# AN ANALYSIS OF VOCAL COMMUNICATION IN THE ADULT BROWN NODDY (*ANOUS STOLIDUS*)

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ABSTRACT.—I analyzed vocal signals of marked adult Brown Noddies (*Anous stolidus*) throughout their nesting season in the Dry Tortugas, Florida from 1979 to 1982. The basic unit of the adult repertoire is a wide-band click, less than 4 msec duration, ranging in frequency from 200 to 3,300 Hz. I identified nine temporal arrangements of these clicks, which form the notes of the calls. These calls differ little in frequency range, but they differ in the mean frequency of the most intense sound energy band, in note duration, in the number of clicks per note, and in internote interval. These calls are used in different contexts, which sometimes overlap. Frequency, note duration, and internote interval do not differ between sexes. Mean frequency and note length varied among individuals for some calls. No tonal elements characteristic of calls of Brown Noddy nestlings remain in the adult repertoire. *Received 5 July 1985, accepted 15 November 1985.*

THE Brown Noddy has been considered to share behavior patterns with gulls and terns (Moynihan 1959), but apart from pioneer studies by Watson (1908) and Lashley (1915) in the Dry Tortugas, Florida, the study by Dorward and Ashmole (1963) on Ascension Island, and Moynihan's (1962) review of sexual and aggressive behavior, little is known of the communication behavior of this species. Approximately 100,000 Sooty Terns (*Sterna fuscata*) nest sympatrically with the Brown Noddy in the Dry Tortugas. Their vocalizations, of higher amplitude than those of the noddies, dominate the acoustic atmosphere in the colony early in the breeding season, and perhaps have led to the impression that vocalizations are relatively unimportant in the Brown Noddy. Using video and sound recordings I recorded vocalizations and the contexts in which they occur during interactions of individuals of known sex and breeding status.

There is a long tradition of study of communication in the Laridae. After examining a number of closely related species of gulls, Tinbergen and others proposed hypotheses about the function and evolution of social signals (Tinbergen 1952, 1959; Cullen 1957; Moynihan 1962; Beer 1975, 1976, 1977, 1979). Some analysis also has been done on the social behavior of terns in the subfamily Sterninae (Cullen 1956). Smith (1970, 1977) concentrated on other avian taxa and stressed that contexts in which social signals are given are important to the information conveyed by the signals (message-meaning analysis). This concept was suggested in the earlier works of Collias (1960) and Marler (1961). The "message" is information encoded in the signal that is descriptive of the signaler and independent of the context. It can be determined by examining the features common to all contexts in which it is used. The "meanings" (to the receivers) are based on the specific details of the context in which a call is given (e.g. location, presence of other individuals, sex and age class, prior experience, season, concurrent activities, or identity of the signaler) and may be interpreted from the responses of the recipients to the signal. Other workers, such as Ainley (1975) and Smith (1972), have also adopted this approach.

Gull and tern vocalizations traditionally were described verbally, but since the mid-1960's they have been portrayed visually on sound spectrograms (Stout et al. 1969, Massey 1976, Conover and Miller 1978, Moseley 1979, Hand 1981). Studies of the vocalizations of Sterninae generally have been of short duration and limited to a few kinds of vocal signals, or to vocalizations of unmarked individuals, and they have not analyzed the entire vocal repertoire spectrographically.

In this study I identify the vocalizations and the type of information carried by these signals. The study serves as a basis for a comparative analysis of Brown Noddy vocal communication with that of the Sooty Tern and other members of the Sterninae (Laridae). An understanding of vocal communication of the Brown Noddy, unusual itself among larids, will be an important addition to the information avail-

TABLE 1. Numbers of individual males and females analyzed and numbers of notes per individual.[a]

| | RC | LC | VIB | HK | LK | SB | RV | RT | BT |
|---|---|---|---|---|---|---|---|---|---|
| No. of males | 8 | 10 | 8 | 6 | 10 | 3 | 7 | 8 | 2 |
| No. of females | 5 | 4 | 3 | 6 | 6 | 8 | 3 | 2 | 2 |
| No. of notes measured/individual | 10 | 5 | 30 | 10 | 15 | 1 | 1 | 5 | 9 |
| Total no. of notes measured | 130 | 70 | 330 | 120 | 240 | 11 | 10 | 50 | 36 |

[a] RC = R-call, LC = Long Caw, VIB = Vibration, HK = High Ker, LK = Low Ker, SB = Soft Buzz, RV = Regurgitation Vocalization, RT = Rattle, BT = Bite Call.

able on breeding strategies employed by members of this family, thereby increasing our understanding of the origin and evolution of these signals.

