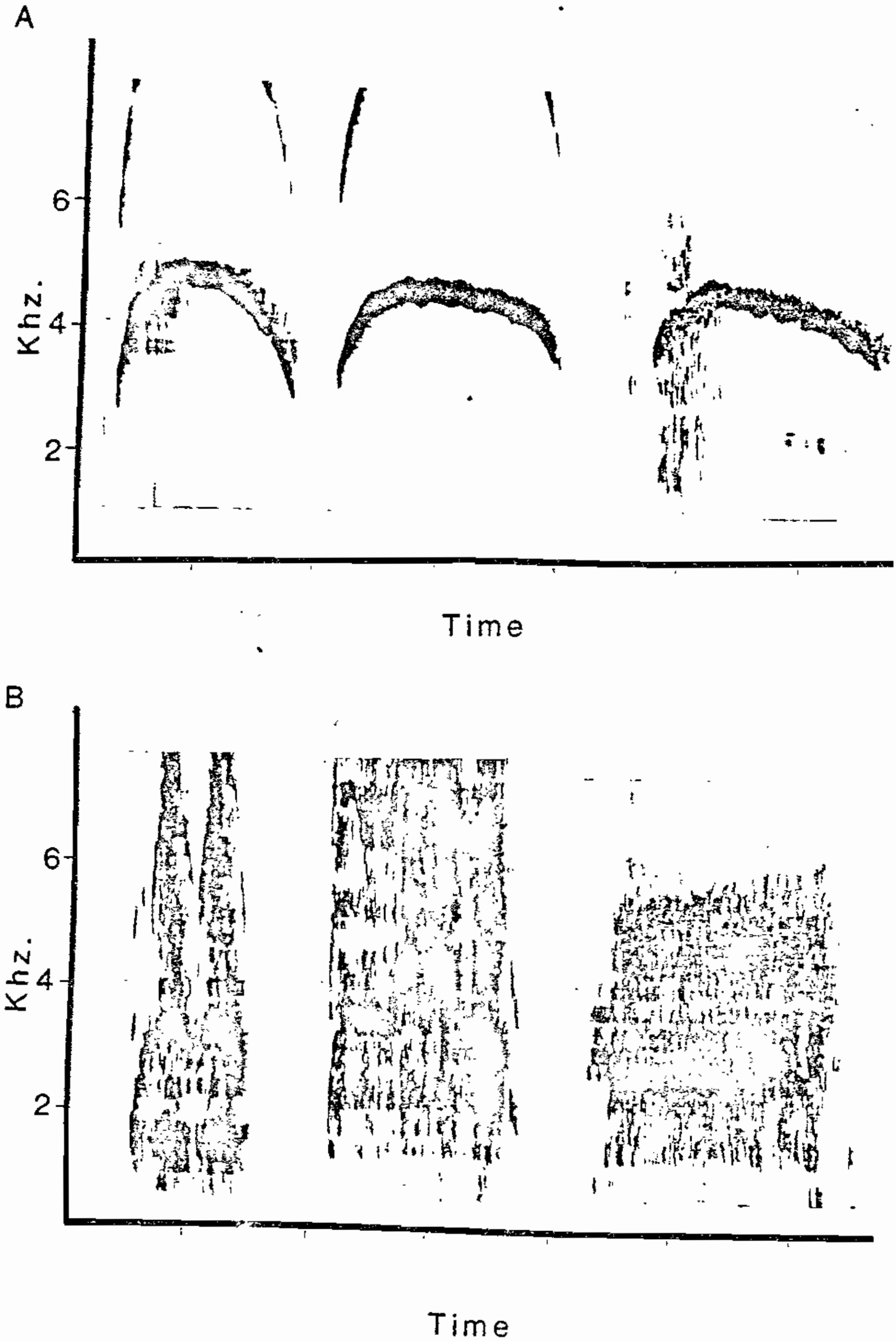
The "vireo" and chick "cheep" were rarely given by the captive birds. Since these calls are normally restricted to the first few days post-hatch it is possible that they went unobserved or that environmental factors necessary to elicit them were not present. Also, the "cheehah" was given only by two chicks, again probably because proper environmental cues were lacking.

The captive birds continued chick "chz-chr" and "peer" vocalizations through August, 1977 ($\sim$2 months post-hatch). However, like the

Figure I-10 - Sonagrams of Captives' Early Vocalizations

A. "Peers"

B. "Chz-Chr"


A
6
Khz.
4
2
Time
B
6
Khz.
4
2
Time

wild fledglings, these birds began to give juvenile vocalizations during August.

The 1Y captives' vocalizations also resemble those of the 1Y wild birds. Figure I-11-A shows examples of juvenile "squeak-whines" given by the captive birds during their first winter. Captive birds' "extended awks" can be seen in Figure I-11-B. The parameters of these calls are similar to those previously described for the wild birds. One quality of these two vocalizations which is more striking in the captive birds' vocalizations is the gradation between "awks" and "squeak-whines". Often a vocalization began sounding like an "extended awk" but because energy was concentrated in one frequency and was held longer than the rest of the vocalization it ended sounding like a "whine". This was present but not as noticeable in the recordings of the wild juveniles.

The captives also regularly gave "uks". (Figure 1-12). The sonagrams of these "uks" appear more pulse-like than those given by the wild 1Y birds although they sound identical. This difference could be a result of recording indoors versus outdoors.

"Juvenile long calls" were first given by the captive birds in October, 1977. ($\sim$ four months post-hatch). The "long calls" given during the first year had the same characteristics as those of the wild birds': a general pattern similar to the adult long call without the adult's highly structured harmonic quality.

Overall, during the first year post-hatch the vocal repertoire of the captive birds matches that of the wild juveniles. The behavior

Figure I-11 - Sonagrams of Captives' Juvenile Vocalizations

A. "Squeak-Whines"

B. "Extended Awks"

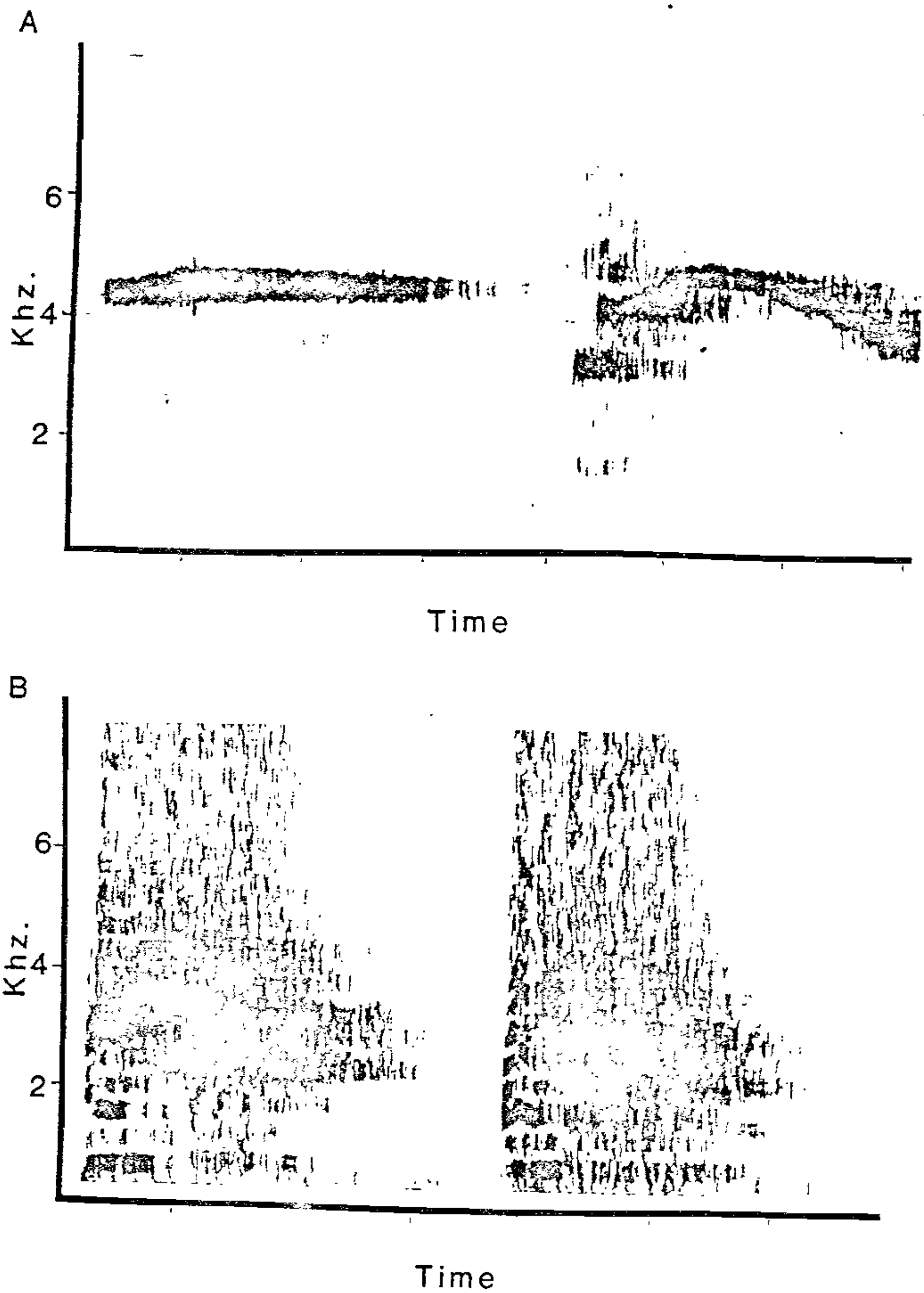
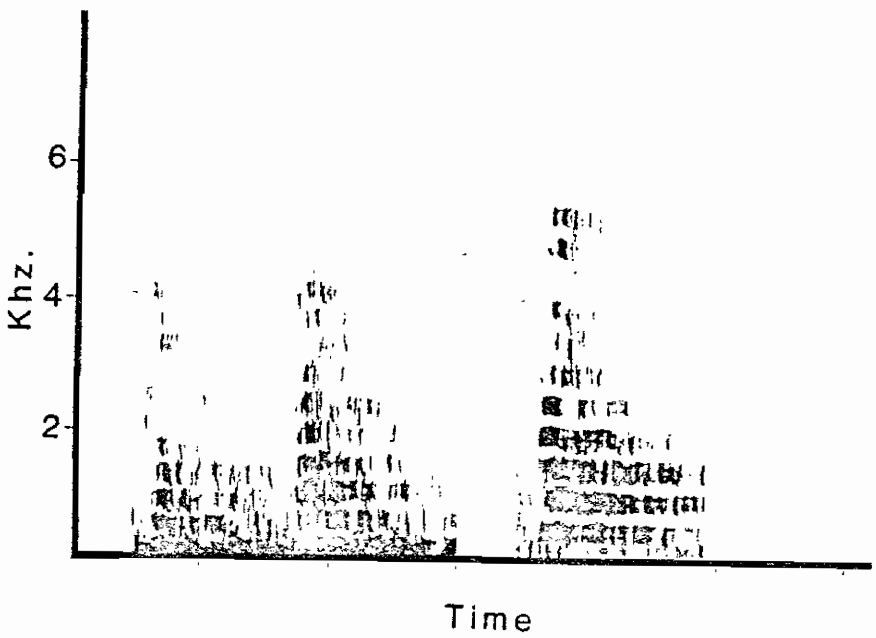

A
6
4
2
Khz.
Time
B
6
4
2
Khz.
Time

Figure I-12 - Sonagrams of Juvenile Vocalizations by Captives - "Uks"


6
4
2
Khz.
Time

of the captives also resembled that of their wild counterparts. Before the 1Y birds had been observed in Panama, it was thought that the high level of aggression associated with their vocalizations was an artifact of the captives' crowded, confined environment. However, as discussed in Chapter 3, the abundant use of these vocalizations in aggressive encounters is the normal condition for 1Y Laughing Gulls.

The vocal repertoire of the captive birds remained stable during their second year. The frequency and pattern of use of the juvenile long call, squeak-whines, extended awk, and uks were unchanged from the previous descriptions.

However, by May, 1979, the vocal repertoire and behavior of the captive birds showed dramatic changes. Beginning at this time, the Laughing Gulls began to develop black-heads and red bills indicating the hormonal changes associated with breeding. Although no actual mating or nest building was observed, early stages of courtship behavior were seen from May through August, 1979. It is well-established that hormones, particularly androgens, can influence both the plumage and vocalizations of birds as they enter the breeding season (for reviews see Andrew, 1969; Nottehohm, 1970). Terkel et al. (1976) have demonstrated that the rate of long-calling in Laughing Gulls is under hormonal control by comparing the rate of long calling of hormonally treated and non-hormonally treated captive juveniles. They were able to show that both testosterone and estrogen treatment will increase the rate of long calling.

The captive birds, as they acquired their breeding plumage and showed courtship behavior began giving adult vocalizations: "keks" "ke-hahs", "kows" and "Gackering". However the "kek" and "ke-hah", though clearly recognizable, did not have the highly structured harmonic pattern of the adult call (see Figures I-13, 14, 15).

The "long calls" given by the captives had a rich-tonal quality due to the well-defined harmonic pattern characteristic of the adult "long call". Figure I-16 shows paired examples of juvenile and adult versions of the "long call" by the captive birds which highlight the change in the harmonic structure of the "long call". The captives often appeared to be straining when giving the early juvenile "long calls". However, "long calls" given during the summer of 1979 seemed to be given effortlessly by the captives. This was particularly reflected in the rapid pace and shortened duration of the short notes.

Although not many examples were available for analysis, the captive birds did show evidence of individual differences in their "long calls". Like the adult "long call" (Beer, 1969, 1970a,b,c, 1972), the number of short notes and their basic structure were similar for all long calls by the same individual. Also, during the summer of 1979, the captives appeared to give only "adult-directed" (Beer, 1975, 1976) "long calls" with the first short notes of lower amplitude than the rest.

