

# INDIVIDUAL AUDITORY RECOGNITION IN THE LEAST TERN (*STERNA ALBIFRONS*)

LYNN J. MOSELEY<sup>1</sup>

*Department of Zoology, University of North Carolina, Chapel Hill, North Carolina 27514 USA*

ABSTRACT.—Playback experiments performed in a colony of Least Terns near Fort Macon, North Carolina, demonstrated that adults can distinguish the call of their mate from that of a stranger. Sonagram analysis of the "Purrit-tit-tit" call, the most common vocalization used when an adult approaches its mate, revealed that both temporal and spectral characteristics of the first note of the call varied significantly among individuals, whereas all measured features of the second note were not significantly different for different birds. Presumably the first note is used to convey an individual's identity, while the second note indicates a tendency to approach the mate and perform certain courtship behaviors. *Received 17 January 1978, accepted 26 March 1978.*

IN his review of individual auditory recognition in birds, Beer (1970a) stated that the best evidence for the existence of vocal recognition comes either from colonial species, for which the omnidirectional properties of sound far exceed those of visual signals in a crowded colony, or from species that inhabit thick vegetation, as foliage obstructs vision but does not greatly hinder sound transmission. This study examines vocal recognition between mates in the Least Tern (*Sterna albifrons*), a colonially-nesting larid.

Individual recognition by voice has been hypothesized for several species of colonial birds and documented for a few. Most investigations deal with auditory communication between members of a mated pair or between parent birds and their young. According to Beer, investigators have used three approaches in the study of vocal recognition in birds: field observation, sound analysis, and playback experiments. Field observation has provided circumstantial evidence for the existence of auditory recognition between mates in several colonial species (e.g. *Sterna hirundo*, Tinbergen 1931 and Palmer 1941; *Larus argentatus*, Tinbergen 1953) and between parents and offspring (e.g. *S. fuscata*, Watson and Lashley 1915; *L. argentatus*, Goethe 1937; *S. sandvicensis*, Hutchinson et al. 1968). However, some method of experimentation is usually necessary to eliminate the possibility that a bird is actually responding to visual rather than auditory stimuli, as in most cases colonial birds can see as well as hear one another (Beer 1970a).

Several investigators have performed experiments to test the ability of parent birds to recognize their own chicks. Although individual recognition of chicks has been demonstrated for several species of colonial nesters (e.g. *Anous stolidus* and *S. fuscata*, Lashley 1913; *S. bergii*, Davies and Carrick 1962; *S. maxima*, Buckley and Buckley 1972), such experiments usually do not reveal the relative importance of visual and auditory modalities for such recognition. However, Miller and Emlen's (1974) study of the effect of altering a chick's voice and appearance on the recognition of young by their parents in the Ring-billed Gull (*Larus delawarensis*) revealed that vocally impaired chicks 12 to 20 days old were accepted whereas visually altered chicks were not. In some species, at least, visual rather than auditory stimuli are important for the development of chick recognition.

Experiments involving the recognition of parents' voices by chicks have met with somewhat more success due to the ease with which chicks can be manipulated.

<sup>1</sup> Present address: Department of Biology, Guilford College, Greensboro, North Carolina 27410 USA.

Controlled playback experiments, performed under both natural and laboratory conditions, demonstrate that in most cases chicks of colonial species clearly distinguish between the voice of a parent and the voice of a strange adult (*Uria aalge*, Tschanz 1968; *L. atricilla*, Beer 1969, 1970b; *S. hirundo*, Stevenson et. al. 1970). White (1971) reported that chicks of the Gannet (*Sula bassana*) seem to have the ability to recognize the voice of a parent in a playback test, but do not always do so. Presumably in this species there is no particular advantage for vocal recognition between parents and young since, unlike the species listed above, Gannet chicks are not mobile and remain on the nest until fledging.