## STUDY SITE 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. This included the period before adults frequented the colony during the day, pair formation, nest building, males feeding females before egg laying, incubation and hatching, feeding young, and young birds beginning to fly. In this colony Brown Noddies nest in trees and bushes, and Sooty Terns nest on the ground (Robertson 1964). In a selected area of the colony, I permanently marked active nests and, using individually distinctive color combinations, color-banded 137 adults caught by hand, with pull-string wire traps, or with butterfly nets. I determined the sex of 90 adults using behavioral cues, such as males feeding or mounting females. I observed no reversals of either during my study. Because I observed the same individuals and the same nest sites over the four study seasons, I believe this to be a reliable method of sexing this species.

Recordings of vocalizations were made 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. In all recording situations, the microphone head was 0.75–1.5 m from two to four nests under observation at one time. It was imperative that the microphone be close to the nest to pick up low-amplitude calls against the high-amplitude background noise of other birds, wind, and surf. Observations on the nature and context of the behavior of individuals were recorded from a blind where a number of nests could be viewed simultaneously. I observed 33–39 nests with color-banded adults each year.

Spectrograms were made on a Kay Sona-Graph model 6061B. These spectrograms were digitized on a Tektronix 4081 Graphic System (Tektronix, Inc. 1978) tablet with a density of 1,550 cross-wires/cm$^2$. The advantage of this technique over the traditional grid overlay is that the grid is finer, and the computer reads and records the x-y coordinates directly. I measured frequency range, frequency of most intense sound energy band (the darkest band in the narrow-band tracing), interclick interval (from midpoint to midpoint of adjacent clicks, for all intervals), note length (from the midpoint of the first click in a note to the last), and internote interval (from the terminal click of one note to the first click of the following note). All frequency measurements were from spectrograms made using the 45-Hz narrow band-pass filter, and all temporal measurements were from spectrograms made using the 300-Hz wide band-pass filter. Average numbers of clicks per note and click rates were calculated. Sample sizes differ among calls because low-amplitude calls were difficult to separate from the background noise of the colony (Table 1). Calls of known individuals of known sex were selected for analysis based upon the relative clarity of recordings.

## RESULTS

The basic unit of the Brown Noddy vocal repertoire is a broad-band click, less than 4 msec in duration (Fig. 1), ranging from 200 to 3,300 Hz. Clicks occur singly, in doublets, triplets, or in short runs, and individual clicks are not resolved completely by the human ear. Sounds formed by a rapid series of pulses have many side bands when analyzed using a narrow-band filter on the sound spectrograph. Many of these bands are harmonically unrelated, and there is unequal emphasis (or intensity) of the bands. This pattern depends on the repetition pattern of the clicks (Watkins 1966).

I identified nine calls composed of different temporal arrangements of these clicks. These different temporal arrangements I refer to as notes. A call is composed of one or more notes. Among the clicks, different frequency bands were emphasized, giving complex substructure to the notes. Notes within a call differed little in the overall frequency range, but the fre-

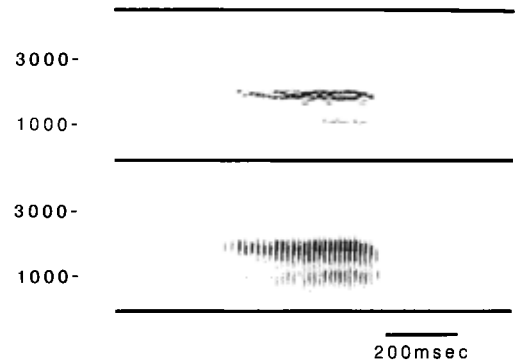


Fig. 1. Spectrograms of individual clicks of vocalizations of adult Brown Noddies (frequency in Hertz vs. time). The upper trace (filter band width 45 Hz) shows better frequency resolution. The lower trace (filter band width 300 Hz) shows better temporal resolution, illustrating the basic structure of the call. Clicks may be grouped in "notes," one or more of which make up each call.

quency of the most intense energy band differed (Fig. 2). Postures of birds while calling also differed among calls, as did positions of the bill and yellow-orange tongue, but the bend

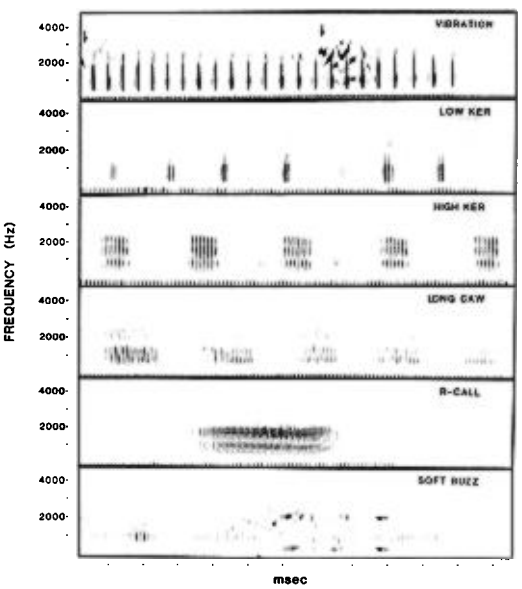


Fig. 2. Spectrograms of six calls from the vocal repertoire of the adult Brown Noddy. Filter band width is 300 Hz. Interval between tick marks on x-axis is 200 msec. Whistles with side bands are Sooty Tern in background (at arrows). The third note of High Ker is preceded and followed by Low Kers of another adult noddy.

