

VOCAL DIFFERENCES BETWEEN AMERICAN LEAST TERNS AND THE EUROPEAN LITTLE TERN

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DURING a study of the breeding biology of *Sterna albifrons browni*, the California Least Tern (Massey 1974), I became interested in the role of vocalizations in mating and parental behavior in this colonially nesting bird. It was apparent that calls were at least as important as visual clues in individual as well as species recognition.

S. a. browni is presently considered to be one of many subspecies of the near-cosmopolitan species *Sterna albifrons* Pallas (Peters 1934: 340; A.O.U. 1957). The nominate race, *S. a. albifrons*, breeds in Great Britain, Europe, and Asia as far east as western Siberia, on the North African coast, and southeast to Iraq and Iran. It winters in Africa, along the coasts and islands of the Arabian Sea, and in central Asia (Witherby 1941, Dement'ev et al. 1969). The three American races are apparently isolated throughout their ranges from the nominate race. They breed on the east coast of the United States, the Gulf Coast and the Caribbean (*antillarum*), the Mississippi River and its drainage system (*athalassos*), and in California and Baja California, Mexico (*browni*), and migrate to Central and South America to winter (A.O.U. 1957).

The subspecies of *S. albifrons* differ very little from each other morphologically. I was curious to determine whether divergence might have occurred in vocalizations and behavior between widely separated races. I therefore chose to investigate the breeding behavior and vocalizations of the nominate race, the European Little Tern, to compare with the California Least Tern. The finding of marked vocal differences between these two subspecies led me to study a third race, the east coast American bird (*antillarum*) to determine whether it was closer behaviorally and vocally to *browni* or *albifrons* or perhaps different from either.

MATERIAL AND METHODS

I studied the California Least Tern for two breeding seasons, 1970 and 1971, at Huntington Beach, California. The importance of calls was noted early in the study and special attention paid to the role of vocalizations in the breeding cycle. I recorded all of the major calls in the field, with observations on accompanying behavior. The study covered the entire breeding period, from time of arrival in late April to departure in mid-August.

In 1973 (11 May to 16 June) I studied breeding behavior and recorded calls of the Little Tern in England, at Blakeney Point, Norfolk, and Minsmere, Suffolk. In

June and July 1974, I studied the east coast American Least Tern in Chatham, Massachusetts.

The rather solitary nature of *S. albifrons* makes it easier to record than most other species of terns, and after a few sessions with a reel-to-reel tape recorder and parabolic reflector I found that the latter was dispensable. I then substituted a cassette for the reel-to-reel recorder and found it quite adequate to cover the bird's vocal range. This simplified recording in the field and my standard equipment was a Sony TC 110 portable cassette recorder and hand-held microphone (Sony ECM 193). Spectrograms in this study were all made from cassettes, on a Kay Electric Sona-graph, Model 662A, at the Moore Laboratory, Occidental College, Los Angeles. I have filed duplicate cassettes of the calls described and pictured here as Moore Laboratory and at the Bioacoustic Archive and Laboratory, Florida State Museum, Gainesville.

To review the taxonomy of the three subspecies under study, I examined and measured specimens from several museum collections. Skins of *albifrons* were from the British Museum (Natural History) and the American Museum of Natural History. All birds had been collected in England and were in breeding plumage. I looked at specimens of *browni* at the Los Angeles County Museum of Natural History, and *antillarum* at the AMNH. In addition, I trapped and examined a number of live, breeding adults in Chatham, Massachusetts in 1974.

I measured wing, tail, and culmen lengths and compared plumages, with special attention to color of back and tail, and number of dark outer primaries, as these traits have been used to differentiate subspecies. The amount of black on the bill, also used, was not measurable with any accuracy because of the age and fading of the bills.

BEHAVIOR

Between the east and west coast races of the American Least Tern no differences in behavior were detectable during the breeding period. As far as I could determine, the aerial phases of courtship, courtship feeding, copulation, nest building, egg-laying, sharing of incubation duties, and care and feeding of the young were the same for both races.

Between Least and Little Terns some behavioral differences were apparent, although the basic breeding biology is very similar on both continents. The behavioral differences may be more quantitative than qualitative. For example, the aerial glide is a regular feature of early Least Tern courtship, with pairs often seen in this particularly beautiful display. I did not see such displays by the Little Tern, although they have been noted by others (Schönert 1961). They do not seem to play the same important role in courtship as in the Least Tern. A more detailed comparative study of behavior must be made before firm conclusions can be drawn.

VOCALIZATIONS

The repertoire of the Least Tern in California contains seven major calls. These are the basic, 4-figure call by which humans identify the bird, three alarm calls, a crooning call used when parents talk to their chicks, a specifically female call associated with courtship feeding, and

a specifically male call made as he flies off after feeding his mate. This basic repertoire is shared by the east coast Least Tern. The European Little Tern has an homologous set of vocalizations, except for the male call, which it apparently lacks.