Investigators have also studied the ability of adult birds to discriminate the call of the mate from that of other adults in the colony. Hutchinson et. al. (1968) recorded "fish calls" from 40 adult Sandwich Terns (*S. sandvicensis*) and analyzed various temporal and spectral parameters of sonagrams of these calls. They concluded that the general "patterning" of the call was always characteristic for each individual. However, they were unable to perform playback experiments to test whether the adults did, in fact, use such characteristics to identify their mates by voice. They were also unable to record more than one sequence of vocalizations from each individual. Intra-individual variation is probably greater among calls from different sequences than among calls in the same sequence (see below). In a more conclusive investigation, playbacks showed that adult Gannets recognize vocalizations of their mates (White 1971). Sonagram analysis of landing calls of individual Gannets suggested that recognition resulted from individually consistent temporal changes in amplitude (White and White 1970).

To demonstrate individual auditory recognition, playback experiments must show that test birds respond selectively to vocalizations from different individuals. Analysis of physical characteristics of the vocalization should reveal one or more sources of interindividual variation. Using this procedure, I investigated auditory recognition between mates in Least Terns. On numerous occasions, I observed that an individual sitting quietly on its nest would suddenly stand and call repeatedly just as its mate, vocalizing loudly, approached the territory. Vocalizations of other individuals were always ignored. Least Terns are colonial nesters that form stable pair bonds for at least one, and possibly several, breeding seasons. Both the male and female participate in incubating the eggs and raising the young. During the incubation period, members of a pair alternate incubation duties approximately every hour (Moseley 1976). On some occasions, particularly during the first few days of incubation, nest relief ceremonies involve a brief period of visual and vocal displays between mates near the nest. However, after about a week of incubation, members of a pair become very efficient at switching places, to the extent that an incubating bird leaves the nest and flies out of the colony, vocalizing repeatedly, at what seems to be the instant it hears the voice of its mate. Auditory signals appeared to be the primary mode of communication in such interactions.

I therefore performed a series of playback experiments designed to test the ability of adult Least Terns to recognize the call of their mates. I have previously identified 10 discrete vocalizations of adult Least Terns (Moseley 1976). The vocalization that is typically associated with approach to the nest and courtship behavior between mates, and the call that occurred most frequently in playback sequences, was the "Purrit-tit-tit," named by Schönert (1961). This vocalization is a 4- or 5-syllabled call approximately 0.5 s in duration, with the dominant frequency of most syllables between 4–5 kHz (Fig. 1). It was nearly impossible to establish by ear which physical

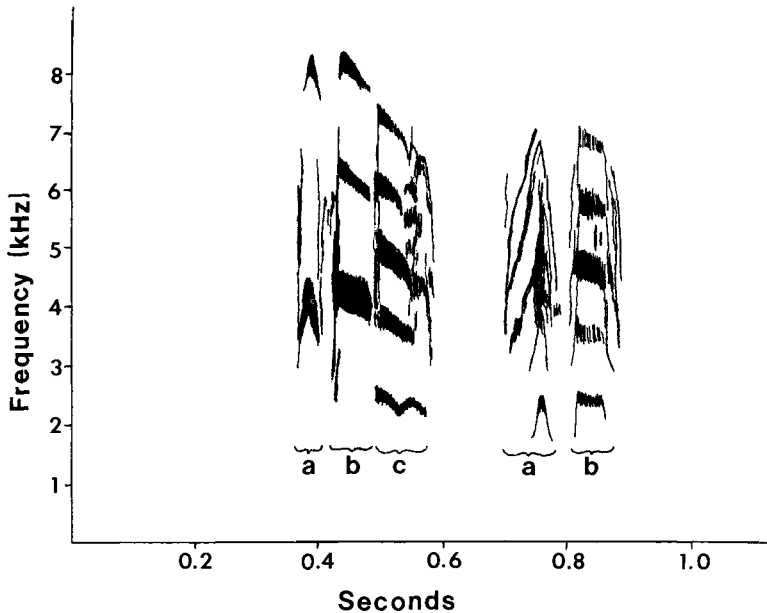


Fig. 1. Representative "Purrit-tit-tit" vocalization, divided into its component segments.

features of the vocalizations differed among various birds. I therefore performed a quantitative analysis to determine which features of the "Purrit-tit-tit" varied sufficiently among birds to permit voice discrimination.