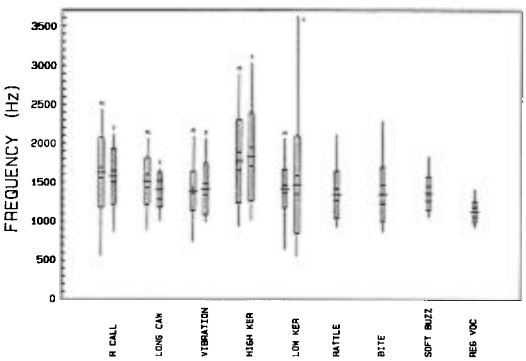


Fig. 3. Frequency of most intense sound energy band of calls from adult Brown Noddy vocal repertoire. Includes mean, 95% confidence limits (horizontal line above and below mean), ±SD (delineated by box), and range. Sexes (m and f) are labeled where analyzed separately.

of the wing remained covered by the contour body feathers.

## Calls of Adult Brown Noddies

*Soft Buzz* (Fig. 2).—Soft Buzz is a slow train of clicks with the most intense energy band at

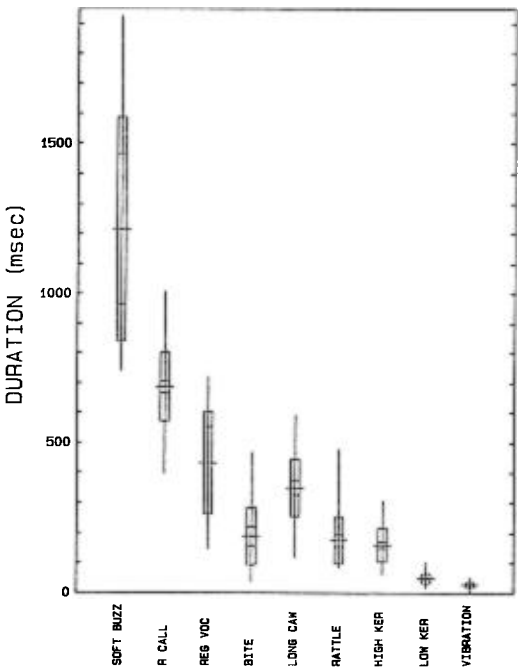


Fig. 4. Note lengths of adult Brown Noddy repertoire. Includes mean, 95% confidence limits (horizontal line above and below mean), ±SD (delineated by box), and range.

TABLE 2. Situations of adult Brown Noddy vocalizations.[a]

| Situation | RC | LC | BT | HK | LK | RT | VIB | SB | RV |
|---|---|---|---|---|---|---|---|---|---|
| Male and/or female on nest as a noddy flies over low or lands on or close to their nest | X | X | | | | X | X | | |
| Adult on nest to intruder (human, egret, Sooty Tern, rat) at or approaching nest | X | X | | | | | | | |
| Adult landing at nest after short absence (attack, feather-wet, defecate, circle) or long absence (feeding) | X | X | | | X | | | | |
| Adult on nest to nestling in neighbor's nest | X | X | | | | | | | |
| Parent on nest to own chick out of nest; not approaching | X | X | | | | | | | |
| Adult to any fledgling flying awkwardly to and from nests | X | X | | | | | | | |
| Adult in air, diving at and striking intruder (human, egret, Sooty Tern, other noddy) | X | | X | | | | | | |
| Adult hand-held by human, biting | | | X | | | | | | |
| Adult attacking another noddy, using bill to jab or bite | | X | X | | | | | | |
| Adult mounted by nonmate; bites throat and bill of intruding male; calls until male dismounts | | X | | | | | | | |
| Adult, while fleeing or pulling from grasp of attacking noddy or Sooty Tern | | X | | | | | | | |
| Adult flying over water or colony, alone or with other noddies | | | | X | | | | | |
| Adult leaving the nest, at initiation of short flights (collect nest material, circle, defecate, attack, feather-wet) or longer (feeding, such as after relieved by mate or in early morning), whether or not mate is present | | | | X | | | | | |
| Adult flying behind another noddy in high flight, following closely with synchronous wing beats | | | | X | X | | | | |
| Adult returning to nest with nest material, flying or walking; mate present, absent, or none | | | | | X | | | | |
| Adult placing nest material on nest | | | | | X | | | | |
| Adult on ground or in bush, in colony or on beach, probing potential nest material | | | | | X | | | | |
| Adult on nest as mate returns with nest material | | | | | X | | | | |
| Adult as it approaches mate on nest, such as during exchange | | | | | X | | | X | |
| Adult as it approaches chick on nest | | | | | X | | | | |
| Adult on nest as mate approaches | | | | | X | | | | |
| Adult on nest as mate leaves the nest | | | | | X | | | | |
| Adult as it leaves mate or chick on nest, such as after relieved or after chick fed | | | | | X | | | | |
| Parent feeding, preening, brooding, or shading chick | | | | | X | | | | |
| Parent approaching chick alone on nest or out of nest | | | | | X | | | | |
| Parent as chick appproaches it on or out of nest | | | | | X | | | | |
| Male or female between bouts of courtship feeding, nest building, copulating | | | | | X | | | | |
| Adult while mate VIB as noddy intruder stands on edge of nest | | | | | X | | | | |
| Male on nest, mate or unmated female near his nest; female may approach male | | | | | X | | | | |
| Male while copulating with female on nest | | | | | X | | | | |
| Female while begging from male | | | | | | | | X | |
| Male and/or female as one preens the other | | | | | | | | X | |
| Male and/or female prior to mounting by male | | | | | | | | X | |
| Male feeding female, just before or during regurgitation of food | | | | | | | | | X |
| Parent regurgitating to chick | | | | | | | | | X |