Basic call.—A 4-figure call, used intensively by adults of both sexes during the breeding season, is the basic specific call of the Least Tern. I named it the fish-flight call (Massey 1974) because of its close association with that behavioral sequence, but it is used in a much wider context and merits a less restrictive name. The call is shrill in quality and has two phrases of two figures each, with emphases on the 2nd and 4th figures. It has been written variously as “k’ee-you-hud-dut” (Wolk 1974), “keedee-cui” (Hardy 1957), and “kee-zink kee-zink” (Davis 1968). It is the call of the courting male carrying a fish in the early courtship period, used also by the female when she joins him in a fish-flight. Frequently a bird will utter half the call several times in a preliminary phase of a behavioral sequence, then change to the full 4-figure call. During the period of courtship feeding the male flies in with a fish to the waiting female, calling continuously as he approaches. The female recognizes the voice of her mate and responds. During the incubation period the male continues to feed the female and uses the call routinely. After the chicks hatch, both parents sound the basic call as they fly in with fish for their young. The chicks learn to recognize it on the first post-hatching day and respond by begging. They soon acknowledge only the calls of their parents, and will not respond to strange adults that fly in calling and offering them fish. The basic call serves for both species recognition and for individual identification within the family group.

Figs. 1a and 1c show the basic call of the Least Tern as recorded in California. (The terminology used to describe the audiospectrograms is that of Bundesen and Davis, as elaborated by Davis (1964)). Duration of the call is 0.45–0.65 sec with an interval of at least 0.1 sec between the 2nd and 3rd figures. The 1st and 3rd figures tend to be short, the 2nd and 4th longer. Each figure is comprised of a fundamental (often weak) and as many as seven harmonics. Usually two harmonics are of greater amplitude than the rest. There is no repetition of figures within a call.

Calls of adults are sufficiently individualized for pairs to recognize each other and for chicks to recognize their parents. This shows up well on spectrograms. No two individuals have calls that are quite alike.

East and west coast Least Terns sound alike and their basic calls look alike spectrographically (Figs. 1b, 1d). The structure of the call is the same on both coasts, despite the wide spectrum of individuality within each race.

The basic call of the European Little Tern sounds quite unlike that of

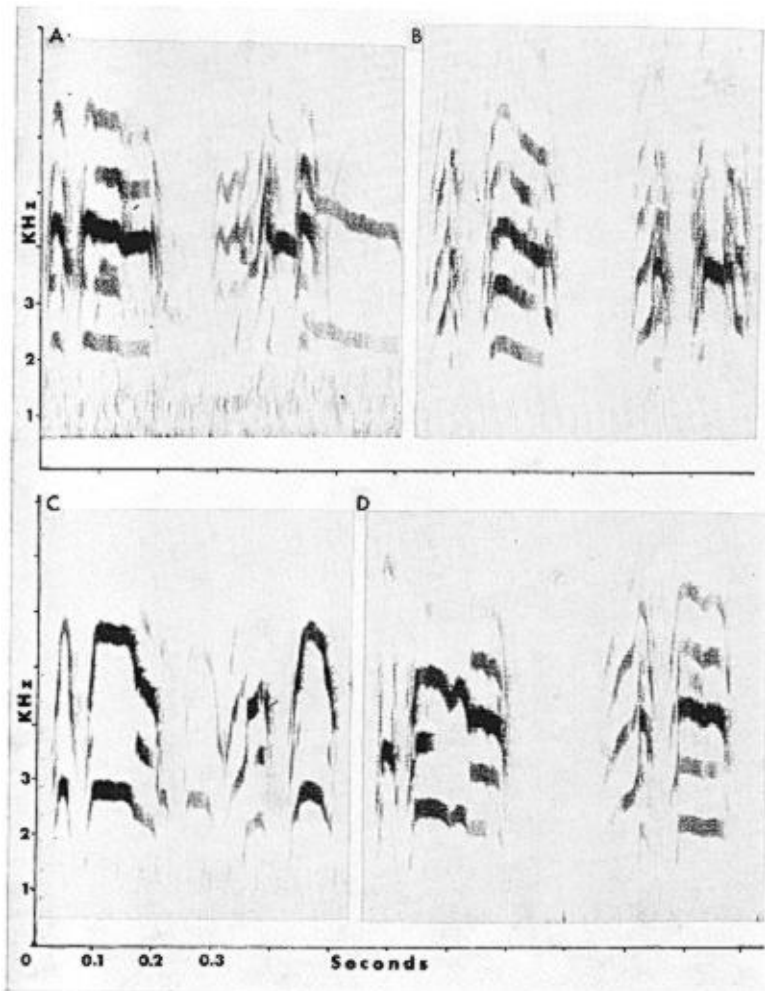


Fig. 1. Basic call of American Least Terns. Each spectrogram represents a different individual: a, c, *Sterna albifrons* "browni" (west coast race); b, d, *S. a. antillarum* (east coast race).

