AN ANALYSIS OF VOCAL COMMUNICATION IN YOUNG BROWN NODDIES (*ANOUS STOLIDUS*)

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ABSTRACT.—Nestlings and young fledglings of the Brown Noddy (*Anous stolidus*) produce three structurally different vocal signals. The postures of the chicks and the contexts in which these signals are produced differ for each call. Nestlings produce all three calls within one day after hatching. One is given during pipping, when the chick is moving on or near the nest, or when it is isolated from the nest. The second is given by begging chicks. The third is given when an intruder approaches. The repertoire is composed of frequency-modulated tonal elements and broad-band bursts of sound. Although changes occur in the temporal and frequency patterns of the calls during the nestling and fledgling stages, there is little resemblance to the adult repertoire during these periods. *Received 4 January 1985, accepted 14 November 1985.*

ONE of the difficulties encountered when studying vocalizations of young birds is distinguishing between differences in the calls associated with different contexts and changes related to maturation. Despite work on the development of song in passerine birds, little is known of the ontogeny of general vocal repertoires for nonpasserines, and the development of vocal communication of only a few has been studied: domestic fowl (*Gallus gallus;* Collias and Joos 1953), the American Coot (*Fulica americana;* Cosens 1981), the European Quail (*Coturnix coturnix;* Schleidt and Shalter 1975), and the Aldabra White-throated Rail (*Dryolimnas cuvieri aldabranus;* Wilkinson and Huxley 1978).

Although the Laridae have been a favored group for the study of communication in adult birds, less is known of the ontogeny of their vocal communication. Moynihan (1959b) examined the function of hostile behavior in captive young Franklin's Gulls (*Larus pipixcan*) and Ring-billed Gulls (*L. delawarensis*) and offered a scheme for the development of the adult calls. Davies and Carrick (1962) noted changes in the vocalizations of very young Great Crested Terns (*Sterna bergii*) prior to the onset of chick recognition by adults. Impekoven (1971) examined motivational control of vocal communication in young Common Black-headed Gulls (*L. ridibundus*). Other workers, such as Cullen (1957) in Black-legged Kittiwakes (*Rissa tridactyla*) and Cullen and Ashmole (1963) in Lesser Noddies (*Anous tenuirostris*), noted the signaling behavior of the young in more general studies of the breeding biology of a species.

The importance of the context in which a signal is used was stressed by Smith (1977) in his analysis of messages and meanings. The "message" is information encoded in the signal that is descriptive of the signaler and independent of the context in which it is given. It can be determined by examining the features common to all contexts in which it is used. The "meaning" to the receiver is based on the specific details of the context, such as location, identity, sex, and age class of the signaler, other individuals present, prior experience, concurrent activities, and season. Meaning can be interpreted from the response of the recipient to the signal.

Although its relationship among larids remains uncertain, the Brown Noddy (*Anous stolidus*) has been considered to be the tern most closely related to the gulls based on the observed behavior of this species (Moynihan 1959a). Detailed analyses of the form and usage of the vocal signals of both adults and young will increase our understanding of the evolution of communication behavior in this family.

STUDY AREA AND METHODS

Observations and recordings were made in a colony of approximately 15,000 adult Brown Noddies on Bush Key, Dry Tortugas, Florida during four breeding seasons from 1979 through 1982. In a selected area of the colony, I securely marked active nests, color-banded adults at these nests, and recorded hatching dates of nestlings and individually banded them. I observed the behavior of known-age nestlings throughout the nestling and early fledgling periods, concentrating on the vocal and visual sig-

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TABLE 1. Numbers of individuals and calls analyzed for each age group.

Call	Age (days)	No. of individuals analyzed	No. of calls analyzed per individual	Total
Harsh Cheep	1–10	5	5	25
	11–20	6	5	30
	21–30	5	5	25
	44–62	2	5	10
Screech	1–10	9	3	27
	11–20	10	3	30
	31–40	9	3	27
	49–61	4	3	12
Frequency-modulated Cheep	1–10	6	5	30
	11–20	5	5	25
	21–30	5	5	25
	44–62	5	5	25

nals used by them during this period of development.