It should also be noted that not only did the captives give adult vocalizations during the summer of 1979, they very rarely gave the vocalizations so prominent in their early juvenile repertoire. The "uk" was the only juvenile vocalization that was regularly given during this period. Although the "uk" is not usually included in the adult

Figure I-13 - Sonagrams of Adult Vocalizations by Captives - "Ke-hah", "Head-toss-note", "Kows"

A. "Ke-hah", "Head-toss-note"

B. "Kows"

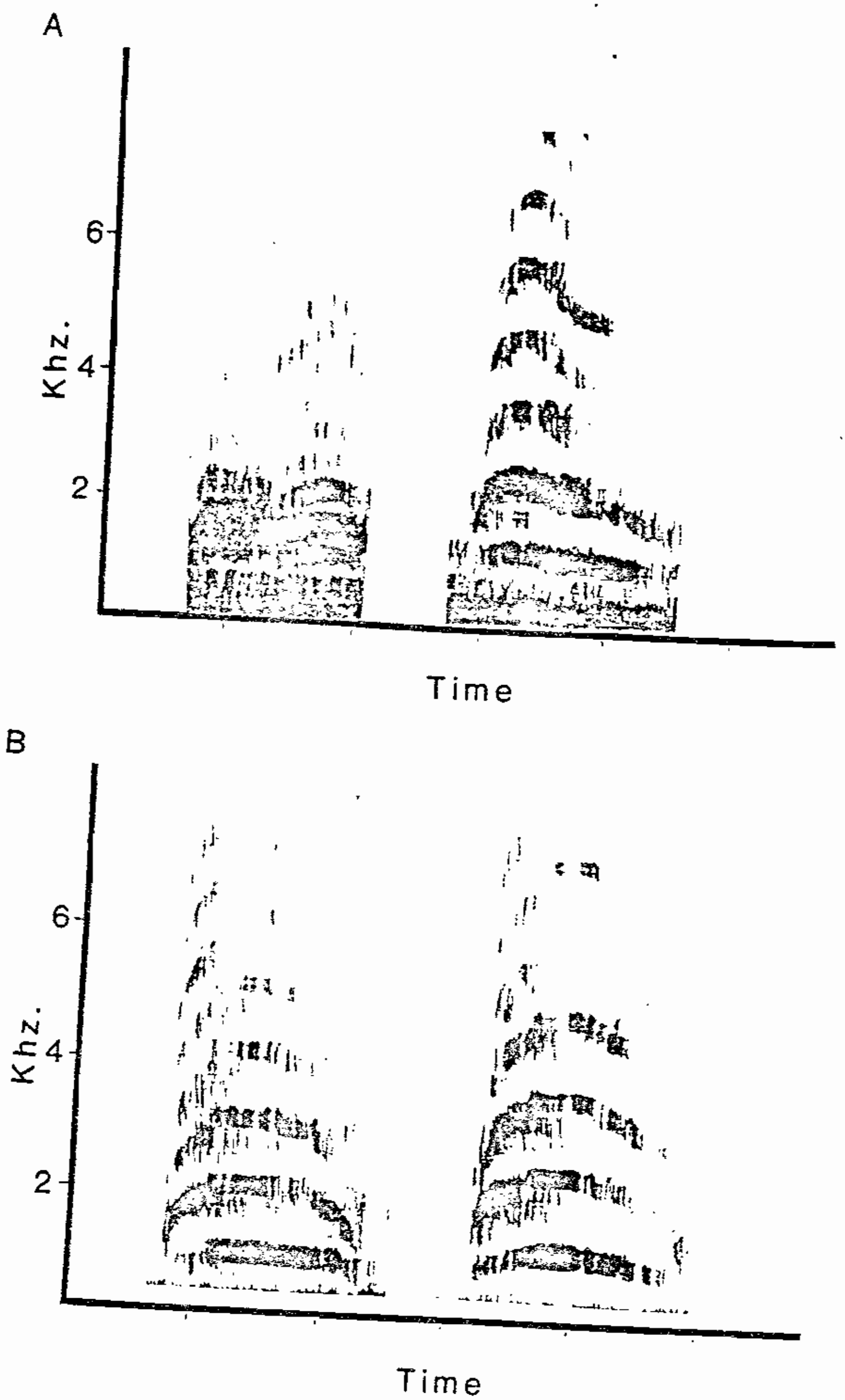
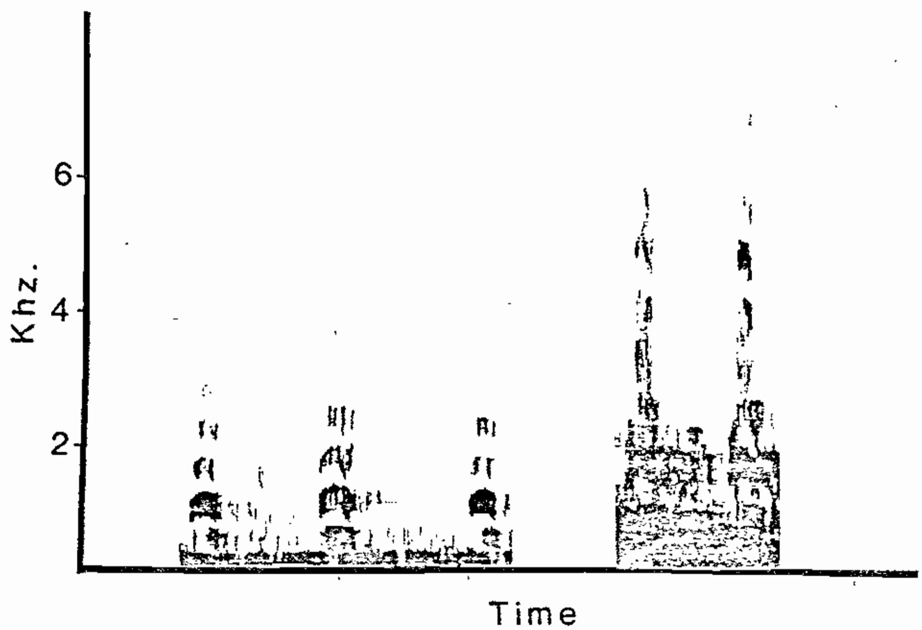

A
Khz.
6
4
2
Time
B
Khz.
6
4
2
Time

Figure I-14 - Sonagrams of Adult Vocalizations by Captives - "Uks", "Keks", "Gackering"

A. "Uks", "Keks"

B. "Gackering"

A



B

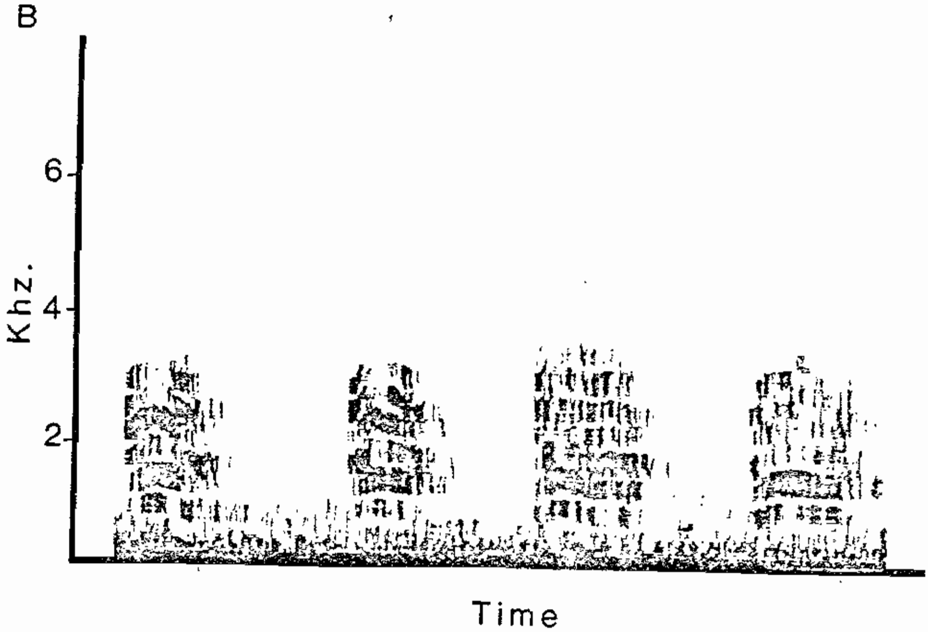
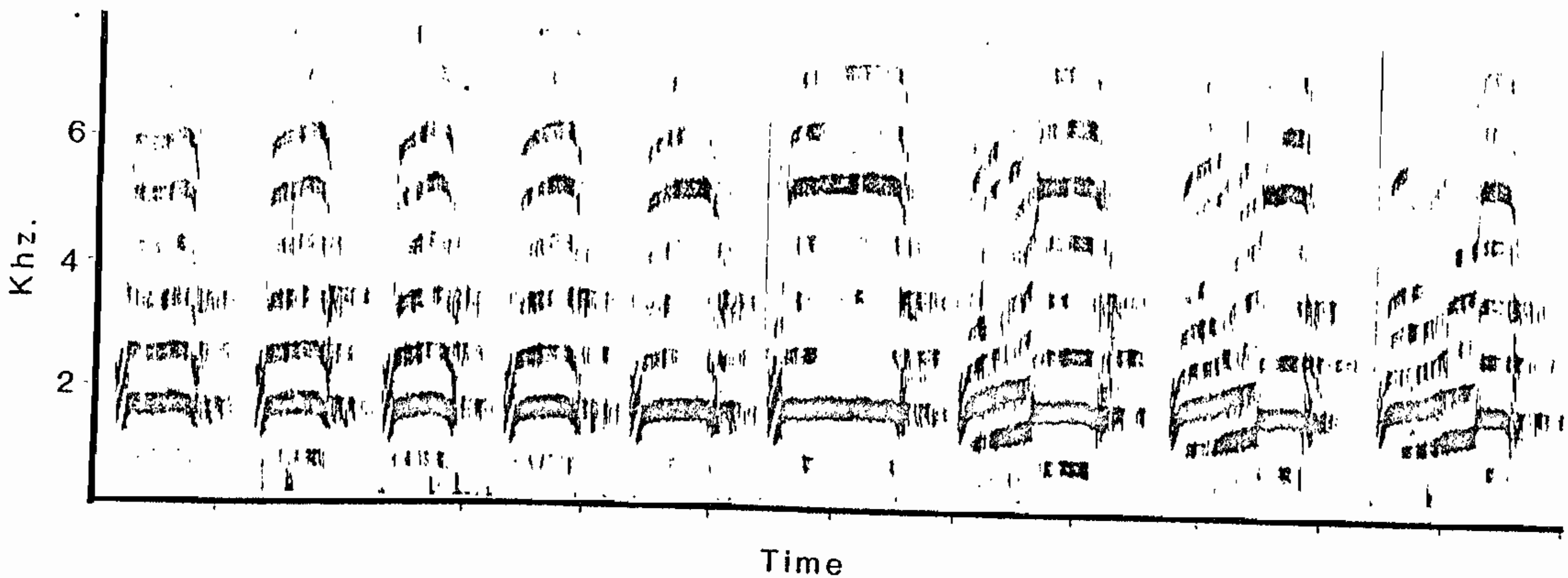


Figure I-15 - Sonagram of Adult Long Call by Captive


Khz.
6
4
2
Time

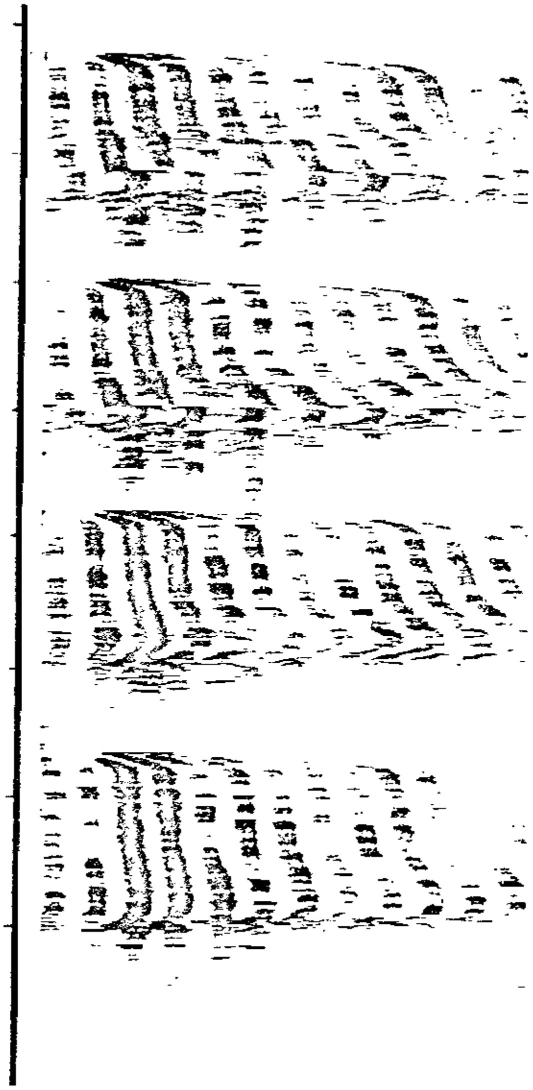
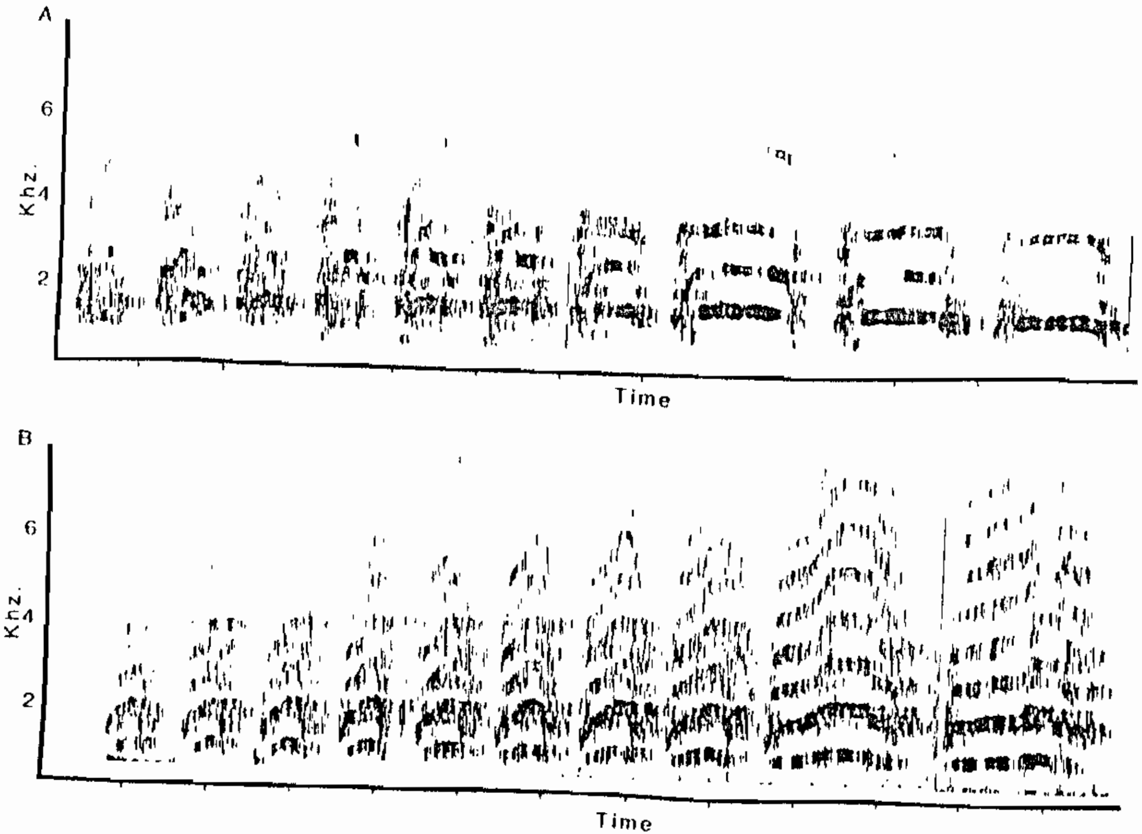
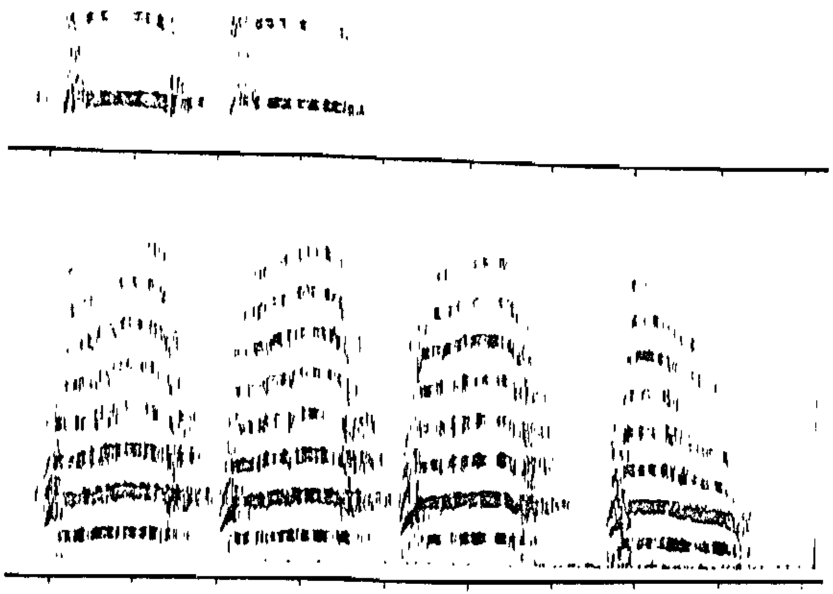


Figure I-16 - Sonagrams of Long Calls by Same Individual

A. Juvenile Long Call

B. Adult Long Call


A
6
Khz.
4
2
Time
B
6
Khz.
4
2
Time



repertoire (Beer, 1975), Bernstein (personal communication) has observed this vocalization among adult wintering Laughing Gulls, raising the possibility that it may be a normal adult call which is not given on the breeding colony.