[a] RC = R-call, LC = Long Caw, BT = Bite Call, HK = High Ker, LK = Low Ker, RT = Rattle, VIB = Vibration, SB = Soft Buzz, RV = Regurgitation Vocalization.

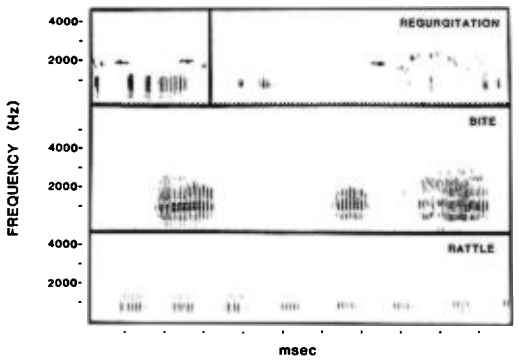


Fig. 5. Spectrograms of three calls from the vocal repertoire of the adult Brown Noddy. Two examples of Regurgitation Vocalization from different birds illustrate the range of variability within the call. Filter band width is 300 Hz. Interval between tick marks on x-axis is 200 msec. Whistles with side bands are high-amplitude calls of Sooty Tern in the background (at arrows).

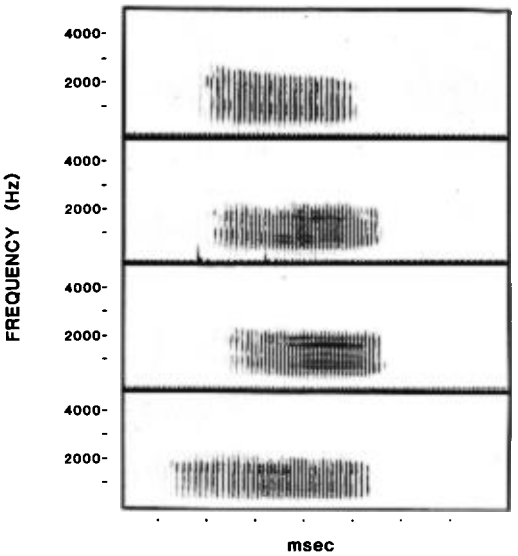


Fig. 6. Four examples of R-call by male L-dgS on his nest as neighboring female lgO-S approaches her own nest. Filter band width is 300 Hz. Interval between tick marks on x-axis is 200 msec. All recordings made at one session.

1,364 Hz (Fig. 3). It may last as long as 2 s but is highly variable in length (Fig. 4). The amplitude rises and falls as the call progresses but remains low relative to other calls. It is given by birds preening or being preened by their mates, by females seeking food from males, or by birds approaching their mates (Table 2). The caller is usually in physical contact with the other bird and stands with the body and neck low and horizontal. The bill is extended toward the mate but remains closed or opens only slightly. Recipients of preening often Soft Buzz or Low Ker (see below) with the bill pointed downward. Before mounting females for copulation, males preen the female while Soft Buzzing, but Soft Buzz does not continue through copulation.

*Regurgitation Vocalization* (Fig. 5).—Regurgitation Vocalization has the lowest amplitude and the lowest frequency of all calls (1,128 Hz, Fig. 3). Long interclick intervals occur in the middle of some calls, giving them a segmented structure, and they are highly variable in length (Fig. 4). The call is given by a male or female as it begins to lower and stretch its neck forward to a begging nestling, or to a female begging from a male (Table 2), and the caller may continue until the recipient begins to feed.