I recorded vocalizations with a Uher Report L5000 tape recorder at 19 cm/s with a Sennheiser ME88 directional condenser microphone. Video recordings were made with a Sony (AVC-3450) black-and-white portable camera and a JVC (CR-4400U) portable cassette recorder, with the Sennheiser microphone. The microphone was placed at one nest or two adjacent nests to allow me to hear the low-amplitude vocalizations of the young. I recorded contextual information and details of the nature of the behavior, along with information about individual identity and age, and examined features common to the contexts in which each call was given.

I made spectrograms of recorded calls on a Kay Elemetrics Corporation Sona-Graph 6061B, using both a 45-Hz (narrow) and a 300-Hz (wide) band-pass filter, and digitized these on a Tektronix 4081 Graphic System tablet (Tektronix, Inc. 1978) with a density of 1,550 cross-wires/cm^2. The advantages of this technique over the traditional grid overlay are that the grid of the digitizing tablet is finer, and the computer reads and records the x-y coordinates directly. I measured the following parameters using spectrograms produced with the narrow filter for frequency measurements and with the wide filter for time measurements: frequency range; frequencies of most intense sound energy band at onset, peak, midpoint, and offset; note length (measured from onset to offset); internote interval (measured from offset of one call to onset of next by the same individual). Low-amplitude calls of nestlings were difficult to separate from the loud background noise of the colony during all stages of the nestling period. Therefore, I selected recordings of known individuals of known age (1–10 days, 11–20, 21–30, 31–40, 44–62, 49–61) with low background noise for the analysis. Numbers of individuals and numbers of calls analyzed per individual are summarized in Table 1. I made all observations from a blind that I positioned in the study area to allow me to observe a number of nests simultaneously, and all recordings were made on birds under natural conditions. In the text, figures, and tables, "adult" refers to any adult Brown Noddy regardless of its relationship with the chick, and "parent" refers to an adult with a known familial relationship with the chick.

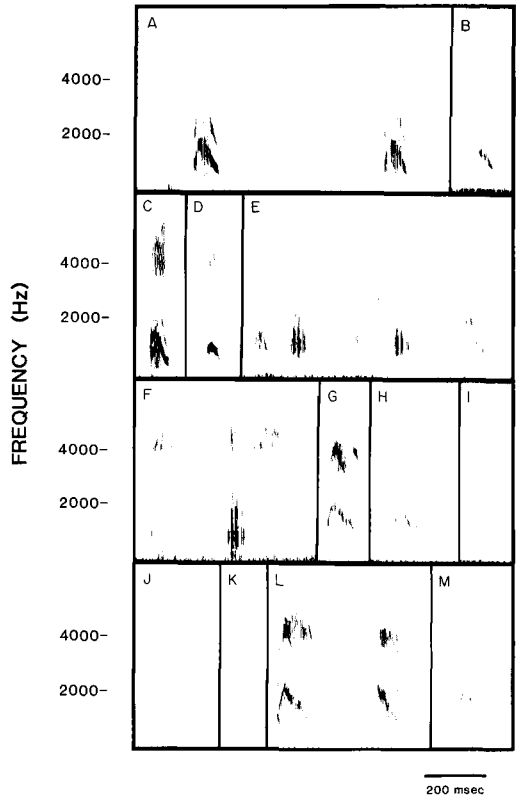

Fig. 1. Spectrograms of Harsh Cheep of young Brown Noddies. Letters grouped below represent calls of the same individual. Chicks A (age 2 days), E (13 days), HI (27 days), and JKL (45 days) show that the forms of the notes may be repeated consistently by an individual. Chicks CD (age 17 days) and FG (27 days) show variation within the repertoires of individuals. Chicks B (3 days) and M (44 days) illustrate other variations in the call. The second and fourth notes in E and second note in F are Low Ker of adults. Filter band width is 300 Hz.