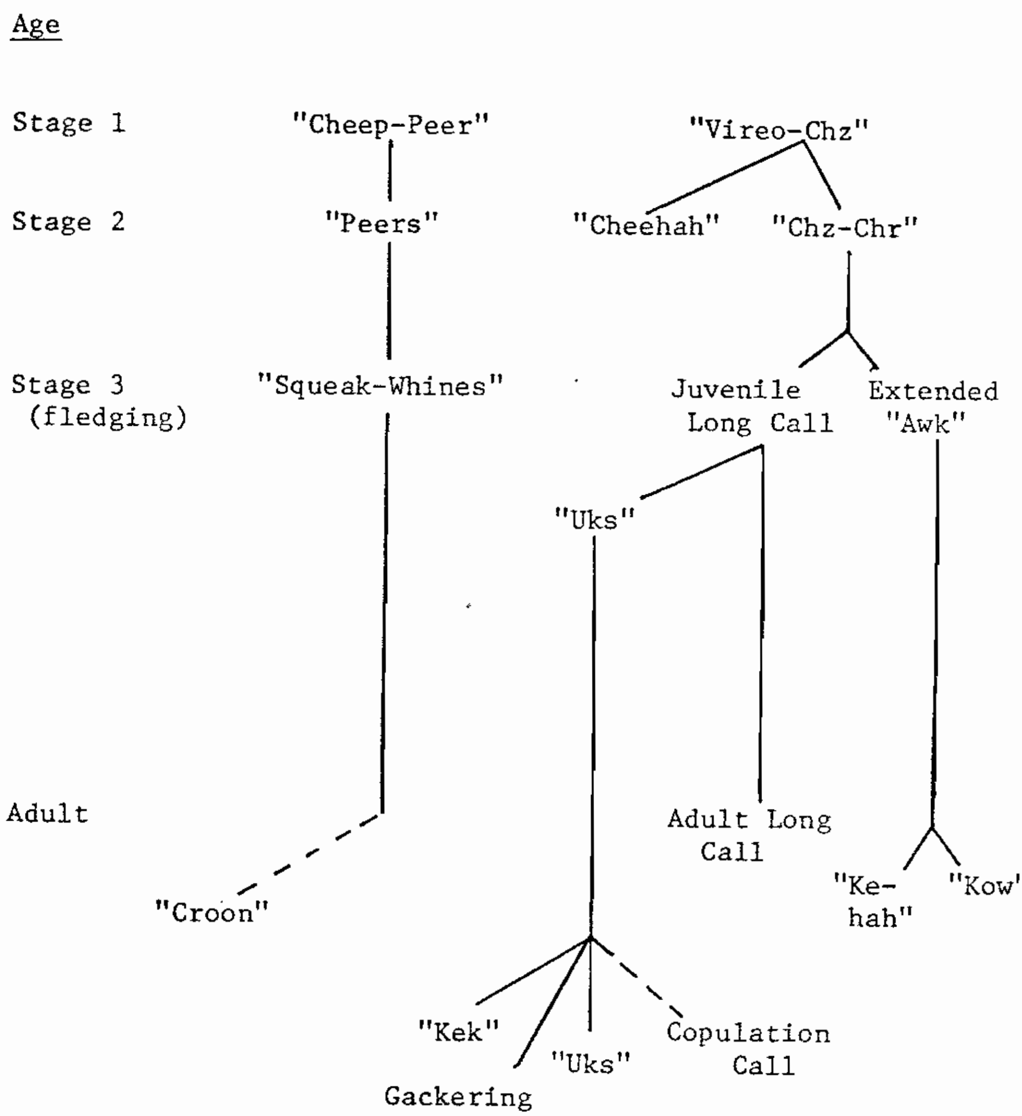
Thus, the captives exhibited most but not all the components of the adult vocal repertoire by their third-year post-hatch. The low prevalence of "choking", "ke-hah", "kek" and "croon" may be related to the low intensity mating behavior observed in these birds. Laughing Gulls can reach sexual maturity by either their third or fourth-year post-hatch, so it is possible that these gulls had not reached full breeding status. Whether this was a function of caging, inappropriate stimuli, or a natural maturational process cannot be answered from these observations.

Discussion

Figure I-17 is an attempt to create an "ontogenetic tree" for Laughing Gulls similar to that described by Moynihan (1959b) for the Franklin's and Ring-billed Gulls. The vocal complexes, "peer-cheep" and "vireo-chz", prominent during the first few days post-hatch are quickly replaced by the "peer" and "chz-chr" calls. Throughout the rest of Stage 1 and Stage 2 these calls are the prevalent vocalizations given by the chicks. The "cheehah" arises during Stage 2 and is dropped from the chick's repertoire by the end of Stage 3. Since the "cheehah" resembles the "chz-chr" calls, it is placed within the "chz-chr" vocal group.

As discussed earlier, Stage 3 chicks give both chick and juvenile vocalizations. "Peers" lead to the juvenile "squeak-whines" and the

Figure I-17 - Ontogenetic Tree of Laughing Gull Vocalizations



"chz-chr" calls are the precursor for both the "juvenile long call" and the "extended awk". The "uk" appears to be a derivative of the "juvenile long call" due to its close resemblance to low intensity short notes.

These juvenile vocalizations are stable throughout the pre-sexual maturity period. Observations of the captive birds indicate that during the bird's second spring adult vocalizations emerge abruptly. The "ke-hah" and the "kow" have characteristics similar to the "extended awk". The "uk" continues into adulthood but new vocalizations also arise from it: the "kek", "gackering", and the "copulation call". The "juvenile long call" takes on the rich adult character as the adult long call and "squeak-whines" appear to be the precursor of the adult "croon".

There are many similarities between this "ontogenetic tree" of the Laughing Gull and those described for the Franklin's and Ring-billed Gull by Moynihan including a monosyllabic and multisyllabic call acting as the building blocks for all later developing vocalization. As discussed by Beer (1980), adult vocalizations of the Laughing Gull consist of "minimum units of sound" which are varied either in amplitude or rate of repetition, making the adult calls distinctive. The branching of the adult vocalizations from only a few chick vocalizations adds strength to this argument if one recognizes that early chick vocalizations can be viewed as the units for later adult calls.

Even with the similar design of the Laughing Gull's "ontogenetic tree" and those described by Moynihan, there is a fundamental difference in interpreting the development of signal function. Moynihan felt that the early displays of his gulls had no signal function but acquired their signal function through a process of "ontogenetic ritualization". It is my belief that the changes in the structure of the vocalizations do not represent a defining of the message but rather reflect a change or acquisition in signal function. The sudden branching of juvenile calls to adult calls as gulls reach sexual maturity is the most striking change during the developmental process and I believe it to be indicative of a dramatic alteration in the social behavior of the Laughing Gulls. As will be described in Chapter 3, the interactions of the juvenile Laughing Gulls are primarily restricted to aggressive encounters aimed at procuring food or roosting spots. However, during the breeding season, the gulls must cooperate with several individuals including mate and chicks in order to ensure reproductive success. This cooperation involves far more complex interactions than those experienced by the juveniles, including pair formation, selection of a nest site, the building and maintenance of a nest, timing of nest reliefs and feeding of the chicks. The variety of adult calls is necessary to match the new social demands on the breeding gulls. Bernstein (personal communication) has found that many of the adult calls which are abundant during the breeding season are rarely heard during the non-breeding season, supporting the contention that their use is restricted to the part of the gull's life cycle which demands an avenue for social cooperation.

The presence of the long call throughout the Laughing Gull's vocal development may underline its importance as a signal. During the breeding season, the adult long call is given in a wide range of contexts as well as providing identification information (Beer, 1975). With such a diversity of uses, it is perhaps not surprising that the long call can serve as a signal for the juveniles. However, in addition, the subtleties of the adult long call may need time to be acquired so the long call's early emergence in the juvenile repertoire may be necessary for developing correct signal function.

It had been my hope that by tracing the development of the form of the vocal repertoire of the Laughing Gull, I would gain insight into the messages of the adult calls. Although I believe that the timing of the emergence of new calls and the persistence of others must be closely linked to their use, only broad generalizations can be made about patterns of message development. For example, it is difficult to see a common link in the messages of the chick "chz-chr" calls and the adult's "kek-kek" which truly fit their use. How the Laughing Gull associates new messages with similar calls remains a mystery.

In the following two chapters the function of the vocalizations present during the pre-adult life of the Laughing Gull will be discussed. From the descriptions, it will become evident that the timing of the emergence of new vocalizations as well as the form and use of pre-adult vocalizations closely reflect the Laughing Gull's age-specific needs.

CHAPTER 2 - FUNCTIONAL SIGNIFICANCE OF LAUGHING GULL CHICK VOCALIZATIONS

Work on vocal development in birds has largely been stimulated by the nature-nurture debate. Insightful experiments on a variety of birds led to the recognition that both a bird's genetic background as well as its acoustic experience shape its final adult vocal pattern (for reviews see: Marler, 1964; Konishi and Nottebohm, 1969; Nottebohm, 1972b). Detailed analyses were performed to classify the types of vocalizations given by immature birds. However, these studies focused on the vocalizations of young birds only as emerging adult vocalizationstions. Little attention was paid to the function the immature vocalizations might serve. Since vocal behavior is the predominant mode of communication in birds, it seems likely that the form and use of immature bird calls are a reflection not only of the eventual adult vocal pattern, but also the requirements of the young bird.

Laughing Gull chicks are particularly well-suited for a functional analysis of immature vocalizations. Since Laughing Gulls are colonial nesters whose chicks are dependent on their parents for nourishment until fledging, the chicks have ample opportunity for social interaction with their parents and other adults and chicks as well. Also, the chicks' vocalizations can be divided into two categories which simplifies a functional analysis of their vocal repertoire. These categories are based on the physical parameters of the vocalizations.

(1) "Chiz-ik" (Nice, 1962; Hailman, 1967)-"Chirirah"(Beer,1970a)

"Chiz-ik-Chirirah" ("Chz-Chr") calls have a wide frequency range with the primary energy concentrated between 2-6 Khz. (see Chapter 1). They are syllabic with sharp onset and termination have sudden changes in pitch and often pronounced overtones. Often, little detail can be seen in a sonagram of these calls with them represented only as bands of noise. The distinction between "chiz-ik" and "chirirah" calls depends solely on the number of syllables: "chiz-ik" calls have two syllables and "chirirah" calls anywhere from three to 10. "Chiz-ik" calls are primarily given in the first 14 days post-hatch and are gradually replaced by "chirirah" vocalizations.

(2) "Peer" (Nice, 1962; Hailman, 1967)

"Peer" vocalizations consist of one or occasionally two tones around 4 Khz. They do not have any syllabic characteristics, and begin and end gradually (see Chapter 1). They are much more whistle-like than the "chz-chr" calls. "Peer" calls are given by the chicks from hatching to fledging.

The structure of the "chz-chr" and "peer" calls may reflect their use. Certain vocal parameters are known to increase the locatability of a call to a binaural animal, specifically a wide frequency range with changes in pitch and a sudden onset and termination (Marler, 1955; Konishi, 1973; Knudsen and Konishi, 1979; Knudsen et al., 1979). According to these specifications "chz-chr" calls should therefore be highly locatable as compared to "peer" vocalizatons. It has also been demonstrated that selection pressures can influence the form of a vocalization. For example, alarm calls in a variety of songbirds have non-locating characteristics to reduce predator detection whereas mobbing calls are known to be highly locatable thereby assisting other birds in finding the caller (Marler, 1955). The striking differences in vocal characteristics of the "chz-chr" and "peer" calls suggest that similar selection pressures may have acted on their form and use.

Descriptions by previous investigators indicate that the form of the "chz-chr" and "peer" vocalizations may reflect their use. Beer (1979) has discussed the "antiphonal duet" which occurs between chicks and a returning parent in which the chicks given "chz-chr" vocalizations. These "antiphonal duets" begin when an adult returns to its nest site and gives a long call vocalization to its chicks who are hidden in the surrounding Spartina marsh grasses. As shown by Beer (1970a,b) the chicks individually recognize their parents from characteristics of their long call. Once the chicks have heard the long call of their parent they respond with "chz-chr" vocalizations. A crude "antiphonal duet" then begins with the chicks giving "chz-chr" calls and the adults giving "ke-hah" vocalizations. During the duet the adult and chicks orient and approach each other through the tall marsh grasses. The chicks continue to give "chz-chr" vocalizations until they reach their parent. These findings suggest that the "chz-chr" calls may have locatable characteristics enabling returning adults to find their hidden chicks. As reviewed by Evans (1980:285) birds whose young wander away from the nest often have developed a vocal exchange between a returning parent and its chicks presumably to aid in their reunion.

Once reaching their parent, the Laughing Gull chicks often switch from giving "chz-chr" to "peer" vocalizations. As reported by Nice (1962) and Hailman (1967), the "peer" vocalization is given by the chicks as they peck at their parent's bill presumably in an attempt to solicit food. Marler (1955) has found that nestling songbirds use non-locatable begging cries to prevent predators from cueing in on their nest site. As Laughing Gull chicks are also subject to predation, it seems likely that when restricted to an area with their parent and having no need to provide location information, they should use a vocalization that has non-locatable characteristics.

The purpose of this study is to verify the proposed function of these two categories of Laughing Gull chick calls and to determine whether the form of the vocalizations matches their use. Specifically, it is hypothesized that the "chz-chr" vocalizations provide location information whereas the "peer" gives the message of seeking care. These two functional categories correspond to descriptions of chick calls and their use by other species of birds. Collias (1952) has described the vocalizations of domestic chicks as falling into two categories: "distress" calls used by the chicks to initiate interactions with their parents and "pleasure" notes given when the chicks are receiving or seeking care. Similarly Conover and Miller (1981) have found that Ring-billed (*Larus delawarensis*) chicks give "distress" calls when in physical discomfort or out of visual contact with their parent whereas the "peer" call is a request for food. It is also suggested that natural selection has led to the "chz-chr" vocalizations having locatable characteristics and the "peer" calls being non-locatable in response to their functions. This analysis will consist of two parts. First, the hypothesized function of the "chz-chr" and "peer" calls will be substantiated by an examination of both chick and adult behaviors associated with the chick calls. Then, an experimental manipulation designed to test the hypothesized function of the two calls will be described.

Part One

In this section the behavior of both adults and chicks will be examined in relation to "chz-chr" and "peer" calls. The aim of this analysis is to show:

(1) "Chz-chr" calls are given when the chick is not in visual contact with its parent and are used to provide the parent with location information.

(2) Chicks will switch from giving "chz-chr" to "peer" calls once they have made visual contact with their parent. This sequence of "chz-chr" to "peer" calls is a frequent and well-established behavioral pattern.

(3) The "peer" call is more often associated with soliciting care than the "chz-chr" vocalizations.

(4) There is a difference in the frequency of use of the calls at various stages of the chick's development reflecting the unique needs of the chicks at these stages.

Methods

Observations of Laughing Gull chicks and parents were conducted from June through August, 1978 at the Brigantine National Wildlife Refuge and at Stone Harbor, New Jersey. All data were collected from blinds constructed in the breeding colonies located on low-lying salt-marsh islands. Three time periods were sampled:

(a) Stage 1 - Chicks and at least one of adults were consistently on the nest. Chicks were being brooded during most of the observations. This period lasted approximately one week to ten days post-hatch. These observations were conducted on the Brigantine colony.

(b) Stage 2- Chicks were still in the nest area but were no longer receiving constant brooding. Adults remained at the site primarily to feed the chicks. When the adults were away collecting food, the chicks stayed hidden in the Spartina grasses surrounding the nests. This sample period was approximately ten days post-hatch to three weeks post-hatch. These observations were conducted both at the Brigantine and Stone Harbor colonies.

(c) Stage 3- Chicks in the Stone Harbor colony were observed after they had moved off their nest sites to a shallow tidal pool. As many as 30 chicks could be seen congregating at the pool at any one time. Chicks were making no attempt to hide when their parents were not present. Although most could fly, they still received food from adults. This period was sampled for two weeks in August, 1979.