#### PLAYBACK EXPERIMENTS

##### METHODS

This study was part of a general investigation of Least Tern behavior and communication conducted in a nesting colony on the north side of Bogue Banks, approximately 1 km northwest of Fort Macon, Carteret County, North Carolina. The center of the colony lies about 200 m inland from Bogue Sound. Between 45 and 50 pairs of Least Terns nested on a former dredge spoil area in May 1975. During my visits to the colony, I observed the terns from a burlap-covered blind, similar to the one described by Robins (1972). Least Terns were unaffected by the presence of the blind and resumed apparently normal behavior within 5 min after I entered the blind.

In order to identify individual birds, I devised a method for color-marking nesting terns with dye from a bottle placed at the nest and activated from within the blind (Moseley and Mueller 1975). The method was easy to repeat if the dye began to fade.

For the playback experiments, I first recorded sequences of vocalizations from 14 marked birds as they approached their nests, either for a courtship feeding or a nest relief. These sequences averaged 25 s in duration ( $SD = 12$ ,  $N = 23$ ) and consisted of one or more of the vocalization types in the Least Tern's repertoire. Occasionally, calls of both members of a pair occurred in a sequence. Recordings were made with a Uher 4000 Report I-C tape recorder and a Dan Gibson Electronic Parabolic Microphone. The most complete sequence from each pair was later incorporated into a test tape for use in the playback experiment.

A test tape consisted of a sequence of vocalizations recorded from the terns at a particular nest, a 30-s interval of silence, a sequence of vocalizations from another pair of birds from the same colony, and a final 30-s interval of silence. I scored the responses of a test bird during the playback and the following 30-s interval according to the following scale of response intensity, based on numerous hours of observing

the responses of incubating terns to the approach of their mate or a strange tern: 0—no response to playback sequence; 1—flies over territory, calling “Purrit,” and returns to nest; 2—rises from nest, looks upward and calls “Purrit” and “Purrit-tit-tit”; 3—remains at nest and “Chatters” continuously; 4—approaches to within 15 cm of speaker while “Chattering”; 5—flies off nest and out of colony, calling “Peedee.” Category 0 describes the typical response of an incubating tern to the approach of a stranger. Categories 1 and 2 describe responses that occur occasionally at the approach of a stranger but more often at the approach of the mate. Categories 3, 4, and 5 include responses and specific vocalizations associated only with the approach of the mate, in order of increasing intensity of response. The order of presentation of calls was randomized during the experimental series. Since most courtship feedings and nest relief ceremonies are accomplished in 15 s or less, I felt that, using the above procedure, I would observe all important responses to the playback and yet keep the test situation similar to a natural interaction.

Prior to each playback experiment, I placed a Magitran speaker (33 × 41 cm, frequency range 40–20,000 Hz) 2 m from a nest on the ground in an upright position aimed at the nest. A 15 m cord attached the speaker to the Uher tape recorder in a nearby blind. Volume of the playback tape was adjusted to a level that, to my ear, was similar to the volume of calls given by a tern approaching its nest. As all test birds had nests within 17 m of the blind, I could easily observe all behaviors and vocal responses to a test tape.

## RESULTS

The test tapes consisted of a variety of vocalization types. Because many sequences contained voices of both mates at a nest, it was necessary to determine the response of a bird to a recording of its own voice to eliminate the possibility that a test bird responded to its own calls rather than those of its mate in a playback experiment. Fortunately I recorded three sequences containing the voice of only one individual. These recordings were obtained as a tern approached its nest when its mate was absent, a situation that arose rarely, and therefore provided only three usable sequences for this test. Following the procedure described above, I broadcast to each bird a recording of its own call and that of a stranger. In all cases, the test birds completely ignored both the recording of their own voice and the call of the strange tern. Thus, although the sample size is small, I conclude that a Least Tern does not respond to a recording of its own voice.