*R-call* (Fig. 2).—This call consists of single notes of mean duration 687 ms (Fig. 4) and of high amplitude. The click rate speeds as the call progresses but may slow again at the end. The most intense energy band is around 1,610 Hz (Fig. 3), but the frequency of this main band may rise or fall during the call. It is given when there is an intruder at or near the nest, and also when a bird's own chick of any age is out of the nest (Table 2). The caller turns toward the receiver, either turning the entire body or only the head and neck, just before the call is given, but turns the head forward again, along the axis of its body, while calling. The neck is extended with the tip of the bill raised slightly, and is retracted at the end of delivery. The caller's bill is open wide and the base of the tongue is raised, but the tip is lower inside the anterior end of the mandible. It is often followed by an attack.

Adult Brown Noddies and Sooty Terns turn away from the R-caller or leave. Birds that are attempting to land continue flying or, if they land, turn away. Birds on the nest when an R-calling mate lands turn away but may turn back and gape, exposing the bright orange tongue and mouth. Chicks in or out of the nest either approach the R-calling parent or the nest (if the parent is out of the chick's reach, such as on a limb above the nest), walking with the body and neck horizontal, or remain standing and turn away. Mates and nestlings also point

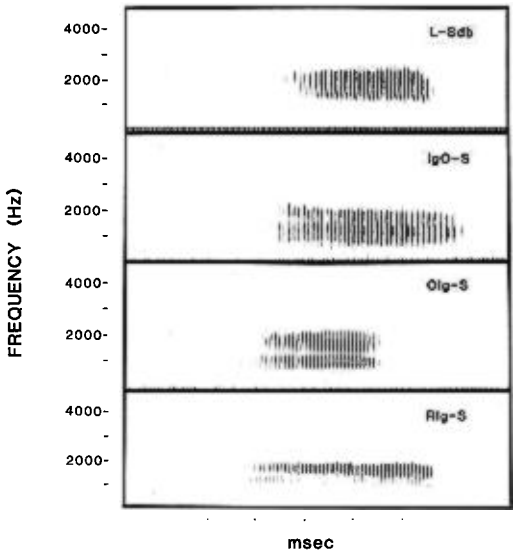


Fig. 7. R-calls from four individual adult Brown Noddies. L-Sdb and lgO-S are female; Olg-S and Rlg-S are male. Filter band width is 300 Hz. Interval between tick marks on x-axis is 200 msec.

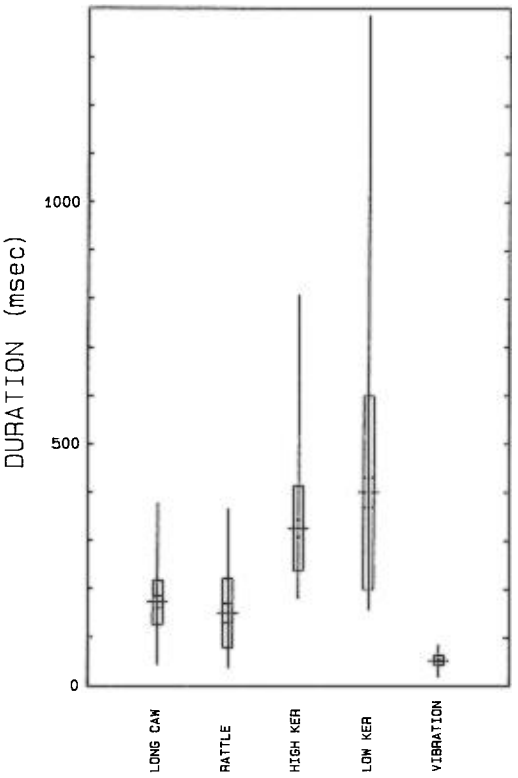


Fig. 8. Internote intervals for calls in adult Brown Noddy vocal repertoire. Includes mean, 95% confidence limits (horizontal line above and below mean), ±SD (delineated by box), and range.

the bill down vertically, and the caller usually responds in turn. These Foot-looks, which are similar to those observed in other larids (Le Croy 1976), also occur among neighboring birds after R-calls are exchanged.

Both the high degree of variation and the consistency among one individual's R-calls is obvious in spectrograms of 4 R-calls of male L-dgS (Fig. 6). Variation in R-call among 4 individuals is illustrated in Fig. 7. Note that all individuals differ from L-dgS, and from each other, in changes in the major energy bands throughout the calls.

*Long Caw* (Fig. 2).—The notes of the Long Caw, which occur in a series, are shorter than the R-call. The number of notes delivered varies from 2 to many, depending on the responses of the intruder or receivers. These notes have the highest amplitude, but the amplitudes of the notes in a series differ. The most intense energy band is around 1,495 Hz (Fig. 3), and the mean note length (Fig. 4) is twice that of the internote interval (Fig. 8). These calls are given in situations similar to those of R-calls (Table 2). The body of the bird extends upward obliquely but becomes horizontal as the call progresses. When calls are directed at a given individual, the caller, as in the R-call, turns toward the individual while calling; the bill is pointed toward or away from the receiver. The tip of the tongue is depressed and the broader base is elevated, as in the R-call, but the bill does not close completely between notes. The caller may attack and continue calling while gripping its adversary in its bill. The Long Caw series is often preceded or followed by R-calls, and responses to Long Caw are similar to those of R-call, although recipients of Long Caw that are not neighbors, mates, or offspring leave almost immediately unless they are grabbed by the caller.