Stage 1 and Stage 2 data were collected by one hour focal samplings of all interactions at nest sites. Stage 1 data consisted of 15 1-hour samplings of 8 nests. Stage 2 data included 16 1-hour samplings of 8 nests. One behavioral score was obtained for each nest by taking the average of repeated samples of the same nest. Different nests were observed for Stage 1 and Stage 2.

Stage 3 data were collected by day observations on one tidal pool. 14 days were sampled for a total of 60 hours.

A Uher M516 microphone was placed at the focal nest site or tidal pool perimeter and connected to a Uher 4200 tape recorder in the blind, making accurate monitoring of the chick calls possible. To ensure relible recording of chick calls only two nests were sampled at any one time.

All vocalizations by either chicks or adults were recorded. If chicks from the same nest vocalized simultaneously the first chick to vocalize was observed. An interaction was considered complete when both adult and chicks were silent for ten seconds.

The behaviors which were noted include:

1. Initiator - The first individual to vocalize -parent or chick.
2. Type of Call-
    a. Adult - (1) croon, (2) long call, (3) ke-hah (Beer,1970b)
    b. Chick - (1) "chz-chr", (2) "peer"
3. Duration of Call
    a. Bout- call repeated 5 times within 10 seconds
    b. Single Call- call not followed by same call within 5 seconds
    c. Switching - change from one call to another within 10 seconds
    d. Quiet - no vocalization for 10 seconds after previous vocalization

<u>Analysis</u>

Stage 1 and Stage 2 results were compared using a one-way ANOVA. An arcsin transformation was used so that the proportions met the assumptions of the ANOVA (Snedcor and Cochran, 1967).

Since Stage 3 observations were not collected by focal sampling these data were not statistically analyzed with the results of Stage 1 or Stage 2.

Results

Since Laughing Gull chicks are vulnerable to predation and attack from parents other than their own, they must be sure of the identity of an adult before vocalizing and potentially revealing their location to a predator. This need is reflected in the finding that chicks initiate fewer interactions with their parents as they grow older and move off the nest losing visual contact with their parents. During Stage 1, chicks initiate significantly more interactions than in Stage 2 (Fig. II-1-A). In Stage 2 chicks wait for the adult to vocalize before calling. Also, the use of "chz-chr" as the first call is significantly higher in Stage 2 than in Stage 1 (Fig. II-1-B) supporting the hypothesis that as visual contact is lost the chicks must increase their use of "chz-chr" presumably to provide location information. Stage 3 chicks, similar to Stage 2, primarily give "chz-chr" calls as their first vocalization to their calling parents ($\bar{X}$= .79, S.E.M.=.06).

As described by Beer (1979) parents and older chicks are sometimes slow to approach each other, often giving the appearance of "contesting" over who will move towards the other. The increase in "chz-chr" calling by Stage 2 and Stage 3 chicks may therefore be a reflection not only of increased distance between parent and chick but also increased time until visual contact is made due to a greater reluctance to approach.

Figure II-1 Vocal Behavior of Chicks at Two Developmental Stages

A. Percentage of Interactions Initiated by Chick

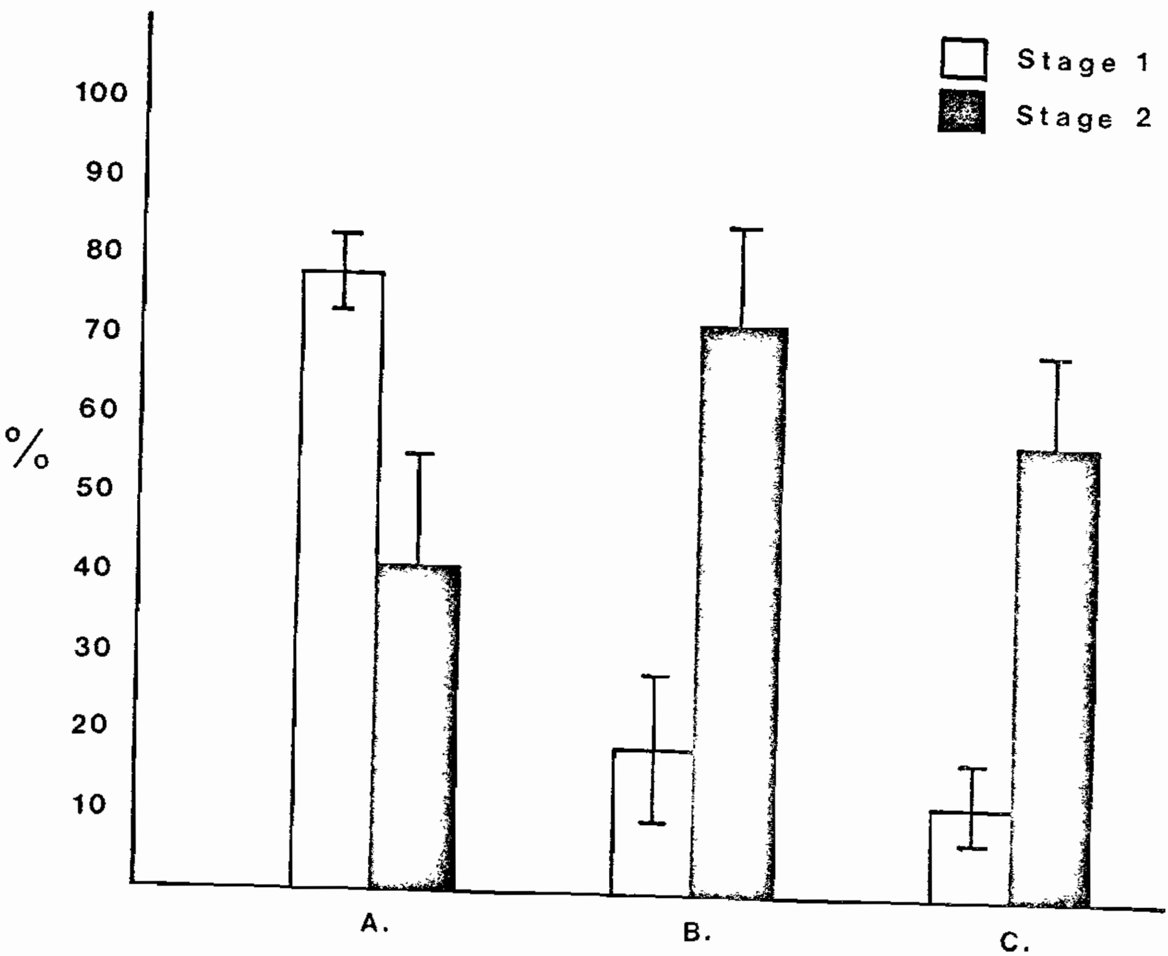
Stage 1- $\bar{X}$= 77.7, S.E.M. = 5.0 Stage 2- $\bar{X}$= 41.0, S.E.M. = 14.0	F= 6.01, p= 0.03

B. Percentage of "Chz-Chr" Given as First Call

Stage 1- $\bar{X}$= 18.0, S.E.M. = 9.0 Stage 2- $\bar{X}$= 72.0, S.E.M. = 13.0	F= 11.71, p= 0.004

C. Percentage of "Chz-Chr" that Switch to "Peer"

Stage 1- $\bar{X}$= 11.0, S.E.M. = 6.0 Stage 2- $\bar{X}$= 57.0, S.E.M. = 12.0	F= 11.34, p= 0.005


Stage 1
Stage 2
100
90
80
70
60
%
50
40
30
20
10
A.
B.
C.

During Stage 2, the frequency of switching from giving "chz-chr" to "peer" calls is significantly greater than in Stage 1. (Fig. II-1-C) The timing of this vocal switch is usually associated with the adult reaching the chick ($\bar{X}$= .83, S.E.M.=.09). In contrast, continuing to give "chz-chr" calls with no switch to "peer" during Stage 2, occurred when the adult failed to make visual contact with its chicks ($\bar{X}$= 1.0, S.E.M. = 0.0). In these cases a parent would often initiate a vocal exchange with its chicks but leave the nesting area before it was visible to its chicks. Similar results were found for Stage 3 chicks with switching from giving "chz-chr" to "peer" occurring when the chicks had reached the adult ($\bar{X}$= .94, S.E.M.=.03) and continuing to give "chz-chr" calls only when visual contact was not made ($\bar{X}$= 1.0, S.E.M.=0.0). Also, as seen in Figure II-2, "peer" calls are most often associated with following "chz-chr" calls in Stage 2 and Stage 3, whereas in Stage 1 the "peer" usually occurs alone.

These results indicate that until visual contact is made between the chicks and adult, the chicks will continue to give "chz-chr" calls. However, once contact is made the necessity to give "chz-chr" calls is removed and "peer" calls can be given.

During all three sampling periods, "peer" calls are most often associated with "No Response" by adult (Stage 1- $\bar{X}$= .64, S.E.M.= .08; Stage 2- $\bar{X}$= .90, S.E.M.=.04; Stage 3- $\bar{X}$= .91, S.E.M.=.04). However, unlike "chz-chr" calls only "peer" calls occur with feeding or begging. Similar results were found by Miller and Conover(1979) in their analysis of Ring-billed Gull chick calls. Laughing Gull chicks are unrelent-

Figure II-2 Use of "Peer" as Related to "Chirirah" (percentage of total peer use by chicks)

Stage 1-	(a)	"Chz-Chr" → "Peer"-	$\overline{X}$= 15.2,	S.E.M. = 8.0
	(b)	"Peer" → "Chz-Chr"-	$\overline{X}$= 3.0,	S.E.M. = 2.0
	(c)	"Peer → Quiet-	$\overline{X}$= 82.0,	S.E.M. = 9.0

Overall F= 15.3, p= 0.0001

a↔b	F= 1.066,	p= 0.31
b↔c	F= 27.32,	p= 0.0000
a↔c	F= 17.59,	p= 0.0004

Stage 2-	(a)	"Chz-Chr" → "Peer"-	$\overline{X}$= 62.0,	S.E.M. = 13.0
	(b)	"Peer" → "Chz-Chr"-	$\overline{X}$= 5.0,	S.E.M. = 2.0
	(c)	"Peer" → Quiet-	$\overline{X}$= 33.0,	S.E.M. = 14.0

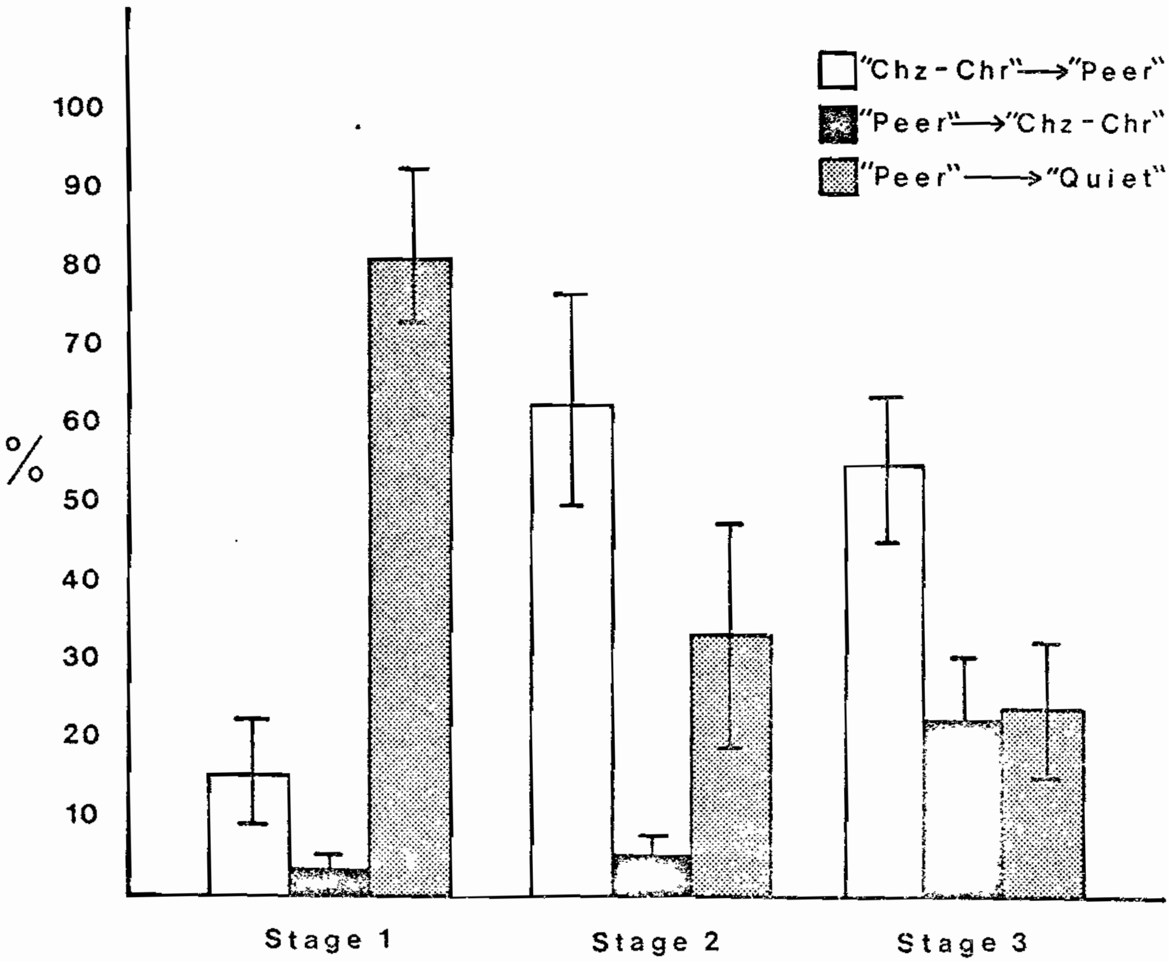
Overall F= 6.85, p= 0.005

a↔b	F= 13.7,	p= 0.0013
b↔c	F= 3.2,	p= 0.09
a↔c	F= 3.6,	p= 0.07

Stage 3-	(a)	"Chz-Chr" → "Peer"-	$\overline{X}$= 54.0,	S.E.M. = 9.0
	(b)	"Peer" → "Chz-Chr"-	$\overline{X}$= 22.0,	S.E.M. = 8.0
	(c)	"Peer" → Quiet-	$\overline{X}$= 23.0,	S.E.M. = 9.0

Overall F= 7.55, p= 0.002

a↔b	F= 11.63,	p= 0.002
b↔c	F= 0.009,	p= 1.16
a↔c	F= 11.01,	p= 0.0020


"Chz - Chr" → "Peer"
"Peer" → "Chz - Chr"
"Peer" → "Quiet"
100
90
80
70
60
%
50
40
30
20
10
Stage 1
Stage 2
Stage 3

ing beggars, sometimes giving "peer" calls as they peck at their parent's bill for as long as 15 minutes. The "peer" call provides information on the likelihood of the chick to feed but other factors, including the adult's willingness to feed, obviously determine whether the chick will be fed. On occasion, adults have been observed regurgitating food with no vocal stimulation from the chicks, so although the "peer" call is very important in soliciting food, the adults can control the timing of regurgitation irrespective of the chicks' vocal demands.

The vocalization of the adults also appear to match the behavior of the chicks (Figure II-3). As previously described by Beer (1970b, 1979) crooning is the prevelant adult vocalization when the chicks are in Stage 1. However, the long call and "ke-hah" are more abundantly used during Stage 2 and Stage 3. The necessity for using the long call and "ke-hah" to communicate with older chicks is two-fold. First, as shown by Beer (1970a,b) the older chicks identify their parents from the individual characteristics of their long call. Second, the "ke-hah" is the primary vocalization used by the adult in the antiphonal duet between the adult and its chicks. Interestingly, like the "chz-chr" vocalizations, the physical parameters of the "ke-hah" (wide frequency range, syllabic, and a sudden onset and termination) make it easily locatable and therefore a beneficial call to use in the antiphonal duet. The rise in the use of the long call and "ke-hah" vocalizations is thus a reflection of the chick's need to obtain both identity and location information of an incoming adult so that the chick can accurately approach the appropriate adult.