RESULTS

I identified three structurally different calls produced by Brown Noddy nestlings and young

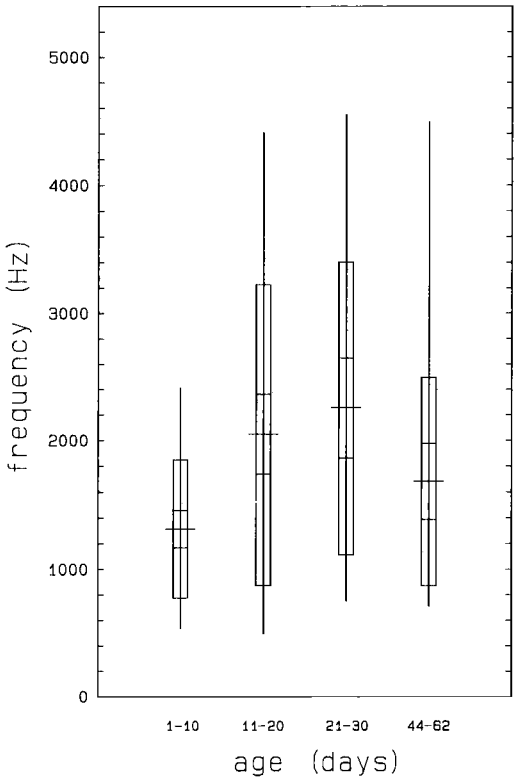

Fig. 2. Frequency of main sound energy bands of Harsh Cheep for four age classes. Includes mean, 95% confidence limits (horizontal line above and below mean), ±SD (delineated by box), and range. There is a change in frequency after age 10 days, and a decline again at the time chicks begin to fly (age 45–50 days).

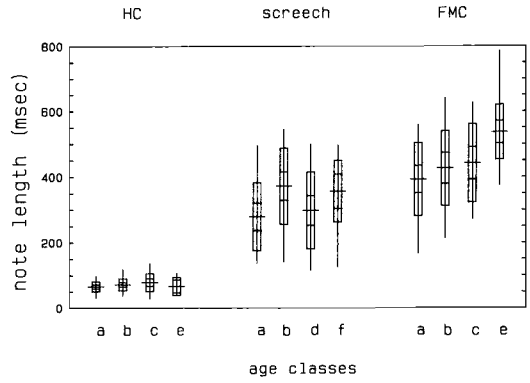

Fig. 3. Note length of Harsh Cheep (HC), Screech, and Frequency-modulated Cheep (FMC) for four age classes: a = 1–10 days, b = 11–20, c = 21–30, d = 31–40, e = 44–62, f = 49–61. Includes mean, 95% confidence limits (horizontal lines above and below mean), ±SD (delineated by box), and range. Length changes little for HC and Screech during the nestling and early fledgling periods, but FMC lengthens as chicks mature.

fledglings, and the contexts in which they are used differ among the calls. Nestlings produce all three calls within one day after hatching, and one (Harsh Cheep) is produced by pipping chicks.

The structures of the vocal signals of young noddies differ greatly from those of the adults. Vocalizations of the young are frequency-modulated whistles and broad-band bursts of sound. The repertoire of adults is composed of notes formed only from discrete clicks, and the frequency-modulated tonal elements characteristic of the young no longer remain (Riska 1986). Although changes occur in the temporal and frequency patterns of the calls during the nestling and fledgling stages, there is little resemblance to the adult repertoire during these periods.

The amplitudes of the vocal signals of young noddies are lower than those of adults, nearly all of which in turn are lower than those of the sympatric Sooty Tern (*Sterna fuscata*). Of the three vocalizations, Screech has the highest amplitude, but all increase in amplitude as the chicks mature. Body postures and bill positions also differ among calls.

Harsh Cheep.—Harsh Cheep (HC) is a short, wide-band note with a terminal downward-sweeping whistle (Fig. 1); the wide-band portion of the call and the whistle are infrequently given alone. Variations exist between individuals and within individual repertoires. At age 1–10 days the mean frequency of the main sound energy band of the wide-band segment is 1,313 Hz (Fig. 2); it increases throughout the nestling period, but drops again by age 40 days. The mean frequency of the onset of the whistle segment remains around 1,400 Hz until about 44 days of age, after which it rises, and the mean of the offset (or end) of the sweep changes little. Note length also changes little from 1 to 62 days (Fig. 3).

HC is given when chicks are out of the nest, when they approach any adult, and when they are approached by any adult, either on or off the nest (Table 2). During bouts of HC, chicks stand or walk in a normal upright posture (Fig. 4), but they may pause and turn the bill downward as they approach or are approached by an adult. HC is also given by nestlings attempting

TABLE 2. *Anous stolidus* nestling and fledgling vocalizations. HC = Harsh Cheep, FMC = Frequency-modulated Cheep.