the American birds. Major points of difference are summarized in Table 1. Where the Least Tern call is shrill and each figure distinctly heard, the Little Tern makes a rapid, more blurred sound of lesser amplitude. The call is very difficult to render phonetically. Schönert (1961) described it as "purririririr." I would essay "widididit," but emphasize that the consonants are chosen arbitrarily, for no letters represent the sound accurately. The call often has 4 figures, but can have 2, 3, or 5 (Fig. 2c-2f).

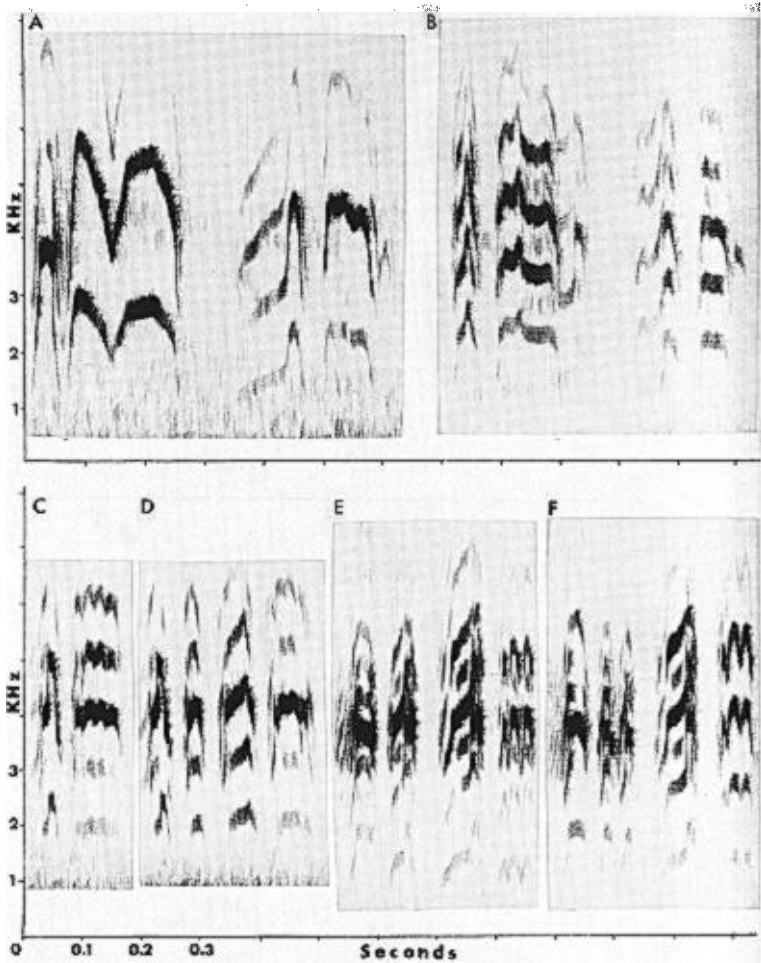


Fig. 2. Basic call of the American Least Tern and the European Little Tern: a, b, *S. a. "browni"*; c-f, *S. a. albifrons*.

Characteristically the male Little Tern makes a 1-figure call while fishing (Fig. 4d) that changes to a 2-figure call after catching a fish, and as he flies toward the waiting female becomes a rapidly repeated one of up to 5 figures. It is often answered in kind by the female. The full call has a duration of 0.275–0.425 sec. The longest one I recorded does not overlap the shortest call of the Least Tern (Table 1).

Differences are also apparent in phrasing and rhythm. The Little Tern's call lacks pauses between the figures; all are uttered rapidly with the

TABLE 1
COMPARISON OF BASIC CALLS OF LEAST AND LITTLE TERNS

	Least Tern	Little Tern
Number of figures in call	4	3-5
Number of figures repeated	0	1
Duration of call (seconds)		
Range	0.45-0.65 ¹	0.275-0.425 ²
Mean	0.504	0.335
Accented figures	2 and 4	Final figure
Number of phrases	2	1

¹ N = 13.

² N = 10.

accent on the final one, regardless of the number of figures in the call. The accented final figure has a distinctive shape on the spectrogram. It shows as a warble with three or more peaks (Fig. 2c-2f). Repetition of figures is another characteristic of the Little Tern's call, as can be seen in Fig. 2f where the first 3 figures are the same and the 4th and 5th both different.