*Bite Call* (Fig. 5).—This is a specific call with the highest click rate (Table 3). It resembles individual Long Caw notes but is shorter and is not repeated in a series. It is given each time a bird grabs an intruder or strikes from the air (Table 2). The most intense sound energy band averages 1,354 Hz (Fig. 3), and, as with R-call and Long Caw, the amplitude is high. Recipients either Long Caw in return, return the peck, or attempt to escape.

*Low Ker* (Fig. 2).—Low Ker is a series of short notes of mean length 49 ms (Fig. 4), and its most intense energy band is around 1,452 Hz (Fig. 3). The internote interval is highly variable (Fig. 8), and I have heard Low Ker notes emitted singly. These calls are given during nest building, changes in incubation and brooding shifts, and during interactions with a mate, potential mate, or chick on the nest (Table 2). The bird stands either with the neck arched and bill pointed down, or with the body and head low and oblique, and the bill pointed forward. The caller may be turned as much as 180° away. Even when facing the receiver, the bill is oriented away (down or to the side) and is opened only slightly.

Low Ker is nearly always given at the nest site, the exception being in nonterritorial areas, such as the beach and the ground beneath nest sites, where birds collect nest material. Birds Low Ker while building on the nest even if their mates are temporarily away or if they have no mate. Unpaired males use loud Low Kers, which attract other birds to the nest site. Females approach the nest standing on the edge, facing away from the nest and the male, and they continue approaching if the male does not R-call, Long Caw, Bite Call, or attack. This pattern of approach and retreat continues with a series of females before a pair is formed. Physical contact usually is made between mates during changes in incubation shifts as they pass on the nest, both Low Kerring; however, the mate ceases Low Kerring or shifts to the High Ker (below) once it is relieved. When parents Low Ker their nestlings approach or remain close, and the nestlings may seek brooding or food from the calling adult.

*High Ker* (Fig. 2).—High Ker is a series of notes given before a bird takes flight and while it is in flight. The most intense energy band is 1,800 Hz (Fig. 3), the highest of all calls. The caller stands in a normal upright posture with the bill at or slightly above horizontal, facing forward or turning its head slowly from side to side. The bill closes completely between notes. The tip of the tongue is raised high above the mandible, but its base is lower in the back of the mouth. Birds that give this call from a perch or from the ground almost without exception take flight while calling, or are in flight either over water or over the colony. High Ker is given before long and short flights (Table 2). The mate of the High Ker caller may Low Ker with the bill pointed down until the High Ker caller leaves the nest, after which the mate immediately ceases Low Ker. Neighboring birds often begin to High Ker and fly after the original caller; some circle and return immediately to their nests while the remainder fly out of the colony.

TABLE 3. Mean numbers of clicks per note and click rates within notes.[a]

| | *n* | Mean clicks/note | Mean clicks/100 msec |
|---|---|---|---|
| RV | 11,670 | 95 | 14 |
| LC | 3,631 | 57 | 16 |
| VIB | 1,389 | 5 | 19 |
| HK | 1,982 | 21 | 13 |
| LK | 1,409 | 9 | 17 |
| SB | 1,103 | 101 | 8 |
| RV | 343 | 35 | 8 |
| RT | 1,277 | 23 | 13 |
| BT | 1,466 | 40 | 21 |

[a] RC = R-call, LC = Long Caw, VIB = Vibration, HK = High Ker, LK = Low Ker, SB = Soft Buzz, RV = Regurgitation Vocalization, RT = Rattle, BT = Bite Call.

*Vibration and Rattle* (Figs. 2 and 5).—Vibration is a series composed of the shortest of the notes. Internote intervals are also shorter than any other call (Fig. 8), and the click rate within notes is high (Table 3). The most intense sound energy band averages 1,429 Hz (Fig. 3). This call is given by a resident when a noddy intruder arrives at the nest while both adults, or an adult and its chick, are present. I never heard this call when a resident was alone as an intruder approached. The calling bird stands with its neck and head obliquely forward and up, and with the bill held slightly above horizontal. It turns its head slowly from side to side and opens the bill only slightly, giving the appearance that the bill and body are vibrating. The tongue and mouth lining are not visible. When the caller is not turning its head, its bill is turned away from both the intruding bird and the other resident bird. The posture and side-to-side movement of the head may continue after the bird ceases calling.