Situation	HC	FMC	Screech
Chick to intruder at nest (other noddy, sooty, human)			X
Displaced from nest, on ground	X		
Out of nest, as parent approaches or calls to it	X		
Approaching parent on nest	X		
As adult lands on nest	X		
Landing on nest	X		
As adult tries to brood, shade it	X		
Walking across nest	X		
In contact with adult after approach		X	
Seeking food from parent		X	

to be brooded and by fledglings landing at the nest after short flights. When seeking brooding, the chick lowers its head as it pushes its way under the body of the adult. Once the chick is brooded or shaded, it immediately stops giving HC. Chicks 1–14 days old ($n = 44$) that I displaced from their nests gave HC when left alone on the ground, but after about age 14 days, all chicks ($n = 31$) remained silent when similarly displaced if not otherwise disturbed. Adults respond to these calls with brooding, shading, and preening, usually calling with the Low Ker, a short contact note composed of discrete low-frequency clicks (around 1,452 Hz), repeated in a series, and with the bill pointed downward.

Screech.—Screech is composed of wide-band segments and whistles that occur in any order within notes (Fig. 5). This call covers the broadest frequency range of the chick vocalizations, from 153 to 7,666 Hz, and the frequency of the main sound energy band changes throughout the note. From 1 to 40 days of age, the mean of the peak frequency of the main sound energy

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Fig. 4. Postures associated with vocal signals of young Brown Noddies. Top: Normal upright associated with Harsh Cheep as 15-day-old chick stands on edge of nest. Center: Defensive threat posture associated with Screech of 15-day-old chick as it stretches its neck and bill forward, spreads its wings, and lunges toward intruder. Bottom: Horizontal body with head and neck low and scapulars slightly lifted is associated with Frequency-modulated Cheep of this 38-day-old nestling.

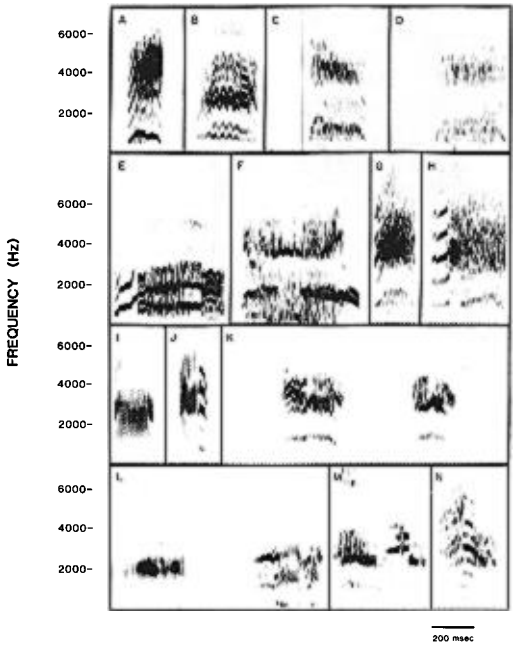

Fig. 5. Spectrograms of Screech of young Brown Noddies. The following grouped letters represent calls of the same individual. Chicks CD (age 3 days) and K (40 days) show that the form of the call of an individual may be consistently repeated. Chicks AB (7 days) and EF (14 days) show variations within individual repertoires. Changes in duration of parts of the note contribute to some of this variation (chick GH, 13 days; chick MN, 59 days). Some chicks begin to produce notes composed of discrete clicks during the nestling period (chick IJ, 37 days; chick L, 49 days), but these notes remain higher in frequency than adult notes. Filter band width is 300 Hz.

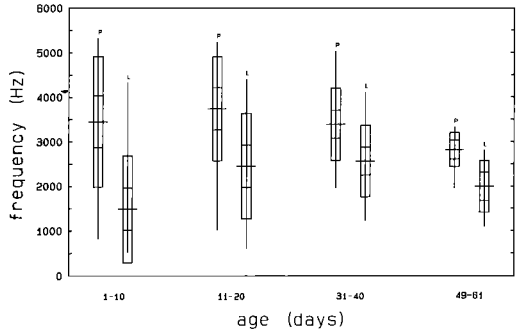

Fig. 6. Frequency of main sound energy band of Screech for four age classes as frequency changes throughout each note. P is the upper limit (peak) of the main sound energy band; L is the lower limit. Includes mean, 95% confidence limits (horizontal lines above and below mean), ±SD (delineated by box), and range.

band drops gradually (Fig. 6). The mean of the lowest frequency rises during the period from 1 to 30 days, after which it falls slightly. Thus, the range of frequencies through which the main sound energy band modulates narrows during the nestling and early fledgling periods, and the mean duration of these notes increases only slightly (Fig. 3).