Figure II-3 Type of Vocalization Given By Adult During Three Chick Developmental Stages (percentages of total interactions)

Stage 1- (a) Croon- $\bar{X}$= 52.0, S.E.M.=16.0
(b) Long Call $\bar{X}$= 21.0, S.E.M.=14.0
(c) Ke-hah $\bar{X}$= 27.0, S.E.M.=16.0

Overall F=1.058, p=0.368

Stage 2- (a) Croon- $\bar{X}$=8.0, S.E.M.=6.0
(b) Long Call $\bar{X}$=24.0.S.E.M.=8.0
(c) Ke-hah $\bar{X}$=68.0,S.E.M.=12.0

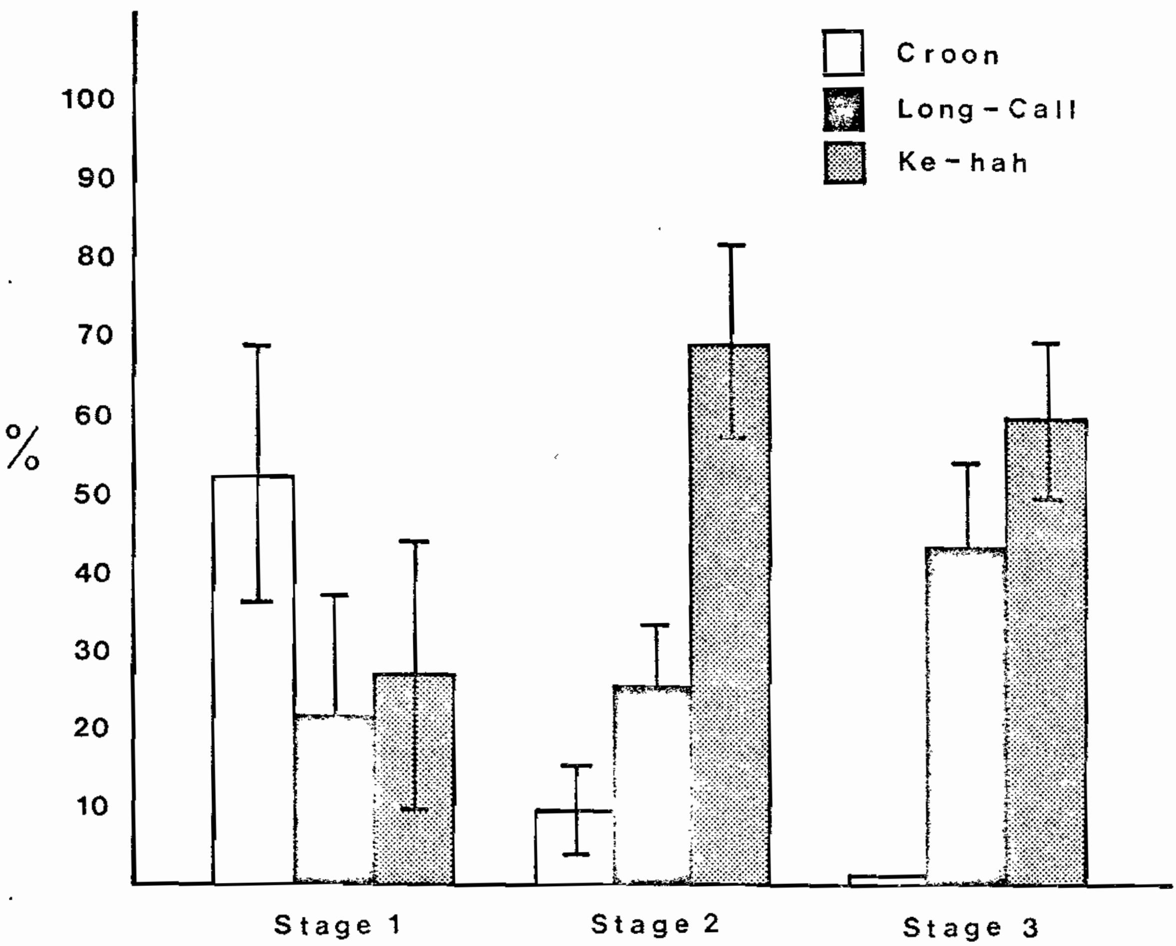
Overall F=11.49, p=0.0006

a↔b - F= 1.72, p=0.21
b↔c - F= 11.15, p=0.004
a↔c - F= 21.61, p=0.0002

Stage 3- (a) Croon- $\bar{X}$=0.0, S.E.M.=0.0
(b) Long Call $\bar{X}$=42.0,S.E.M.=10.0
(c) Ke-hah $\bar{X}$=58.0,S.E.M.=10.0

Overall F= 13.20, p=0.0001

a↔b - F=13.53, p=0.0008
b↔c - F=1.61, p=0.213
a↔c - F=24.47, p=0.0000


Croon
Long-Call
Ke-hah
100
90
80
70
60
%
50
40
30
20
10
Stage 1
Stage 2
Stage 3

Although these results suggest that "chz-chr" calls are given to provide location information and that "peer" vocalizations are used to solicit care from the adults, determining what causes the chicks to stop giving "chz-chr" vocalizations and begin giving "peer" calls is still unclear and essential for a complete understanding of the use of these vocalizations. If the main factor acting on the use of these calls is whether location information needs to be provided then the chicks should switch vocalizations only when they are assured of the location of their parent. Although visual contact seems to be the eliciting factor, the above field observations cannot verify that it is a necessary one. Possibly, the chicks switch when they reach a feeding site or when they respond to vocal cues from their parents.

The purpose of the next section is to experimentally determine if visual contact with the parent is necessary to cause the chick to switch from giving "chz-chr" to "peer" vocalizations.

Part Two

Methods

The experiment was conducted in Stone Harbor, New Jersey during the 1979 breeding season. Ten chicks (seven to ten days of age) from ten nests were randomly assigned to two test conditions. In one condition a chick was placed under a cloth-covered box which eliminated visual cues (test box approximately 1/3 meter x 1/3 meter x 1/3 meter). In the other condition a chick was placed in a wire-covered box which restricted physical but not visual contact.

During a test session all but the one test chick was removed from the nesting area. The test box was placed over the chick two meters from the original nest area. Several 1/2 meter stakes were placed around the nest so that distances of 1 meter and 2 meters from the test box were known.

Data were collected from a blind. The experiment started when the adult returned to the area and began a vocal exchange with its chick. A Uher M516 microphone was hidden in the grass at the test box so that the chick's vocalizations could be accurately monitored in the blind using a Uher 4200 tape recorder. The Type and Number of calls given by both the chick and adult in relation to the location of the adult was scored for 15 minutes.

If in 15 minutes the adult never was within 1 meter of the box, or if in 30 minutes the chick had not responded the trial was eliminated.

Analysis

Due to the small sample size and numerous 0 and 1.0 scores in the results, it was unsatisfactory to use an arcsin transformation and perform an ANOVA. Therefore, the probability of obtaining the results was estimated from the ranks of the scores.

Results

The rate of overall calling by the chicks was not significantly different for the two conditions (wire-covered- $\overline{X}$= 195.4 calls/trial, S.E.M. =33.7; cloth-covered- $\overline{X}$=252.8 calls/trial, S.E.M. = 36.34; + = 1.91-N.S.). The rate of giving "chz-chr" calls also did not differ (wire-covered- $\overline{X}$= 159.6 calls/trial, S.E.M. = 32.11; cloth-covered- $\overline{X}$= 252.6 calls/trial, S.E.M. = 36.3; + = 1.16-N.S.). The mean peer rate in wire-covered condition was 35.8 calls/trial, S.E.M. = 12.97. Only one chick in the cloth-covered condition gaye any peers.

Table (II-1) shows the percentage of "peer" and "chz-chr" calls given by the chicks in the two test conditions. As can be seen "peers" were given almost exclusively by chicks in the wire-covered condition. The probability of all five chicks in the wire-covered condition giving "peer" calls more frequently than the chicks in the covered condition is .004. These results indicate that the switch from giving "chz-chr" to "peer" calls will occur only if the chick can make visual contact with its parent. If visual contact is not made then the chick will continue to use "chz-chr" calls.

There is also a significant interaction between the distance the adult is from the wire-covered box and the type of call given by the chick (Table II-2). The percentage of "peer" calls given by the test chick was always higher when the adult was less than 1 meter from the wire-covered box than when the adult was either between 1 and 2 meters from the box or greater than 2 meters from the test box ($p = 0.0003$). Thus the probability that the chick will give a "peer" call increases as the adult approaches the chick.

As previously described, the long call and "ke-hah" vocalizations are the primary vocalizations used in the antiphonal duet probably because of their identifying and localizing characteristics. The croon call, on the other hand, seems to be used by the adult when in close contact with its chicks as it attempts to feed or brood them. (Beer, 1970b). Thus, it would seem likely, that in this testing paradigm the adult should give long call or "ke-hah" vocalizations until it has made

Table II-1 Test Condition and Percentage of "Peer" Calls Given by Test Chick

(1) Wire- Covered Condition	-	2.0
		3.0
		20.0
		34.0
		35.0
		$\overline{X}$= 18.8
		S.E.M. = .72
(2) Cloth- Covered Condition	-	0.0
		0.0
		0.0
		0.0
		1.0
		$\overline{X}$= 0.2
		S.E.M. = 0.0

Table II-2 Distance Adult is From Wire-Covered Box and Percentage of "Peer" Calls Given by Test Chick

(a) 1 Meter - 9.0
11.0
27.0
60.0
80.0

$\overline{X}$=37.4
S.E.M. = 1.4

(b) 1 - 2 Meters- 0.0
0.0
0.0
0.0
7.0

$\overline{X}$= 1.5
S.E.M. = .14

(c) 2 Meters - 0.0
0.0
0.0
2.0
6.0

$\overline{X}$= 1.6
S.E.M. = .12

physical or at least visual contact with its chicks, whereupon it should switch to the croon call. Table II-3 shows the percentage of vocalizations given by the adults in the two test conditions. With only one exception, croons were more frequently given in the uncovered than covered condition ($p = 0.02$). However, as can be seen in Table II-4, unlike that found for the chick vocalizations, there is not a significant interaction in the wire-covered condition between the type of vocalization given by the adult and the distance the adult was from the test box. The adult was as likely to give croons at the nest area as it was near the chick.

For the adult, therefore, it appears that two factors may control when it switches from giving long call or "ke-hah" to croon vocalizations. Both visual contact with the chick as well as the adult reaching a location where it anticipates the arrival of the chick seem to elicit the vocal switch. This finding adds further support to the contention that visual contact determines when the chick will switch its vocalizations. Since the adults gave croon calls when on the nest but the test chicks did not respond with "peers" demonstrates that the chicks were not merely responding to the vocalizations of the adults but rather were relying on visual contact. These results are supported by Beer's (1970b) "chickarena" tests where he found that positive filial response by young chicks tends to be initiated by "crooning", however "ke-hah" and long-calling become more potent stimuli by the time the chicks were 12 days post-hatch.

It is possible that if the cloth-covered test box had been placed

Table II-3 Test Condition and Percentage of "Croons" Given by Adult

(1) Wire- Covered Condition - 26.0
58.0
66.0
73.0
84.0

$\bar{X}$= 61.4
S.E.M. = .98

(2) Cloth- Covered Condition - 0.0
3.0
7.0
44.0
47.0

$\bar{X}$= 20.2
S.E.M. = 1.04

Table II-4 Distance Adult is From Wire-Covered Box and Percentage of "Croon" Calls Given by Adult

(a)	1 Meter -	23.0
		25.0
		48.0
		77.0
		84.0
		$\bar{X}$= 51.4
		S.E.M. = 1.26
(b)	1 - 2 Meters -	0.0
		65.0
		73.0
		74.0
		82.0
		$\bar{X}$= 58.8
		S.E.M. = 1.49
(c)	2 Meters -	7.0
		57.0
		60.0
		63.0
		71.0
		$\bar{X}$= 51.6
		S.E.M. = 1.14

on the nest area that the test chick would have given "peer" vocalizations when it was not in visual contact with its parent. However, in light of the findings of the reported experiment, it seems likely that giving the "peer" vocalization at the nest area without visual contact with the parent is a learned response and that the crucial factor determining the switch is visual contact.

Conclusion

Laughing Gull chicks have few needs. They must remain inconspicuous to avoid predators, and must be found and fed by their parents. The above findings demonstrate that in both form and the use of the chicks' vocalizations serve these needs well. In particular, the regular pattern of giving the locatable "chz-chr" vocalizations until visual contact is made, followed by a switch to the non-locatable "peer" vocalization is consistent with the requirement that the chicks reveal their location only to their parents. The use of the "chz-chr" vocalizations in the antiphonal duet also matches the need of the chicks to be located by their parents. Antiphonal duetting has been shown to be advantageous among song birds as a means of maintaining the pair-bond in dense habitats where visibility is difficult (Thorpe, 1972).

However, the form and use of the chick vocalizations may also reflect some of their adult requirements. As previously described (Chapter 1), both the "chz-chr" and "peer" vocalizations can be viewed as precursors to later adult vocalizations. Also, as discussed by Beer (1979) the antiphonal duet between the chicks and their parents may help to prepare the chicks for more complex social interactions later in life that depend on the ability to deliver and perceive subtle differences in vocal signals.

Thus Laughing Gull chick vocalizations should not be viewed solely as growing approximations of adult calls or self-contained products of the chicks' immediate needs, but rather as a compromise ensuring their survival and eventual reproductive success.

CHAPTER 3 - FEEDING AND VOCAL BEHAVIOR OF JUVENILE LAUGHING GULLS

The ability of immature birds to compete successfully for food with adults has been examined in a variety of species. The young of Brown Pelicans (Pelecanus occidentalis; Orians, 1969), Sandwich Terns (Sterna sandvicensis; Dunn, 1972), Herring Gulls (Larus argentatus, Ingolfsson and Estrella, 1978; Verbeek, 1977a,b), Glaucous-winged Gulls (Larus glaucescens, Barash et al., 1975; Searcy, 1973), Ruddy Turnstones (Atenaria interpres; Groves, 1978) and Olivaceous Cormorants (Phalacrocorax olivaceus; Morrison et al., 1973) all exhibit reduced ability at capturing or handling food items as compared to adults. Buckley and Buckley (1974) found that juvenile Royal Terns (Sterna maxima) were as successful as adults in capturing prey, but due to their lower diving rates, the juveniles had to increase their feeding time. These studies support the theory developed by Lack (1966) and Ashmole (1963) that delayed breeding observed in birds maximizes their eventual reproductive success by preventing young, inexperienced birds from breeding until they can sufficiently feed their offspring without jeopardizing later clutches.

Laughing Gulls (Larus atricilla) generally do not reach sexual maturation until their third year post-hatch (Dwight, 1925; Bent, 1921). Burger (1980) and Burger and Gochfeld (1981) have examined age-differences in the feeding ability of Laughing Gulls on dumps and have found that although juveniles are as capable as adults at finding food in dumps, they are more susceptible to piracy. Similarly, young gulls were less proficient at picking up bait and protecting it from pirates.

The purpose of this paper is to examine the differences in the ability of juvenile and adult Laughing Gulls to compete for food and roosting sites in Panama. The most consistent and striking finding of this study was that the juveniles did not exhibit a relative inefficiency when competing for food or roosting sites as compared to adults. However, unlike the adults, the juveniles had to rely on using aggressive vocalizations in order to obtain either food or a roosting site.

This research was conducted from January through April, 1979 at various sites along the bay front of Panama City, Panama or from a motorboat in the Bay of Panama. During this time both adults and juveniles can be found in large numbers around Panama City. Although all ages of Laughing Gulls probably are present at this time in Panama, this paper will compare only the behavior of juveniles that had hatched during the summer of 1978 (First-year or 1Y) to the behavior of birds that were at least three years of age (Third-year or 3Y). These two ages have the most distinctive plumage (Dwight, 1925) and therefore are most reliably identified.