Figure 2 summarizes the results of playback experiments conducted during May of 1975. Least Terns responded significantly more ( $P < 0.005$ ) to playbacks of calls of their mates than to calls of other individuals in the colony. Thirteen out of 14 test birds exhibited no response to the playback of vocalizations of a strange tern. However, each sequence of calls of a test bird's mate elicited a response, usually of the type typically observed when an incubating tern is approached by its mate. Because responses of test birds were scored on an ordinal scale, I used the non-parametric Wilcoxon Matched-Pairs Signed-Ranks test to compare responses of each individual to the two playback situations (Siegel 1956). This technique has been used effectively in previous studies of individual recognition (Emlen 1971).

## SONAGRAM ANALYSIS OF INDIVIDUAL VARIATION

### METHODS

After completing the playback experiments, I prepared sonagrams of all recordings containing “Purrit-tit-tit” calls attributable to birds of known identity, most of which had been subjects in the playback experiments. Vocalizations were analyzed on a Kay Elemetrics 7029A Sonagraph, using both the wide (300 Hz) and narrow (45 Hz) bandwidth filters and the 80–8000 frequency setting. I then measured 10 temporal and 5 spectral characteristics of 45 “Purrit-tit-tit” calls of 10 individuals. To measure temporal and spectral parameters, I used an overlay of 0.1-in ruled tracing paper, calibrated to the frequency and

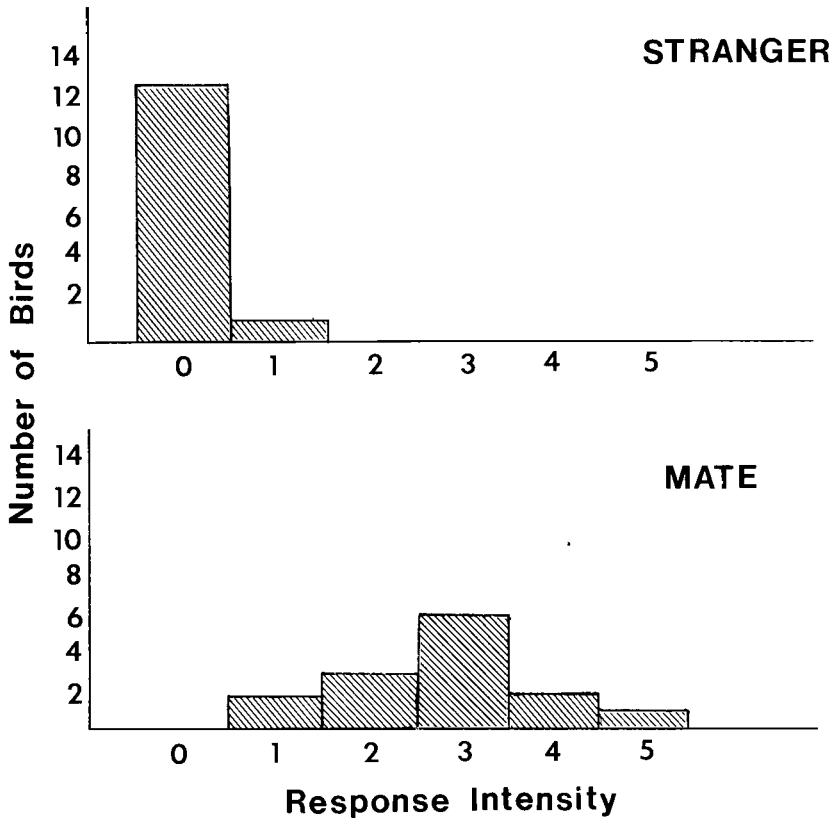


Fig. 2. Responses of test birds to playback experiments. The top histogram illustrates the responses of 14 test birds to a recording of calls by a strange tern; the lower figure illustrates the responses of these birds to a recording of calls by their mates. Significance by the Wilcoxon Matched-Pairs Signed-Ranks Test:  $P < 0.005$ .

time scales of the sonagraph. I measured the duration of notes and syllables to within 2 ms and dominant frequency of syllables to the nearest 50 Hz. Standard deviations of all parameters consistently exceeded any error that might have resulted from measurements at this level of precision.