Chicks that are alone on the nest Screech when an intruder appears (Table 2). Chicks turn toward and face the intruder, spread the wings to the side, and Screech (Fig. 4). Many also lunge toward and attempt to bite the intruder. These attacks continue until the intruder stops approaching or leaves, or until the nestling backs up and turns to face into the vegetation. Intruders remaining on the nest do not attack in return but turn away from the chick, point the bill down to the ground (Foot-looking, Cullen and Ashmole 1963), and stand on one edge of the nest until the chick moves to the opposite edge.

In each of the four age classes, the frequency of the main sound energy band of Screech is higher than that of Harsh Cheep, and the note lengths are longer. In many examples, Screech resembles a string of Harsh Cheeps with no internote intervals but with the main sound energy at a higher frequency.

Frequency-modulated Cheep.—Frequency-modulated Cheep (FMC) is a tone or whistle, often with side-bands, that rises in frequency after the onset and falls again after reaching a peak frequency (Fig. 7). The mean frequency of the peak is 1,777 Hz at age 1–10 days and generally increases throughout the nestling period, as do the means of the onset and offset (Fig. 8). The mean duration at 1–10 days of age is 392 ms, and this also increases throughout the nestling period (Fig. 3).

Nestlings give this call when they beg from adults, facing the adult at a right angle from the side (Table 2). Their bodies are horizontal with the head and neck low (hunched), and the crown is often lower than the scapulars on the back (Fig. 4). They raise the tip of the bill as they reach toward and nibble at the bill of the adult, calling simultaneously. A chick also gives this call when it is in contact with a parent after approaching the parent or after the parent moves toward it. Unlike HC, the chick is always stationary when giving FMC. The chick's

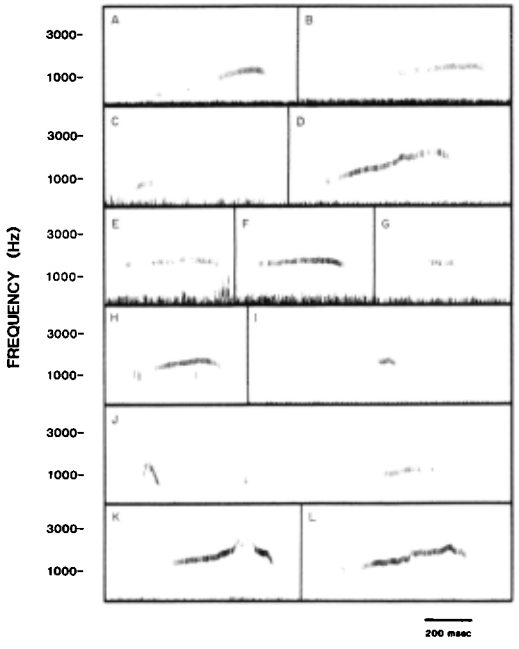

Fig. 7. Spectrograms of Frequency-modulated Cheep of young Brown Noddies. The following grouped letters represent calls of the same individual. The FMCs of chick AB (age 7 days) were recorded at the same time, but the onset of note A is lower than that of B, and the rates of change in frequency also differ. Chicks HI (23 days) and KL (45 days) show some variability within the individual repertoires. The notes of chick EFG (12 days) show that the forms are often consistently repeated. Chicks C (9 days) and D (13 days) show variation among individuals for their age classes. In some contexts, chicks may Harsh Cheep as they approach the parent, before they being to beg with FMC (chick J, age 24 days). Note Low Ker of adult is also given in these contexts (sections E, H, J). Filter band width is 300 Hz.