Description of Vocalizations

The types of calls given by the 1Y gulls is a significant factor in determining their ability to compete for food and roosting sites. From laboratory observations of captive Laughing Gulls prior to this field study, the form of the calls used by the 1Y birds was known. Although there is gradation between the calls, for this paper two classes of calls will be discussed.

(1) Whines and Squeaks

These vocalizations vary significantly from a very brief "squeak" ($<$ .05 seconds) to a long "whine" ($>$ 1.7 seconds). However, the tonal quality is similar in all variations with the major energy concentrated around 4000 Hz. sometimes with 1 or 2 harmonics. These calls resemble the Laughing Gull chick "peer" call (see Chapter 1). Often these calls are given in a hunched posture similar in form to the begging posture of the chicks.

(2) Juvenile Long Call and Extended "Awks"

The juvenile long call is very similar to the adult long call (see Chapter 1). The highly structured harmonic pattern is not as clear in the juvenile long call but the rhythmic pattern strongly resembles the adult long call. To human ears it sounds like a hoarse, squeak adult call.

Often the juveniles use what appears to be just the long note section of the juvenile long call which in this paper will be referred to as extended "awk". This call can be given singly or repeated, and has a raspy quality due to strong harmonics and many overtones. The extended "awk" is usually given in an oblique posture with a gaping bill. Due to the similarity in form and use of the extended "awk", it is analyzed in the same category as the juvenile long call.

From laboratory observations of captive juveniles, I suspected that the messages of these calls could be understood as a continuum of likelihood of attack with the "squeak-whines" representing the lowest probability of attack and the juvenile long call-extended "awks" the highest probability of attack. The amount of aggressive behavior seemed unusually large in the captive group and before any field observations were conducted I thought this might represent an aberration due to high densities and confinement. However, as will be shown, the abundant use of these vocalizations in potentially aggressive encounters is the normal condition for 1Y Laughing Gulls.

Three competitive situations will be described: 1Y and 3Y birds' attempts to obtain roosting sites and two feeding situations.

Displacement from Pilings

Adjacent to a sewer pipe on the beach below Balboa Avenue in Panama City was a group of 15 pilings used by the gulls as a resting area during the high tide. At low tide, gulls were usually seen feeding in the sewer stream and standing on the surrounding exposed beach. At high tide, the beach in this area and the sewer pipe were completely covered by water. The pilings offered both a resting area from the water as well as a good vantage point from which the gulls would swoop down and scoop up particles (small pieces of garbage and insects) that had floated to the water's surface from the submerged sewer pipe. During the months of January and February, 1979, observations were taken at this site to determine how frequently and with what success individuals attempted to land on occupied or unoccupied pilings. The significance of vocalizations used by the gulls either when displacing another gull from a piling or when defending a position on a piling was examined as well.

Methods

Observations were taken one hour before the daytime high tide. The sampling period lasted 30 minutes. Ten hours of reliable observations are included in the analysis. Notes were dictated onto a cassette tape recorder listing all displacement "attempts". An "attempt" was scored anytime a gull ("intruder") approached a piling which was already occupied by another gull ("sitter") and tried to land. The observations of "attempts" included the location of the "attempt", the age of both the "intruder" and the "sitter", vocalizations used by either bird, the number of vacant pilings at the time of the "attempt", and the outcome of the "attempt". Similar records were kept for landing on vacant posts.

Results

There is no significant difference between 1Y and 3Y birds successfully displacing a "sitter" from a piling (Table III-1-A). Also 1Y "intruders" are as likely as 3Y "intruders" to attempt to displace either 1Y or 3Y "sitters" (X^2=0.16, 1df, not significant). However, 1Y gulls are much more likely to vocalize than 3Y birds when attempting to displace another gull (Table III-1-B), and the use of vocalizations by the 1Y birds is correlated with a successful displacement (Table III-1-C).

The two age groups show no statistical difference in their ability to defend a piling from an "intruder". (Table III-2-A). Unlike the displacement findings there is no statistical difference between the number of 1Y and 3Y birds which vocalized when defending a piling site (Table III-2-B).

The vocalizations used by either 1Y "intruders" or "sitters" were primarily the juvenile long call and the extended "awk". When giving either of these vocalizations a 1Y "sitter" was usually in a semi-

Table III-1 - Competitive Behavior For Pilings by 1Y and 3Y Gulls

	1Y	3Y	X^2	p
Success	22	14	N.S.*	
No Success	20	13		

A. Outcomes of displacement "attempts" by 1Y and 3Y "intruders"

	1Y	3Y	X^2	p
Vocalize	16	2		
No Vocalize	26	25	6.52	0.02

B. The number of 1Y and 3Y "intruders" which did or did not vocalize in a displacement "attempt"

	Vocalize	No Vocalize	X^2	p
Success	12	10		
No Success	4	16	3.94	0.05

C. "Attempt" success by 1Y gulls as related to use of vocalizations

*N.S. = Not Significant- p 0.05

Table III-2 - Behavior of Gulls Defending A Piling

	1Y	3Y	X^2	p
Success	11	22	N.S.	
No Success	16	21		

A. Outcomes of defending a piling by 1Y and 3Y "sitters"

	1Y	3Y	X^2	p
Vocalize	11	14	N.S.	
No Vocalize	16	29		

B. The number of vocalizers who were successful in defending a piling oblique posture with its bill open, pointing toward the "intruder". The calls would be followed by a gape-jab if the "intruder" flew close to the "sitter" of an occupied piling. Head tosses frequently followed the juvenile long call.

Discussion

The acquisition of a piling was a competitive situation for the gulls since there were far fewer pilings than gulls and the pilings were favored locations as resting spots and vantage points for food. The results indicate that although the 1Y birds were as successful at acquiring and maintaining a position on the pilings, their ability was directly correlated to the use of vocalizations, particularly the juvenile long call and the extended "awk". As described earlier, I suspected that the extended "awk" and the juvenile long call are used by the juveniles to indicate a high likelihood of attack. Since the use of these vocalizations by the 1Y gulls is correlated with the "sitter" leaving his piling, it would appear that in this context this interpretation is upheld. The use of these vocalizations seems necessary for the 1Y birds to successfully compete with the 3Y birds. Probably some aspect of the 3Y birds' age and experience allows them to be as successful as the 1Y birds without the use of vocalizations. Although 3Y birds would defer their pilings to vocalizing 1Y birds, 3Y birds were often seen arriving at a piling and, with no obvious behavioral signal, were able to supplant a "sitter". Bernstein (person communication) is examining whether the adults are capable of individually recognizing other gulls and if this allows them to do without aggressive displays since they "know" which adults can defend and acquire pilings.

Feeding Situations

Two feeding situations (Sewer Stream Feeding and Kleptoparasitism from Brown Pelicans) were examined in order to determine if feeding success was different for 1Y and 3Y Laughing Gulls and whether the use of vocalizations affected the two age groups' feeding success. From the displacement results, it was suspected that in competitive feeding situations the 1Y gulls would vocalize more than the 3Y gulls and that the use of vocalizations by the 1Y gulls would be positively correlated with feeding success.

(1) Sewer Stream Feeding

During low tide at several locations along Balboa Avenue, streams were formed in the sand by the spilling of sewer pipes into the Bay of Panama. Groups of gulls ranging from 2 to 40 could be seen during low tide feeding in these streams on a wide variety of material including small pieces of garbage and insects.

Since gulls could reliably be found at these feeding areas and because it was possible to get within 15 meters of the feeding birds without disturbing them, this was a good situation for observing feeding success and collecting observations of the gulls' vocal behavior.

Methods

During the months of February and March, 1979 I observed gulls feeding at two sewer streams. Twenty observation days are included in this analysis. I divided each stream in half giving four locations for data collection. One minute samples were taken in a random order of up to 5 birds in both age categories in each location. Care was taken to avoid sampling a bird more than once in a daily sampling session. Observations were spoken into a cassette tape recorder and later transcribed and analyzed. The number of "jabs", defined as anytime a gull quickly dipped his bill into the stream, were recorded as well as whether the "jab" was a success or a miss. A "jab" was determined to be a success if the gull was seen manipulating an object in its bill and swallowing. Also, vocalizations given by the observed bird were noted.

Results

No significant difference was found between 1Y and 3Y birds' feeding success at any of the four sewer stream locations (Table III-3-A). There was also no difference in feeding rates between 1Y and 3Y birds (10.27 jabs/min., 8.87 jabs/min. respectively; $F= 2.94$, $p= 0.089$). However, in all four locations there was a significant difference between the number of 1Y and 3Y birds which vocalized while feeding (Table III-3-B). A 1Y gull was much more likely to vocalize than a 3Y bird.

Feeding success was not correlated with the use of vocalizations. Comparisons were made between the frequency of vocalizing and feeding success, and the type of call given and feeding success, but neither of these two analyses provided significant results.

Discussion

These results indicate that vocalizations do not appear to affect either the 1Y or 3Y birds' feeding success in a sewer stream. The high proportion of observed 1Y birds using vocalizations as compared to 3Y birds in this context is at first not readily explained. However, a

Table III-3 - Feeding Behavior of Gulls at Sewer Streams

		1Y	3Y	X^2	p
Stream A	Success	191	195	N.S.	
	No Success	310	258		
Stream B	Success	235	190	N.S.	
	No Success	209	200		
Both Streams	Success	426	385	N.S.	
	No Success	519	458		

A. Feeding success of 1Y and 3Y birds at two stream locations and combined

	1Y	3Y	X^2	p
Vocalize	57	13		
No Vocalize	35	77	43.39	0.01

B. The number of 1Y and 3Y birds which vocalized while feeding in the sewer streams possible explanation is that the degree of skill necessary in this feeding situation is low and that the use of vocalizations cannot increase the feeding success of an individual. Juvenile long calls and extended "awks" were often used by the 1Y birds in this situation and usually were given with a gape-jab towards another bird. Although this behavior often did serve to move close individuals away from a vocalizing 1Y bird, this did not help the 1Y birds' feeding ability. The 1Y birds' behavior may be a reflection of the need to use calls in more demanding feeding contexts. Since sewer streams are a relatively new resource exploited by gulls, it is perhaps not surprising to find that some of the gulls' behavior is unnecessary in this context. A more demanding feeding situation which is historically significant in terms of the evolution of behavior patterns in the Laughing Gull will be discussed in the following section, and should illuminate the necessity for the high use of vocalizations among 1Y birds.

(2) Kleptoparasitism from Brown Pelicans(Pelecnaus occidentalis)

After observing the gulls feeding in the sewer streams, it became apparent that other types of feeding situations had to be examined. From the end of February to the end of March, 1979, the behavior of the juvenile Laughing Gulls as they fed among Brown Pelicans was observed. During this period it was common to see flocks of gulls and pelicans as well as terns and cormornats feeding in the Bay of Panama on schools of fish attracted by the nutrient-rich waters of seasonal upwellings.

Although one could see gulls feeding alone on the schools, the location and timing of this type of feeding were very difficult to predict and therefore almost impossible to study. However, it was very common to see flocks of gulls, primarily 1Y birds feeding among the diving pelicans. Most of the 1Y gulls involved in this feeding situation were attempting to use the collecting skill of the Brown Pelicans for obtaining food either by directly stealing part of the pelican's catch or by taking remains of what the pelicans did not actually swallow from the water's surface. Rarely was any form of aggression used either by the gulls to steal food or by the pelicans to protect their catch. This behavior has been previously described by Baldwin (1946).

Kleptoparasitism has been observed in twenty-three species of the Family Laridae (for review see Brockman and Barnard, 1979) including Herring Gulls (*Larus argerntatus*; Morrison, 1978), and Black-headed Gulls (*Larus ridibudus*; Fuchs, 1977; Kallander, 1977). Kleptoparasitism has been previously described in Laughing Gulls by Hatch (1970, 1975), Baldwin (1946) and Zusi (1958). Since kleptoparasitism is considered a common behavior among the Laridae (Brockman and Barnard, 1979; Morrison, 1978), it probably represents an evolutionary significant feeding strategy.

Methods

Observations were collected either from a motorboat in the Bay of Panama or close to the causeway connecting the mainland with a small offshore island (Flamenco Island). When a diving pelican was spotted, observations were dictated to a recorder on whether a gull approached the pelican within a 5 meter area, and, if so, if the gull landed on the pelican or within a 2 meter area around the pelican.

All vocalizations were noted as well as the feeding success of both the gull and pelican. If more than one gull approached, an attempt was made to score the behavior of up to three gulls.

In order not to oversample a particualr flock of Laughing Gulls, the total number of observations was limited to no more than half of the number of gulls in any flock. If the flock was small enough so that individuals could be followed, an attempt was made not to sample any gull or pelican more than once.

Most of the observations were taken between 0700 and 1100 hours, as the afternoon winds made sampling extremely difficult.

Results

Due to strong winds and bad reflections off the water's surface, not all of the desired observations could be collected on each recorded pelican dive. However, it was decided to analyze any information which was considered accurate and did not depend on missing data. Since the light and wind conditions did not appear to affect the birds' behavior, it is assumed that such an analysis does not bias the results.

There was no significant difference in feeding success between 1Y and 3Y birds (Table III-4-A). As one can see from Table III-4-A, the number of observations of 3Y birds is quite small compared to those collected of 1Y birds. Kleptoparasitism from Brown Pelicans appears to be predominantly a 1Y bird activity.

Similar to previous findings, the number of 1Y birds that vocalized in this situation was significantly greater than the number of 3Y birds that gave vocalizations (Table III-4-B).

Table III-4 - Kleptoparasitism by 1Y and 3Y Gulls

	1Y	3Y	X^2	p
Success	28	7	N.S.	
No Success	185	39		

A. Success at kleptoparasitism from brown pelicans by 1Y and 3Y laughing gulls

	1Y	3Y	X^2	p
Vocalize	100	3		
No Vocalize	60	30	28.5	0.01

B. 1Y and 3Y laughing gulls that vocalized while feeding off brown pelicans

Of the 213 juvenile approaches that were scored 105 resulted in the gull either landing within a 2 meter area around the pelican or on the pelican's head and accounted for almost all of the gulls' successful feeding attempts. As can be seen in Table III-5-A, feeding success was not significantly different in these two areas. However, the frequency of landing beside the pelican was much higher than landing on the pelican's head. This may represent two different strategies for feeding. Landing beside the pelican allowed the gull to quickly collect fish that appeared to be stunned by the pelican's dive, from the water's surface. Gulls that landed on the pelican's head seemed to use this position as a vantage point for spotting stunned fish but also would attempt to grab fish hanging from the pelican's bill.

Since the juvenile gulls appeared to be relying on either stunned fish or fish dangling from the pelican's bill, they had to land close to or on a pelican which had just completed a dive. The use of vocalizations was correlated with the likelihood that a 1Y gull with either land beside or on a pelican (Table III-5-B). In particular, the use of the juvenile long call and the extended "awk" were the best predictors of landing on or within a 2 meter area of a pelican (Table III-5-C).

The type of vocalization given by the 1Y birds compared to extended "awks" given more frequently (Table III-6-A). However, the juvenile long call and the extended "awk" were given significantly more often in a group approach than either a "whine" or "squeak". (Table III-6-B) Also, if an individual in a group approach gave a juvenile long call

Table III-5 - Behavior of 1Y Gulls During Kleptoparasitism

	Head	Beside- 2 meters	X^2	p
Success	5	20	N.S.	
No Success	17	63		

A. 1Y laughing gull's success at kleptoparasitism either from the brown pelican's head or beside the pelican

	Vocalize	No Vocalize	X^2	p
Head or 2 meters	71	13	19.63	0.01
Pass Over or Flutter Beside	29	29		

B. The relationship between the use of vocalizations by 1Y gulls and the proximity to the brown pelicans

	Long Call/ Awk	Squeak/ Whine	X^2	p
Head or 2 meters	60	11	24.54	0.01
Pass or Flutter	10	19		

C. The relationship between the type of call given by a 1Y laughing gull and proximity to a brown pelican

Table III-6 - Vocal Behavior and Kleptoparasitism by 1Y Gulls

	Long Call/ Awk	Squeak/ Whine	X^2	p
Success	13	2		
No Success	47	28	2.25	0.06

A. The relationship between the type of call given by a 1Y Laughing Gull and its feeding success when among Brown Pelicans

	Long Call/ Awk	Squeak/ Whine	X^2	p
Group	49	7	18.24	0.01
Single	19	23		

B. Type of call given by 1Y gull if in a group or individaul attack on a brown pelican

	Long Call/ Awk	Squeak/ Whine	X^2	p
Remain Closest	29	3	6.81	0.01
No Remain Closest	1	3		

C. Type of call given by 1Y gull and ability to remain the closest to a brown pelican in a group attack or extended "awk", it was significantly more likely to remain with the pelican at the closest distance for the longest amount of time (Table III-6-C).