Vibration usually grades into Rattle; however, Rattle may occur alone. It resembles the High Ker but has shorter internote intervals (Fig. 8), and the individual notes often are not resolved by the human listener, giving the call a rolling quality. The posture and movements of the bill are the same as for Vibration, or the

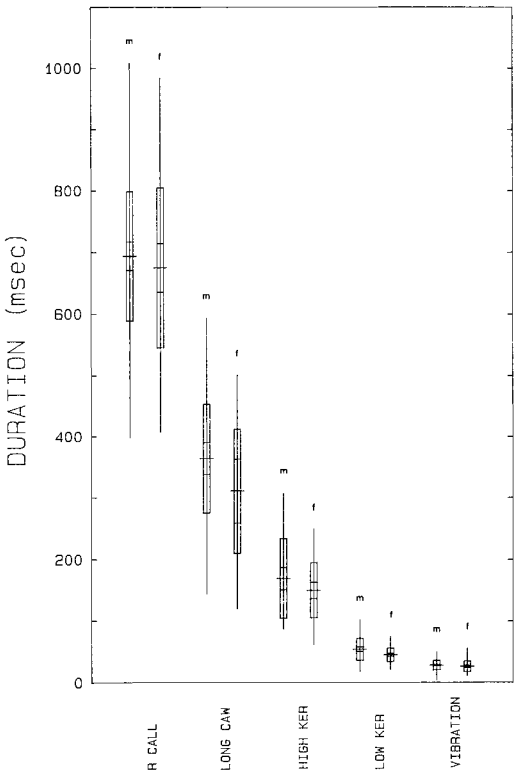


Fig. 9. Note lengths of adult Brown Noddy vocal repertoire. Males (m) and females (f) are labeled. Includes mean, 95% confidence limits (horizontal line above and below mean), ±SD (delineated by box), and range.

bill may be momentarily vertically downward. Amplitude rises and falls throughout the series. Call length varies, and bouts of Vibration and Rattle often alternate with little pause. If the caller's mate is present, it may join in with the Vibration and Rattle, or it may give a bout of Low Ker with the head low and bill pointed downward. Intruders turn away and leave or continue flying if they were attempting to land. Vibration and Rattle continue until the intruder leaves, or until a resident Long Caws and then attacks.

### Temporal Patterns of Calls

The calls can be distinguished easily from one another by a combination of factors including note length, internote interval, number of clicks per note, and whether the call consists of a single note or a series of notes.

Soft Buzz, R-call, Regurgitation Vocalization, and Bite Call occur as single notes, and the others are series of repeated notes. Bite Call, Rattle, and High Ker are notes of similar length, but Bite Call is composed of twice as many clicks per note as either Rattle or High Ker (Table 3), and it is not repeated in a series. Notes of Rattle and High Ker have similar numbers of clicks, but the mean internote interval of High Ker is twice that of Rattle (Fig. 8). Long Caw notes are repeated at the same internote intervals, are longer, and have 2.5 times as many clicks as Rattle does.

Low Ker and Vibration notes, the shortest notes in the repertoire, overlap in their note-length ranges but differ in internote interval by a factor of 8 (Table 3). The same number of clicks in the Soft Buzz (mean values of 101 clicks in 1,205 ms) are compressed in the shorter R-call (mean values of 95 clicks in 687 ms).

### Comparison of Sexes

There were no sex differences in the frequency of the most intense sound energy bands for the five calls for which sexes were analyzed separately (Fig. 3). Male notes tended to be slightly longer in duration than those of females in all calls except Vibration, but the 95% confidence intervals overlapped for all calls except Low Ker (Fig. 9). Thus, the mean values for males and females are the same.

### Comparison with Young Noddies

Vocalizations of Brown Noddy nestlings (Riska 1986) are different from those of adults in that they are composed of tonal elements with side bands as well as bursts of sound over a wide frequency range, and the major sound energy bands are 500–2,000 Hz higher. Short discrete clicks like those in adult notes are extremely rare.

## Discussion

In the Dry Tortugas, the amplitude of the noise of the Sooty Tern colony is higher than that of the Brown Noddies, and without a microphone at the nest many of the noddy vocalizations would be missed. For Low Ker, Soft Buzz, and Vibration, direct observation of the birds is often necessary to determine which are calling. The structure of the vocalizations also leads to confusion when the calls are first heard

by a human observer, but they become unmistakably distinguishable to the listener with experience. In dense colonies it is difficult (and often would be wrong) to say that a caller is directing its message to only a single bird. Recipients pick up signals from many individuals calling simultaneously. When analyzing calls, one must account for an obvious individual near the nest and also for birds flying low over the nest and birds active at neighboring nests.