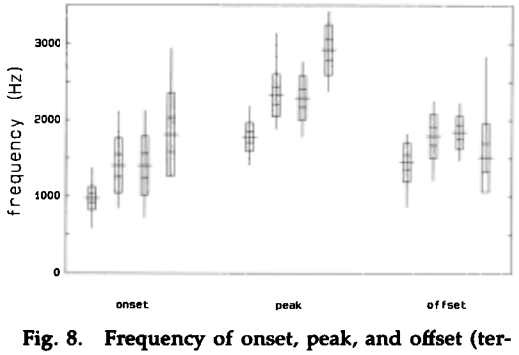

Fig. 8. Frequency of onset, peak, and offset (termination) of Frequency-modulated Cheep for four age classes. From left to right for each section: 1-10 days, 11-20, 21-30, 44-62. Includes mean, 95% confidence limits (horizontal lines above and below mean), ±SD (delineated by box), and range.

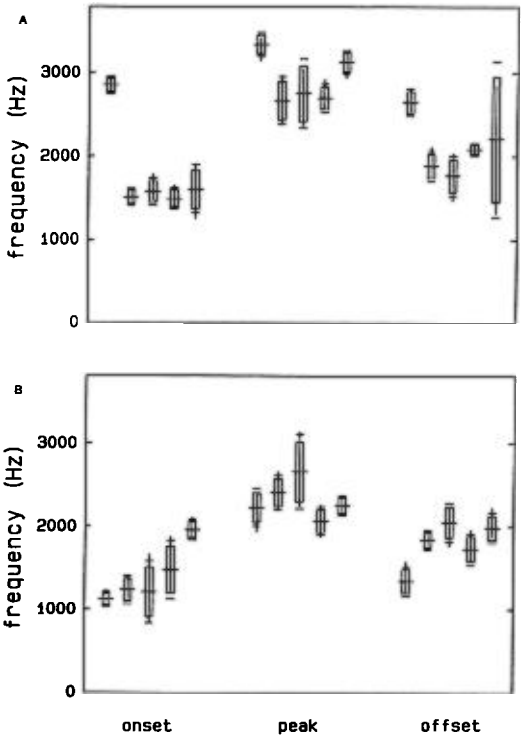

Fig. 9. Frequency of onset, peak, and offset of Frequency-modulated Cheep of five individuals from each of age classes 11-20 days (A) and 44-62 days (B). Order of individuals is the same for each section. Includes mean, 95% confidence limits (horizontal lines above and below mean), ±SD (delineated by box), and range.

body is horizontal, and it often has its neck withdrawn. It sometimes begins to beg as it continues to FMC, or it may stand silently near the parent.

I examined 5 calls from each of five individuals in the 11-20 and the 44-62 (days) age classes. Differences exist among individuals in the mean frequency of the onset, peak, and offset of FMC in both age classes (Fig. 9). As with HC and Screech, variation occurs among successive calls of one individual and between individual repertoires.

DISCUSSION

The common element among the contexts in which Harsh Cheep is given is that a chick is in motion or that it is out of the nest. The meaning to the adult is that it should locate and monitor the chick, approach it, and pro-

vide care. The type of care depends upon the location, condition, and subsequent behavior of the nestling. Harsh Cheep of nestlings is analogous to Low Ker of adults, as adults give Low Ker in the same contexts in which nestlings give Harsh Cheep, and both calls precede a decrease in distance between mates or between adults and young. Low Ker may be derived from Harsh Cheep, but there are no data on the vocal behavior of one- and two-year-old juveniles.

The common element among the contexts in which Screech is given is that the chick is endangered by an intruder. The message of the caller is threat of attack to an intruder or of retaliation. The meaning to the receiver is that it risks attack if it continues to approach. The nestlings' Screech is analogous to various aggressive calls of the adults' repertoire, as they are used in similar contexts and precede or accompany the departure of an intruder. Screech probably develops into these three adult calls, shortening as the Bite Call, lengthening as the R-call, and becoming repetitive as the Long Caw as the clicks became more distinct and the tonal elements disappeared. The frequency of the most intense sound energy band is higher in Screech than in these adult calls, even though it decreases throughout the nestling period.

The common elements among contexts for Frequency-modulated Cheep are that the chick is stationary, horizontal, and seeking food from the adult, in close contact with the adult, or reaching across the nest toward the adult. The message of the caller is that it is hungry, and the meaning to the adult is that it should feed the chick on the nest. FMC may stimulate regurgitation by adults, and it may facilitate the coordination of adult and young during feeding bouts as chicks remove partially digested food directly from the throat of the parent. FMC is used in similar contexts as Soft Buzz (an irregular string of low-amplitude clicks) by adult noddies, although the structures of the calls differ greatly. FMCs of young birds increase from one-third to only one-half the length of Soft Buzz of adults by age 62 days, but they remain whistles throughout this period and are higher in frequency than Soft Buzz. These FMCs increase in amplitude throughout the nestling period and dominate the acoustic atmosphere in the colony well after chicks that have begun to fly are still being fed at the nest by their parents.