Generally, when two or more birds approached a diving pelican, one of the 1Y birds would give a juvenile long call or extended "awk". The other juvenile usually would then veer away either silently or as it gave a "squeak" or "whine". Thus, the juvenile long call and the extended "awk" seem to be vocalizations given by competitive and potentially aggressive individuals, whereas the "squeak" and "whine" vocalizations are given by juveniles less likely to be aggressive and more likely to "retreat". The advantage of at least appearing aggressive through the use of vocalizations is demonstrated by the higher feeding success of individuals using the juvenile long call and the extended "awk".

Although individual gulls were not systematically followed, it appeared that the juveniles often followed a single pelican for a few dives. Kallander (1977) found similar behavior among parasitic Black-headed Gulls and suggested that the aggressive behavior exhibited by these gulls may be an attempt to defend a "mobile territory" from other intruding gulls. Laughing Gulls are highly opportunistic feeders and as described by Hatch (1970, 1975) often use the sight of another gull as a cue to a potential food resource. Therefore, aggressive threats may be necessary for a defending 1Y gull to gain the advantage in utilizing the food provided by the diving pelican.

Conclusion

In all three situations described, the 1Y birds were much more vocal than the 3Y birds. Except when the 1Y birds were feeding at the sewer stream, which may not be an accurate reflection of their feeding behavior, the use of vocalizations, particularly the extended "awk" and long call, increased the success of 1Y birds in obtaining or maintaining a desired resource. A possible interpretation of these results would be that the extended "awk" and long call encode a message of high probability of attack, leading to the retreat of the recipient and the communicator's success.

However, the amount of actual aggressive behavior exhibited by the 1Y birds was quite low. Five minute observation periods of 120 birds at sewer streams were used to examine the level of aggressive behavior associated with the 1Y birds' vocalizations. Table III-7 shows that the extended "awk" and long call were the best predictors of aggressive behavior (Gape-Jabs at receipient) by the communicator. However, the association between aggressiveness and these vocalizations is so small that their reliability as a predictor of aggressiveness is low. This finding is common when analyzing aggressive displays, and lead to difficulties in interpreting the communicator's behavior, since the retreat of the recipient must be relied upon as a measure of likelihood of attack.

Recent discusssions have centered on whether animals provide accurate information by aggressive displays or, rather, "manipulate" or deceive" the recipient about their likelihood or ability to attack

Table III-7 - Behavior of 1Y Communicators Following Each Type of Vocalization While Feeding in Sewer Streams

Type of Vocalization	Behaviors: Gape/ Jab	Stand	Feed	Move
Awk	19 (.12)*	88 (.56)	26 (.16)	25 (.16)
Long Calls	4 (.11)	20 (.57)	4 (.11)	7 (.20)
Squeak/Whines	14 (.04)	167 (.51)	51 (.16)	96 (.29)

*(percentage of all cases)

(Dawkins and Krebs,1978; Carlyl,1979). These authors contend that, particularly in situations where the benefit is low, contests between a communicator and recipient are settled without probing or escalation and therefore can lead to a high incidence of "decitful" signals. It is possible that in the three situations described the benefit for 1Y birds is greater than that for 3Y Laughing Gulls. Table III-8 shows one census that was taken of the number of 1Y and 3Y gulls that were either feeding in the sewer streams or standing on surrounding,exposed mud flats. If one assumes that the population of 1Y and 3Y birds available to feed at the sewer streams is the total mumber of each at both locations, then one sees that a much smaller proportion of 3Y birds utilize the streams than 1Y birds. Also, of the total number of birds feeding in the sewer streams, fewer are 3Y birds. These results, as well as the low number lf 3Y birds observed feeding with the pelicans, suggest that these two feeding situations may be a marginal resource for 3Y Laughing Gulls. In contrast, high utilization by 1Y gulls is a strong indicator that feeding at the sewer streams or with the pelicans are important resources for the 1Y birds. The value of these resources may be great for the 1Y gulls as they may lack skills necessary to obtain food in more competitive situations. Large flocks of adult Laughing Gulls were often observed feeding in the abundant schools of fish in the Bay of Panama during the upwelling. This feeding situation was very difficult to study due to the frenzy of activity, but it was obvious that with a high degree of skill a gull could obtain sufficient quantities of food quickly. Few 1Y birds were seen feeding with these

Table III-8 Census of IY and 3Y Birds Feeding on Sewer Streams or Standing on Exposed Surrounding Mudflats - 3/12/79

½ Hour From Low Tide	Stream Totals 1Y	Stream Totals 3Y	Mudflat Totals 1Y	Mudflat Totals 3Y	% Overall Stream 1Y	% Overall Stream 3Y
-5	22 (.64)*	12 (.36)	22 (.56)	17 (.44)	.5	.41
-4	43 (.75)	14 (.25)	27 (.13)	180 (.87)	.61	.07
-3	50 (.77)	15 (.24)	22 (.11)	170 (.89)	.69	.08
-2	41 (.55)	33 (.45)	14 (.10)	133 (.90)	.75	.2
-1	34 (.5)	34 (.5)	16 (.11)	131 (.89)	.68	.21
Low Tide	42 (.65)	23 (.35)	13 (.14)	82 (.86)	.76	.22
1	38 (.55)	31 (.45)	21 (.14)	125 (.86)	.64	.2
2	21 (.57)	16 (.43)	34 (.15)	200 (.85)	.38	.07
3	33 (.67)	16 (.33)	34 (.14)	210 (.86)	.49	.07
4	25 (.66)	13 (.34)	21 (.23)	70 (.73)	.54	.16
5	25 (.66)	13 (.37)	6 (.14)	38 (.86)	.81	.25
6	16 (.89)	2 (.11)	11 (.24)	35 (.76)	.59	.05
7	7 (.78)	2 (.22)	-	-	1.0	1.0

*- percentage of total on stream or mudflat

adult flocks suggesting that they may not be able to succeed in this highly competitive situation. Thus, 1Y gulls may be forced to depend on food they can obtain from the sewer stream and the pelicans. The reliance of 1Y birds on aggressive displays may be a necessary substitute for their lack of skill, providing enough time and/or space to obtain the desired resource.

Due to the high benefit of these resources to 1Y gulls, it is possible that 1Y gulls may be attempting to "deceive" the adults about their aggressiveness in order to secure the food resource, and that 3Y gulls may comply with the 1Y gulls' message since the resource is of little value to them. However, to decide that a display is "deceptive" because aggression is not highly correlated with it is a limited view of displays. As discussed by Hinde (1981), ethologists (e.g. Moynihan, 1955; Smith, 1977; Stokes, 1962) have always stressed that signals do not forecast precisely what the communicator will do next, since other environmental cues including the behavior of the recipient can alter subsequent behavior. A 1Y gull's use of a vocalization depends in part on its assessment of the recipient, which can be inaccurate and lead to a change in behavior. Thus, to determine if a 1Y gull is using "deceptive" displays requires a much more complete understanding of the relative costs and benefits of not only the resource but of each interaction. With the present data it is impossible to answer this question, but it is my suspicion that the vocal behavior used by the 1Y gulls represents both their need of the desired resource and their lack of feeding skills, and if confronted by an equally "needy"

3Y bird, the 1Y bird might resort to overt aggression.

It has been theorized by Zahavi (1977a, b) that a signal can be considered reliable when the cost of its performance is directly related to its meaning. He has named this theory the "handicap principle" (Zahavi, 1975) and suggests that the form of a variety of threat displays, including the side display used by many species, have evolved because they communicate the risk the signaller can incur and presumably its ability to win the encounter. Therefore, according to Zahavi, the aggressive behavior of the 1Y gulls should be examined as a "handicap" which highlights their ability and willingness to succeed in an aggressive encounter. Given the present data, this interpretation can only remain speculative.

If the high level of vocal behavior exhibited by 1Y birds is a reflection of their competitive skill, it would be predicted that second-year birds would represent a transition between 1Y and 3Y birds in their use of vocalizations, an hypothesis yet to be tested in the field. Also, if 1Y birds are not only very apparent because of their vocalizations but also because of their distinctive plumage. It is possible that the juvenile plumage represents more than a maturation point, serving as a signal to other birds that the individual is immature and likely to act aggressively. The juvenile plumage may be a "badge" or a characteristic of an animal's appearance that has been modified to provide information (W.J.Smith, 1974, 1977:238-240) similar to the species-isolating function of the eye-ring colors of arctic gulls (N.G. Smith, 1966).

A general relationship may exist between maintaining a juvenile plumage for an extended period and use of aggressive vocalizations.

This study has demonstrated that immature birds can successfully compete with adults for limited resources. However, it appears that lack of skill is supplemented by an increased reliance on aggressive vocal behavior.

CHAPTER 4 - A COMPARISON OF CHICK VOCAL BEHAVIOR IN THE HERRING GULL, GREAT BLACK-BACKED GULL, AND LAUGHING GULL

Comparative behavioral studies have been used by ethologists both to determine phylogenetic relationships between closely related species and to determine the adaptive function of behavior patterns. The classic works by Moynihan (1959) on the Family Laridae and Johnsgard (1961, 1965) on the Family Anatinae showed that behavior could be used as a taxonomic character to clarify classification within a bird group. By contrasting the behavior of closely related species in diverse ecological conditions, ethologists have discovered correlations between ecological factors and behavior, leading to an understanding of the adaptive function of behavior patterns. Work on colonial nesters in the Family Laridae has been particularly instructive. Cullen's (1957) comparison of the cliff-nesting Kittiwake (*Rissa tridactyla*) to ground-nesting gulls, Tinbergen's (1959) compiled report on the behavior of a variety of gull species and Beer's (1966) study of nesting behavior of the Black-billed Gull (*L. bulleri*) have all demonstrated that through analysis of the association of behavior homologies and ecological factors, the adaptive function of behavior patterns can be determined.

The purpose of this study was to compare chick vocalizations given by Herring Gulls (*Larus argentatus*) and Great Black-backed Gulls (*L. marinus*) to the Laughing Gull (*L. atricilla*) chick calls. Since homologies are common in adult gull vocal repertoires, it seemed likely that they would be found in the early chick calls. However, differences in nesting habitat between these gull species, could potentially alter both the type and use of the chick calls.

From previous work on Laughing Gulls (see Chapter 1), it was known that two types of calls predominate the chick's vocal repertoire: the "peer" and "chiz-ik-chirirah" ("chz-chr") calls. When their parents are away collecting food, Laughing Gull chicks hide in the tall Spartina marsh grasses surrounding their nest sites. As an adult returns, the chicks give "chz-chr" calls in an "antiphonal" response to either the adult's ke-hah or long call. Once they are in visual contact with their parents, the chicks immediately switch to the "peer" vocalization. These observations, along with the physical parameters of the calls (see Chapter 2) were evidence that the "peer" is given by the chicks to solicit care-giving whereas the "chz-chr" call is used to provide location information to a newly arrived adult.

Both Herring Gulls and Black-backed Gulls can be found on Elder Island, a small island located in the Brigantine National Wildlife Refuge, New Jersey. Unlike the marsh islands used by the Laughing Gulls, vegetations where the large gulls nest is sparse. From initial observation, it appeared that visual contact between Herring Gull and Black-backed chicks and their parents was minimally hindered by vegetation in contrast to the situation observed in Laughing Gulls. It was therefore of interest to determine if "chz-chr" calls were present in the Herring Gull and Black-backed vocal repertoire, and, if so, if they were used to provide location information.

Methods

Observations were conducted at the Brigantine National Wildlife Refuge, New Jersey for one week in July during the 1978 breeding season. Recordings of the Herring Gull chicks were gathered from their nesting colony on Elder Island. Two chicks from a Black-backed Gull nest located within the Herring Gull colony were also recorded.

All vocalizations reported in this study were from Stage 1 and Stage 2 (see Chapter 1). The vocalizations were gathered from blinds constructed in the breeding colonies. Recordings were made at 7½ IPS on a Uher 4200 series tape recorder using a Uher M516 microphone hidden at the nest site.

Recordings were anlayzed on a Kay Elemetrics 6061B Sona-Graph using the wide band filter on the .8-8 Khz scale.

The categories previously described for Laughing Gull chick vocalizations (Chapter 1) were used to describe the vocalizations reported in this study.

Unfortunately time did not permit collection of enough Black-backed and Herring Gull vocalizations to merit a strict statistical comparison between their vocalizations and Laughing Gull chick calls. Therefore, ranges measured from available sonagrams will be used in the discussion.

Results

Great Black-backed Vocalizations

Figure IV-1-A shows examples of Stage 1 vocalizations given by

Black-backed gull chicks that resemble the Laughing Gull's Stage 1 "peer" and "cheeps". Like the Laughing Gull "peer" and "cheep" the Up-down pattern is present in both of these Black-backed calls. Short duration (range .13-.18 sec.) "cheeps" are prevalent in the Black-backed's early repertoire with a variable frequency range between vocalizations. (frequency change range 1-1.5 Khz.; low range 2-3.5 Khz.; high range 3.5-4.5 Khz.). "Peers" are quite similar to the Laughing Gull "peers" except for a considerably longer duration ($\sim$ .5 sec vs. $\bar{X}$- .32 sec.).

Examples of Black-backed calls which resemble the Laughing Gull "chz-chr" vocalizations can be seen in Figure IV-1-B. Similar to the Laughing Gull chick vocalizations, these calls are syllabic, with a wide frequency range (generally from 1-8 Khz.). However, the repetition of form in each syllable is less consistent in Black-backed's "chz-chr" vocalizations than that seen in Laughing Gull "chz-chr" calls producing a more variable sound. Also, unlike the Laughing Gull's "chz-chr" calls, a principal frequency is not usually present but rather distinct harmonics predominate lending a richer tone to the call.

The duration of these calls ranges from .3-.5 sec., longer than that previously reported for Laughing Gull chicks' "chz-chr" calls (range .15-.33 sec; $\bar{X}$- .24 sec.).