To analyze the data, I selected the F statistic, defined as  $F = s_1^2/s_2^2$  where  $s_1^2$  equals the variance of sample 1 and  $s_2^2$  equals the variance of sample 2 (Hays 1973). For each parameter, I compared the variance of a sample of calls from 9 different birds ( $s_1^2$ ) with the variance of a sample of 9 calls by the same individual on different occasions ( $s_2^2$ ). If the ratio was greater than the tabled value of F for the appropriate degrees of freedom, I concluded that the calls of different birds vary significantly more with respect to the parameter than calls by the same bird.

## RESULTS

Figure 1 illustrates a typical "Purrit-tit-tit" vocalization, divided into its component segments (notes, syllables, inter-note and inter-syllable intervals). "Purrit-tit-tits" of different individuals varied considerably in structure (Fig. 3). One method of analyzing physical characteristics of vocalizations for individual differences is to compare calls given by one bird with vocalizations given by several other birds. Presumably if 10 calls by the same bird show significantly less variability with

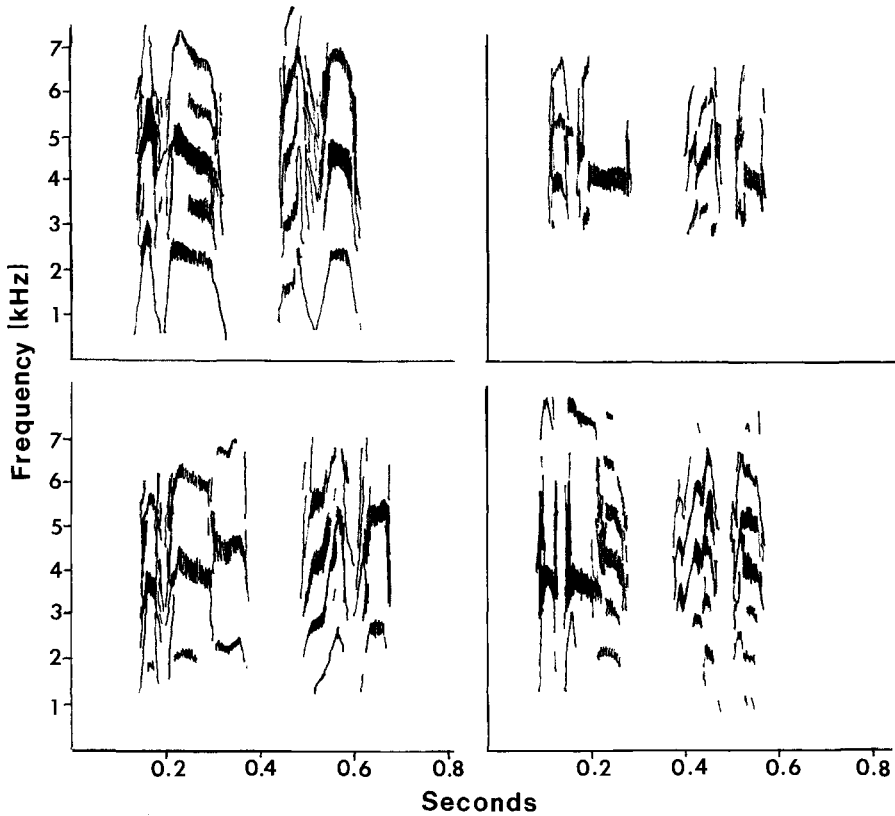


Fig. 3. "Purrit-tit-tit" vocalizations of four different individuals.