Nest defense and self-defense by young Brown Noddies (with Screech) is unusual among young larids, particularly for 1-day-old nestlings. Noddy nests in the Dry Tortugas serve as fixed sites where young are fed by their parents for an extended period of time even after they have begun to fly (Riska 1984). When breeding adults are away from the colony and feeding at sea, nonbreeding birds commonly attempt to perform nest-building and courtship activities on, and steal nest material from, temporarily unattended nests. Many of these nests contain chicks that successfully drive off intruders. Cullen and Ashmole (1963) also observed that nestling Black Noddies defend their ledge nests against intruding adults on Ascension Island. Moynihan (1959b) observed attack behavior in young Franklin's and Ring-billed gulls within one week after hatching.

The similarity in plumage pattern of feathered young Brown Noddies to the adults is also unusual among larids. These nestlings have dull brown body, wing, and tail feathers like those of adults and white on the top of the head, but the white may be limited to the forehead only. Many of the dark downy nestlings also have a white crown. Black Noddy nestlings have the color pattern of the adults in both their downy and feathered plumage; they are also fed at the nest for an extended period of time after they have begun to fly. Plumage patterns of young of ground-nesting species that do not defend their nest sites do not resemble those of adults.

The vocal repertoire of young Sooty Terns, which is composed of tonal elements with side bands and elaborate patterns of frequency modulation, changes during the nestling period, resulting in more adultlike calls. Moynihan also observed modifications in Juvenile Long Calls and adultlike Pumping in Franklin's and Ring-billed gulls during the nestling period. Unlike these species, young Brown Noddy vocalizations change little during the nestling and early fledgling periods and have little resemblance to the adult repertoire.

Literature Cited

Collias, N., & M. Joos. 1953. The spectrographic analysis of sound signals of the domestic fowl. Behaviour 5: 175–188.

Cosens, S. E. 1981. Development of vocalizations in the American Coot. Can. J. Zool. 59: 1921–1928.

CULLEN, E. 1957. Adaptations of the Kittiwake to cliff-nesting. Ibis 99: 275–302.

CULLEN, J. M., & N. P. ASHMOLE. 1963. The Black Noddy *Anous tenuirostris* on Ascension Island. Part 2. Behaviour. Ibis 103b: 423–446.

DAVIES, S. J. J. F., & R. CARRICK. 1962. On the ability of Crested Terns, *Sterna bergii*, to recognize their own chicks. Australian J. Zool. 10: 171–177.

IMPEKOVEN, M. 1971. Calls of very young Black-headed Gull chicks under different motivational states. Ibis 113: 91–96.

MOYNIHAN, M. 1959a. A revision of the family Laridae (Aves). Amer. Mus. Novitates No. 1928.

———. 1959b. Notes on the behavior of some North American gulls. IV. The ontogeny of hostile behaviour and display patterns. Behaviour 14: 214–239.

RISKA, D. 1984. Experiments on nestling recognition by Brown Noddies (*Anous stolidus*). Auk 101: 605–609.

———. 1986. An analysis of vocal communication in the adult Brown Noddy (*Anous stolidus*). Auk 103: 359–369.

SCHLEIDT, W. M., & M. D. SHALTER. 1975. Stereotypy of a fixed action pattern during ontogeny in *Coturnix coturnix coturnix*. Z. Tierpsychol. 33: 35–37.

TEKTRONIX, INC. 1978. 4081 Graphic System operator's reference. Manual #070-1950-00. Beaverton, Oregon, Tektronix, Inc.

SMITH, W. J. 1977. The behavior of communicating. Cambridge, Massachusetts, Harvard Univ. Press.

WILKINSON, R., & C. R. HUXLEY. 1978. Vocalizations of chicks and juveniles and the development of adult calls in the Aldabra White-throated Rail *Dryolimnas cuvieri aldabranus* (Aves: Rallidae). J. Zool., London 186: 487–505.