R-call and Long Caw may have similar messages that warn an intruder of attack if the caller is approached or if the intruder fails to retreat. Birds that give Long Caw while they are being attacked warn of possible return attacks. The meanings to receivers also may be similar. Intruders should retreat from the caller because the latter will attack if approached further. It is difficult to state which of these calls is of higher intensity because both Bite Call and Long Caw are given during actual fighting. When approached on the nest by a human intruder, R-calls are given well before Long Caw, and Long Caw may not be given until the intruder is next to the calling bird. When a bird gives the Long Caw as it flies to its nest, the meaning to neighbors may be that it is ready to defend its territory, or it may be responding to birds that R-call and Long Caw as it flies over their nests. In addition, Long Caw may signal readiness to interact with its mate (in nest exchange) or chicks (feeding, brooding, shading).

Multiple meanings of R-call and Long Caw are also illustrated in the context of calling to chicks outside the nest. While an adult may use these calls to warn of attack to any potential source of harm to its chick, the meaning to the chick may be that the adult is ready to defend it and that its route to the nest or to the adult is safe. The chick can detect intruders as well as detect an adult on its nest, and it may use this contextual information to determine the relative safety of moving toward the nest.

The message of High Ker is intent to leave the nest for short or long periods. Because it is never given by birds returning to the nest, to the caller's mate or its nestling it may mean that the caller is leaving the territory and terminating interaction. It may also mean that the bird flying over other nests is not a territorial challenger. Brown Noddies feed in flocks at sea, and data based on marked individuals show that neighbors return to their nests in groups. Thus, advertising a departure may recruit foraging partners and facilitate locating schools of fish. At sea, High Ker may signal the location of individuals.

The message of Low Ker may be willingness to approach, allow approach, or maintain contact or interaction. When given by a bird gathering nest material near territories of other birds, the meaning to recipients may be that the individual intends to move near without challenging. To mates, potential mates, or offspring Low Ker may mean that it is safe to continue approach or remain near the caller, but to intruders the meaning may be based on the inference that the caller is part of an established family unit or that the nest site has current residents.

The message of Vibration and Rattle may be readiness to attack an intruder, for they occur only when an intruder is at the nest. The message is also readiness to remain with the site and associate. The meanings of these calls differ for the intruder and for the chick or the mate of the caller, as the responses are different. To the intruder, it means the caller will attack. Because the caller drives off an intruder but not the mate or offspring, to mates and offspring it means they will not be attacked. Vibration resembles Low Ker in that notes are short and repetitive, but the shorter internote intervals may give Vibration some characteristics of R-call while retaining features of Low Ker.

The message of Regurgitation Vocalization may be that the caller is about to disgorge partially digested food. The meaning to females and nestlings may be that they must move into position to take the food. Birds seeking food enter with their own bill at a right angle to the feeder's bill, scooping out partially digested food. This orientation is similar to the Black-legged Kittiwake (*Rissa tridactyla*; Cullen 1957) when feeding offspring at the nest.

The message of Soft Buzz is that the caller seeks or seeks to maintain close physical contact for some nonattack interaction. To the receiver, it means the caller wants food, is ready to preen or mate, or will remain in contact; the specifics depend on the consequent or subsequent behavior of the caller.

Darwin (1872) hypothesized that in a species' communication repertoire, signals of opposite function would be sufficiently distinguishable in form to reduce or prevent ambiguity. R-call and Long Caw are given during attack or as a

warning of attack, while the short repetitive notes of Low Ker are given during close interaction between mates or between parents and young. Soft Buzz is the longest note in the repertoire, longer than R-call, and facilitates close contact between members of a pair. Vibration, which is a regular and rapid series of the shortest notes in the repertoire, drives conspecific intruders away from the territory of a mated pair. Soft Buzz is, however, lower in amplitude and in frequency than Long Caw and R-call (Fig. 1).

The postures of the bird during these calls are also different. During Vibration, the bill is raised slightly above horizontal while the neck is stretched obliquely upward. During Long Caw and R-call, the neck and bill are stretched nearly horizontal. During Low Ker, the neck is either stretched obliquely downward and the bill is in line with the neck, or the neck is withdrawn and the bill is pointed downward, often vertically.

Moynihan's (1962) extensive observations in the central Pacific offered much insight into Brown Noddy behavior. However, he did not record vocalizations at the nest. He divided noddy vocalizations into three categories: Long Caws, which I believe are the same as my category of R-call; Rapid Caws, the same as my category of Long Caw; and Rattles, a grouping of my categories of Low Ker, Vibration, Rattle, and perhaps Soft Buzz. Moynihan may have observed only one context in which Low Ker occurs (Choking display) and no Soft Buzz or High Ker because he stated that all Rattles "are almost certainly threat." He also stated that landing birds are often silent, even when landing beside other birds. In the Dry Tortugas, Long Caw, R-call, and Low Ker are given regularly upon returning to the nest, whether or not the mate is present, and the loudest Low Kers are given in this context. Moynihan stated that Rapid Cawing is "by far the most common, almost only, call uttered by birds during real aerial flights," suggesting he lumps High Ker with Long Caw; as indicated in my study, however, the uses of these calls do not overlap.

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