respect to a certain parameter than 10 calls each from a different bird, individuals should be able to identify each other by voice alone. A group of calls in the same sequence by the same individual is, however, an inadequate sample with which to compare vocalizations of different individuals. For example, five repeated "Purrit-tit-tit" calls by one bird on the same occasion are likely to show less variability than "Purrit-tit-tits" by the same bird on five different occasions. Slight changes in relative strengths of tendencies associated with delivery of the calls at different times, differences in transmission of the signal, and the physical condition of the bird could contribute to increased variability in different sequences. If only calls from the same sequence are used, it is possible that statistical analysis could indicate sufficient variability among individuals to allow for individual recognition where, in fact, none exists. To be conservative in this analysis, I selected only calls by marked birds for which I had recordings on two or more occasions separated by at least 30 min.

Table 1 presents the results of statistical analysis of temporal and spectral features of this vocalization. The duration and dominant frequency of all components of the "Purrit" note are significantly more variable for calls by different birds than for calls by the same individual ( $P < 0.05$ ). However, the duration and frequency of the components of the second note are not significantly different among birds. Selected F-values are given in the last row of Table 1.

TABLE 1. F-results: individual variation among temporal and spectral characteristics of the "Purrit-tit-tit" vocalization of Least Terns.

| Note      | Segment                | Temporal characteristics <sup>a</sup> | Spectral characteristics <sup>a</sup> | Actual F-values <sup>b</sup> |
|-----------|------------------------|---------------------------------------|---------------------------------------|------------------------------|
| "Purrit"  | Syllable a             | +                                     | +                                     | 24.4 (3.6)                   |
|           | Syllable b             | +                                     | +                                     | 10.3 (3.4)                   |
|           | Syllable c             | +                                     | +                                     | 9.8 (3.4)                    |
|           | Total "Purrit"         | +                                     | *                                     | 10.2 (3.4)                   |
| "Tit-tit" | Syllable a             | -                                     | -                                     | 3.1 (3.7)                    |
|           | Syllable b             | -                                     | -                                     | 3.2 (3.5)                    |
|           | Interval between a & b | -                                     | *                                     | 2.4 (3.5)                    |
|           | Total "Tit-tit"        | -                                     | *                                     | 3.3 (3.5)                    |
|           | Inter-note interval    | +                                     | *                                     | 43.6 (3.4)                   |
|           | Total "Purrit-tit-tit" | +                                     | *                                     | 10.0 (3.4)                   |

<sup>a</sup> + = significant ( $P < 0.05$ ); - = not significant; \* = not applicable to spectral analysis.

<sup>b</sup> F-value for vocalizations from one individual compared with vocalizations from nine other birds. Number in parentheses is tabled value of F ( $P < 0.05$ ) for appropriate degrees of freedom. Where actual value exceeds tabled value of F, the vocalizations of nine different birds are significantly more variable than calls given by the same individual.

## DISCUSSION

My results indicate that, for each parameter tested, sufficient variability exists in the temporal and spectral features of the "Purrit" note to permit discrimination by voice. It is possible that only one or two features of the note are actually necessary for individual recognition. To establish which feature or combination of features is most important, one must artificially alter the calls on tape and conduct additional playback experiments. This work is presently in progress with the Least Tern.