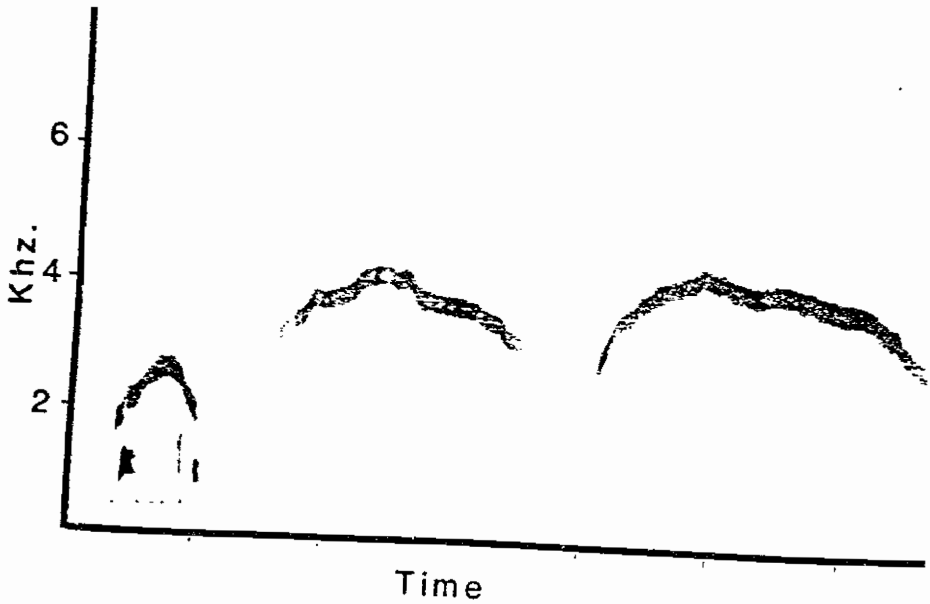
Black-backed "peers" and "cheeps" like the Laughing Gull counterparts are given when the chicks are attempting to solicit food or brooding from their parents. Generally "peers" were given in bouts as the black-backed chicks begged for food with accompanying head movements

Figure IV-1 - Sonagrams of Black-Backed Chick Calls

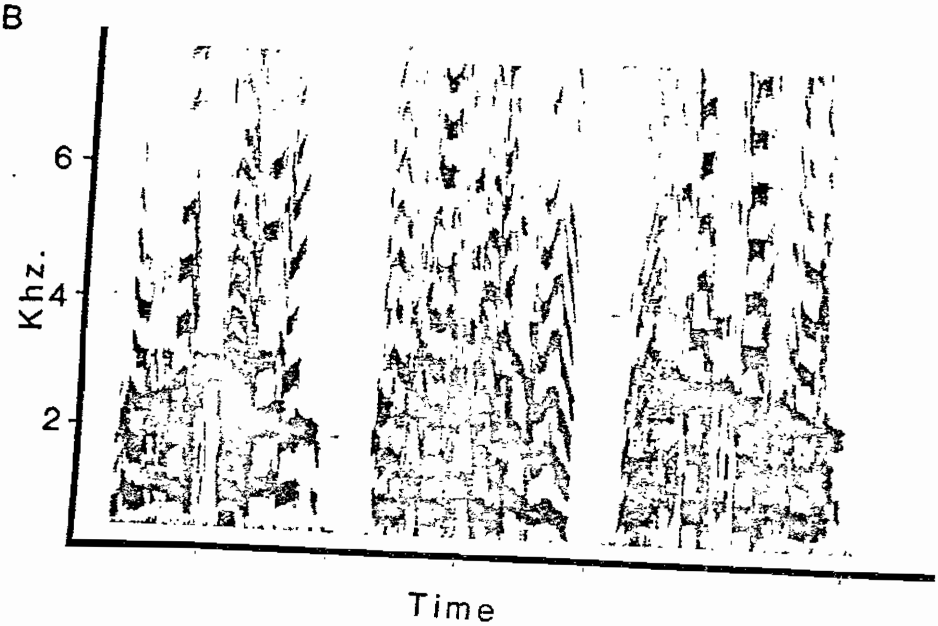
A. "Peers"

B. "Chz-Chr"

A



B



similar to the Laughing Gull chicks' head-pumping (see Chapter 1). However, the use of the "chz-chr" calls differed from that described for Laughing Gull "chz-chr" calls. Similar to the Laughing Gull chicks, the Black-backed chicks usually gave the "chz-chr" calls as an antiphonal repsonse to an adult vocalization (either "mew", "kow" or long call) at the beginning of an interaction, but the characteristic switching from "chz-chr" to "peer" once visual contact was made was not strictly adhered to. Chicks were observed giving the "chz-chr" call not only when the adult was visible but even when they were within a few inches of each other.

Thus, although the form of the Black-backed chick vocalizations closely resembles that of the Laughing Gull chick vocalizations, the contexts in which the calls were given differed.

Herring Gull Chick Vocalizations

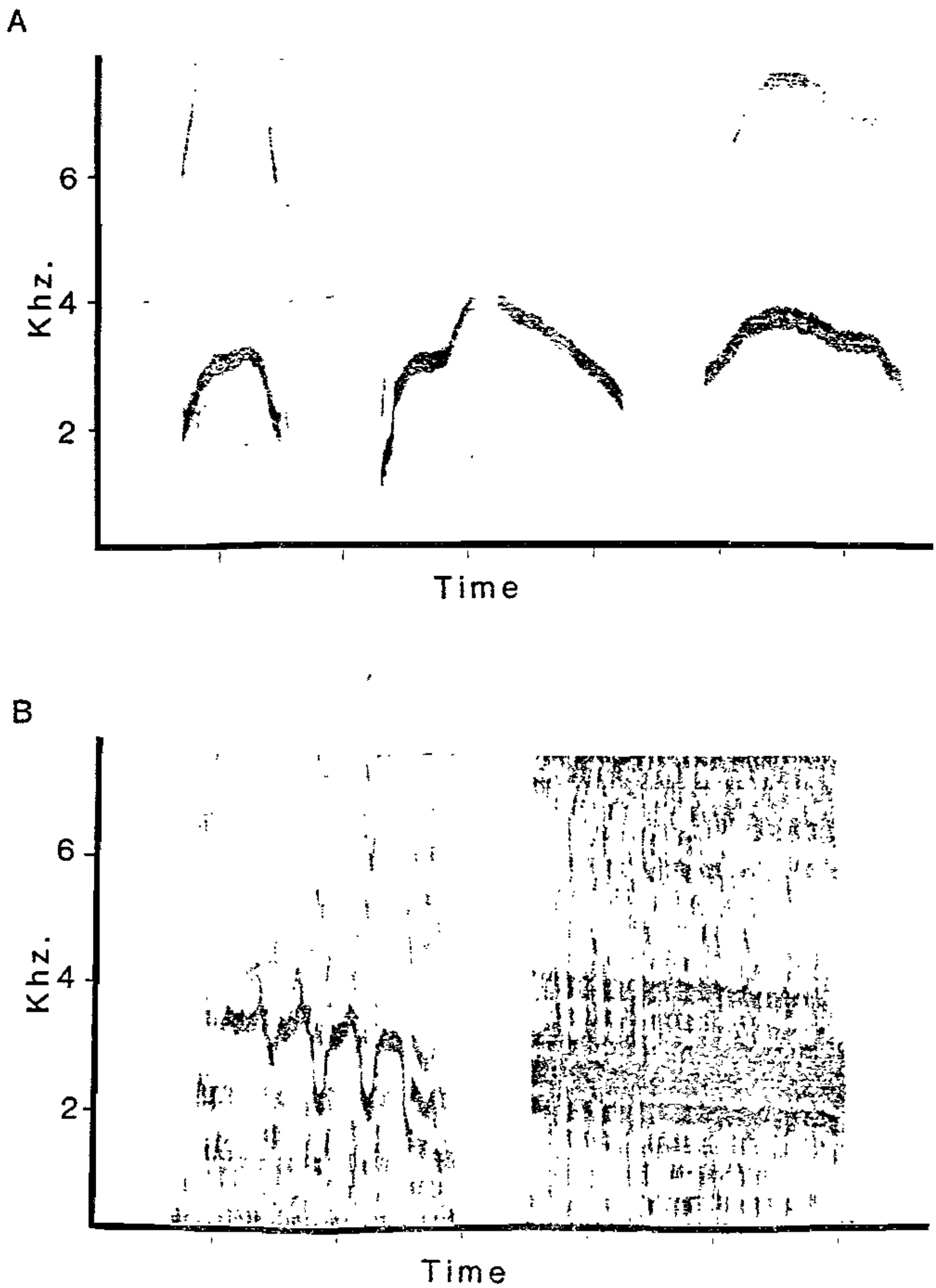
Herring Gull chick vocalizations can be divided into two categories similar to the division between Laughing Gull "peer-cheeps" and :"chz-chr" calls. Figure IV-2-A shows examples of Herring Gull "peers" and "cheeps". Like those given by Laughing Gull chicks, these calls are monosyllabic with the characteristic Rise-Fall pattern. "Cheeps" are short duration (range .15-.2 sec.) "peers" (range .32-.5 sec.).

Vocalizations in Figure IV-2-B are examples of the Herring Gull's version of the chick "chz-chr" calls. Similar to that previously described for the Laughing Gull, they are multisyllabic calls with a wide frequency range (generally from 1 - 8 Khz.). Repetition of form between syllables is common with energy concentrated in a few frequencies-

Figure IV-2 - Sonagrams of Herring Gull Chick Calls

A. "Peers"

B. "Chz-Chr"


A
6
Khz.4
2
Time
B
6
Khz.4
2
Time

harmonics are not as prevalent as those observed in the Black-backed chick vocalizations. The total duration of these calls ranges from .3 to .5 sec. making them longer than the early Laughing Gull "chz-chr" calls but similar to the duration reported for the Black-backed's "chz-chr" vocalizations.

The behaviors associated with these vocalizations were similar to those described for Laughing Gull chicks. "Cheeps" were given by chicks still being brooded and occurred in irregular bursts. "Peers" tended to be associated with either soliciting of food or brooding, and were generally given in bouts lasting up to several minutes.

"Chz-chr" calls were usually given in a semi-antiphonal response to an adult vocalization (ke-hah, long call or kow) and were generally followed by the "peer" call once the chicks had neared the adult. However, there was less reliance on visual contact between the adult and chick in determining the timing of this switch than observed in Laughing Gulls. On several occasions chicks were seen giving "chz-chr" calls when the adult was clearly visible and often less than 1 meter away. In general there was little correlation between distance and visibility from the adult and the timing of the switch, although the basic pattern was consistent with the behavior described for Laughing Gull chicks.

Conclusion

Several general observations can be made from these data. First, the overall structures of the chick calls are similar in the Laughing Gull, Herring Gull and Great Black-backed Gull. In all three species, the chick calls can be divided into two groups: monosyllabic, monofrequency calls and multisyllabic, multifrequency calls. Similarly, the basic behaviors associated with these calls are consistent among these three gull species. "Cheeps-peers" are given in bouts when the chicks are soliciting care and "chz-chr" calls are given antiphonally when initiating a vocal interaction with the parent. The most striking difference between the three species is the factor controlling the switch from giving "chz-chr" to "peer" vocalizations. Laughing Gull chicks depend on visual contact with their parent, whereas both Herring Gull and Great Black-backed chicks appear to rely very little on visual contact.

Although the Black-backed and Herring Gulls were not followed even through fledging, these results suggest that like the Laughing Gull the two early forms of chick calls may act as the basic units for later adult calls. Descriptions of vocal development in the Ring-billed and Franklin's Gull by Moynihan (1959b) and in the Black-headed Gull by Impekoven(1971) indicate that this also is the pattern in these species. The consistency of these results between species suggest that the ancestral form of vocal development in Laridae may have been an elaboration of a two call chick repertoire which has been preserved in the surviving species.

It is unclear, however, if the reliance on visual contact with the adult is the determining factor controlling the switch from giving "chz-chr" to "peer" calls represents an ancestral behavior or is a modification by the Laughing Gull. It is possible that in response both to the dense vegetation of their nesting habitat and predation pressure from larger gulls and other predators,specialization of chick calls has been selected for in the Laughing Gull which maximizes the ability of the adult to locate the chicks while keeping predator cues to a minimum. However, the Laughing Gull is a member of the primitive, hooded gulls (Xema) which are considered to be representative of the ancestral ground nesting gull from which other Larus forms diverged (Moynihan, 1959). Also, Burger (1974) has suggested that the ancestral gull was a marsh nester. Thus, the behavior of the Laughing Gull may well represent that of the ancestral Larus and the differences in the Herring Gull and Black-backed chicks' vocal behavior may reflect subsequent loss or alteration to the basic behavioral patterns reflecting their specific ecological needs.

The important point is that the differences in vocal behavior of these three species of gulls is a response to their breeding habitat. The importance of habitat on adult nesting behavior has already been demonstrated by Burger (1978). Burger showed that increasing vegetation density is negatively correlated with inter-nest distance in gull colonies. It would be interesting to examine Laughing Gull chick behaviors in colonies nesting in drier and more open areas and Herring Gulls that have invaded the marsh areas originally occupied by the Laughing Gull to determine the flexibility of these behaviors and if the breakdown in the association of visual contact and vocal change depends on the visibility within the nesting area.

Further studies on the vocal behavior of Larus chicks should prove quite fruitful, as these results indicate that an analysis of the relationship between habitat and chick vocal behavior can lead to an understanding of the ultimate function of chick calls.

SUMMARY AND CONCLUSIONS

In this thesis I have attempted to make several points about Laught Gull vocal development which I believe are important in understanding the acquisition of display patterns.

First, there is a continuity in form between the early chick calls and those given by adults. The division of the early chick calls into either monosyllabic, monofrequency calls or multisyllabic, multifrequency calls is maintained throughout the Laughing Gulls' vocal development. It is possible that this consistency of pattern allows the Laughing Gulls to practice those sounds which will be used in later adult vocal interactions. Gaining vocal competency has been used as an explanation for the path of vocal development in songbirds. Observations like those of Carolina Chicadees (*Parus carolinensis*, S.T. Smith, 1972) indicate that juvenile songbirds often give jumbled versions of adult vocalizations when alone which appear to have no social signalling function. The complexity of sounds in final adult song and the timing of the critical period to the presence of necessary acoustical stimuli are additional reasons to suspect that early pre-adult songs may be practising stages and carry no communication information.

However, the situation is different for Laughing Gulls. At all points during vocal development, their calls provide information about subsequent behavior. Vocalizations are not given in a random pattern but are used consistently immediately post-hatch. Chick vocalizations give information on the chicks' likelihood to interact and feed and are specially modified to provide location information. Juvenile calls can be viewed as a continuum of likelihood to attack and allow the juveniles to compete with adults for limited resources. The branching of vocalizations when the birds fledge and reach sexual maturity underline the necessity of the Laughing Gull repertoire to match the communication requirements of their social environment. Therefore, it appears that while passing through stages of vocal development Laughing Gulls do not pass through progressive stages of vocal competency, rather the messages of their vocalizatons change according to their age-specific needs.

With no obvious need to practise the sounds of later adult calls, the consistency in form during all stages of vocal development suggests that there may be a physiological constraint on the types of vocalizations given by Laughing Gulls. It is possible that the vocal apparatus of the Laughing Gull may be capable of producing only sounds which fall into two categories. Although it is suspected that the two internal tympaniform membranes of a gull's syrinx may act as separate sound sources (Greenwalt, 1968) it is not known if they produce different sounds as has been reported for some songbirds (Nottebohm, 1971, 1972 a,b; Nottebohm and Nottebohm, 1976; Lemon, 1973). It is possible that the types of sounds produced by Laughing Gulls may be related to the sounds and/or the combination of sounds produced by the two tympaniform membranes.

The consistency in form not only between early and later Laughing Gull vocalizations but the structural similarities of the adult repertoire (Beer, 1980) leads one to question how the Laughing Gulls differentiate between vocalizations and associate specific meaning to each call. As discussed by Beer (1975, 1976, 1980) reaction to adult vocalizations are context dependent - distinctions being made on a wide variety of sources of information including the timing of the vocalization and the posture and location of the signaller. Contextual sources of information are most likely important during all stages of vocal development in Laughing Gulls and, combined with the subtle variation in the calls themselves, make each vocalization distinctive to the gulls. As suggested by Beer (1979), the dynamic interactions which occur between parent and chicks during the nesting period may prepare the chicks for recognizing and using subtle differences in signalling behavior.

From my work on vocal development in the Laughing Gull, it is clear that only describing the emergence of vocal patterns will not provide a complete understanding of the acquisition of a display behavior. In order to approach a full appreciation of the path a developing display must take, the social and ecology requirements must be examined at each intervening stage. Vocal communication is fundamental to almost all social behavior in gulls, and many other kinds of birds, and therefore is vital to the survival of an individual. I believe that closer examination of the juvenile repertoires of song birds within their social context, will reveal vocalizations specially suited to the birds' age-specific communication needs and may demonstrate a signalling function of pre-adult songs. The ontogenetic path of a display must not be viewed as a random process leading to the final adult product, but as a series of finely tuned stages which serve to maximize an individual's reproductive success.

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