The "tit-tit" note is remarkably consistent among all birds. Whereas the "Purrit" note is frequently used alone, the "tit-tit" note rarely occurs alone in a sequence. Presumably the "Purrit" and "tit-tit" convey different messages. The contexts in which the "Purrit" note occurs alone indicate that the major message conveyed by this vocalization is identification of the signaler. A Least Tern typically calls repeated "Purrits" as it leaves the colony (following a "Peedee" series, Moseley 1976), or when feeding alone or in small groups. In addition, a tern on its nest occasionally calls "Purrit" in answer to the "Purrit-tit-tits" of its approaching mate. In aerial courtship, the tern without the fish (the presumed female) also uses the "Purrit" (Moseley 1976). In each context, the adaptive value of a vocalization that conveys a bird's identity is clear. The use of the "Purrit" by the presumed female in aerial courtship aids in familiarizing the male with her voice. Later in the breeding cycle, when nest reliefs occur frequently, repeated "Purrits" by an incubating bird in answer to its mate could help the arriving bird locate its nest in the midst of a uniform colony and thus permit rapid incubation shifts. The use of this vocalization by foraging birds could serve to orient others from the colony to a plentiful source of food. The value of vocalization that conveys identity in this context, however, is not clear, and it may be that the "Purrit" is used by feeding birds simply because it is the most appropriate vocalization in the species' repertoire for communicating a bird's presence without implying any erroneous information about its motivational state.

The complete "Purrit-tit-tit" vocalization is highly associated with two social contexts: when approaching the mate, or when carrying a fish either during aerial courtship displays or prior to a courtship feeding (Moseley 1976). A Least Tern calling "Purrit-tit-tit" is therefore conveying at least two discrete messages. It iden-

tifies itself with the "Purrit" note, and, with the "tit-tit" note, indicates a tendency to approach the mate and perform certain non-agonistic behaviors, such as courtship feeding or assuming incubation of the eggs. The "tit-tit" note, because of its structural consistency, conveys an easily recognizable message of intent to approach without aggression. Because it is always accompanied by the "Purrit," no structural variability in the "tit-tit" is required for individual recognition to occur.

The ability to communicate auditorily both identity and a tendency to behave sexually with a mate or potential mate is an advantage in a crowded colony of morphologically similar birds. During early courtship, each member of a pair learns to recognize its mate by voice and probably by sight so that efficient trading of incubation duties can occur later. After the first week of incubation, members of a pair rely heavily upon auditory communication during nest reliefs. An incubating bird simply flies off its nest when it hears the "Purrit-tit-tits" of its approaching mate, and the nest relief is accomplished rapidly with little or no visual communication between birds. The frequent use of the "Purrit-tit-tit" during early courtship also helps to insure that strangers do not later interfere with or participate in incubation activities at the wrong nest. It is not uncommon for a strange bird with a fish to land or attempt to land near an incubating bird (Moseley 1976). On such occasions, the intruder is often driven off before it lands. Apparently the occupant of the nest recognizes a strange "Purrit-tit-tit" call before it visually recognizes the intruder, and reacts aggressively to prevent the stranger's continued approach.

For a colonially-nesting species of morphologically similar birds, the ability to identify individuals by auditory signals probably permits recognition at greater distances than visual signals would allow. When a tern approaches its mate on a nest, the subsequent interaction occurs very rapidly. The use of auditory signals is therefore an expedient strategy for enabling rapid localization of an individual in a crowded colony.

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A symposium on **The Integrated Study of Bird Populations** will be held at Wageningen, the Netherlands, from 17-21 September 1979 on the occasion of the 25th anniversary of The Institute for Ecological Research of the Royal Netherlands Academy of Arts and Sciences. Invited speakers will address bird populations in relation to food supplies and territorial behavior, optimal foraging strategies, energetics of free-living birds, and Red Grouse and Great Tit population dynamics, and facilities will be available for display of posters on related subjects. Further information may be obtained from **I.A.C., Postbus 88, 6700 AB Wageningen, The Netherlands**.

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The second **International Congress of Systematic and Evolutionary Biology** will be held at the University of British Columbia, Vancouver, Canada on 17-24 July 1980. A number of symposia will be offered, and sessions for contributed papers will also be organized. Those interested in receiving an information circular in the spring of 1979 should write to **Dr. G. G. E. Scudder, Department of Zoology, University of British Columbia, 2075 Wesbrook Mall, Vancouver, B.C. V6T 1W5 Canada**.