Amplitude has not been measured, but there is a clearly heard difference between Least and Little Terns in this respect; American birds are louder than their English relatives. Their voices are also more strident.

Alarm calls.—Least and Little Terns of both sexes use several alarm calls to express various levels of anxiety. Fig. 3 shows two of them spectrographically. The mildest of the Least Tern alarm calls sounds the same on both coasts (Fig. 3a, 3b) and can be written as "zwreep" (Wolk 1974). It is not at all like that of the Little Tern (Fig. 3c), verbalized as "wiik." The call of medium intensity made by the Least Tern (Fig. 3d) is a repeated staccato note that sounds like "kit kit kit" (Massey 1974). The homologous call of the Little Tern is also a staccato, but each note is of shorter duration (Fig. 3e). The alarm call of greatest intensity (not illustrated) is used against a hostile intruder on the nesting grounds. In a situation of maximum stress, as when a human is handling its eggs or chicks, the Least Tern utters a sharp, repeated staccato note while mobbing, and at the low point of the dive, a harsh scream as it defecates on the offender. The Little Tern makes a chattering sound, with a harsh "bzzz" at the low point of the arc, as when mobbing an European Oystercatcher (*Haematopus ostralegus*). Defecation is not usually a feature of mobbing behavior in Little Terns.

Sex-specific calls.—Both Least and Little Terns have a sex-specific call uttered only by the female. It is used during the courtship period by a bird signaling her mate her willingness to be fed. The male flies in with a fish, sounding the basic call, and the female may respond with a "wu-du-du." The call as made by the east coast Least Tern is shown in Fig.

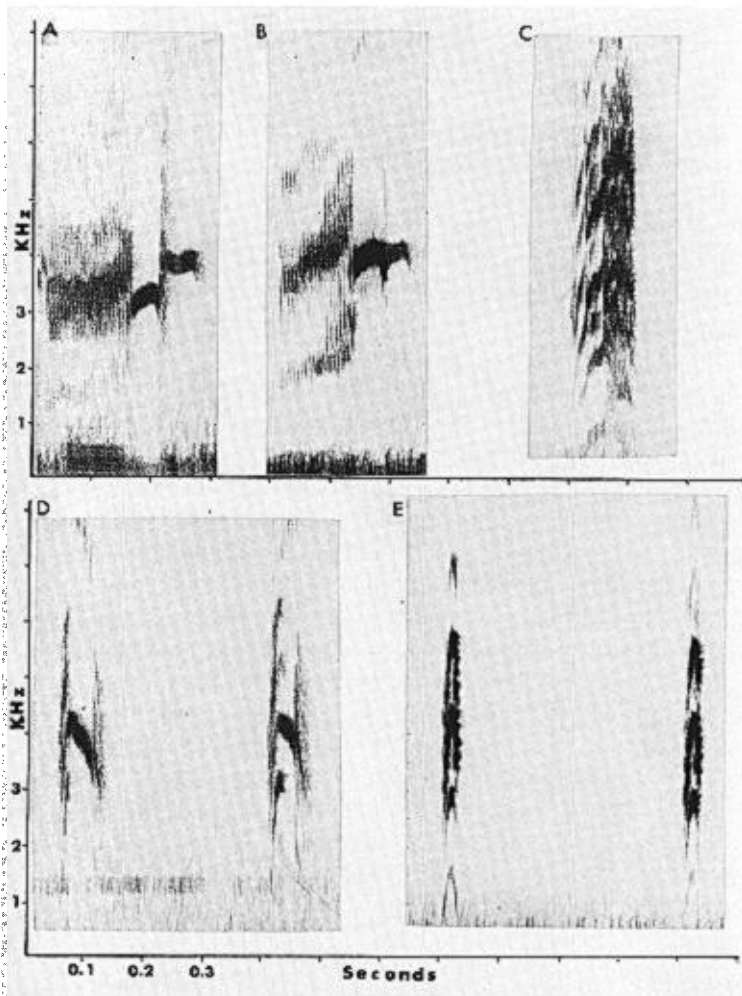


Fig. 3. Alarm calls. Low intensity alarm call of: a, *antillarum*; b, "*browni*"; c, *albifrons*. Middle intensity alarm call of: d, "*browni*"; e, *albifrons*.

4a; the homologous call of the female Little Tern in Fig. 4b. Although these calls sound more alike than do other homologous calls, there is again a difference in duration, with the American bird making a longer call. I noted also a marked difference in frequency of usage; both *antillarum* and *browni* females use it regularly throughout the courtship feeding and incubation periods, during which time the male is feeding his mate. In the vocabulary of *albifrons* it is rare; I have only two examples on all of the tapes made during a breeding season in England.

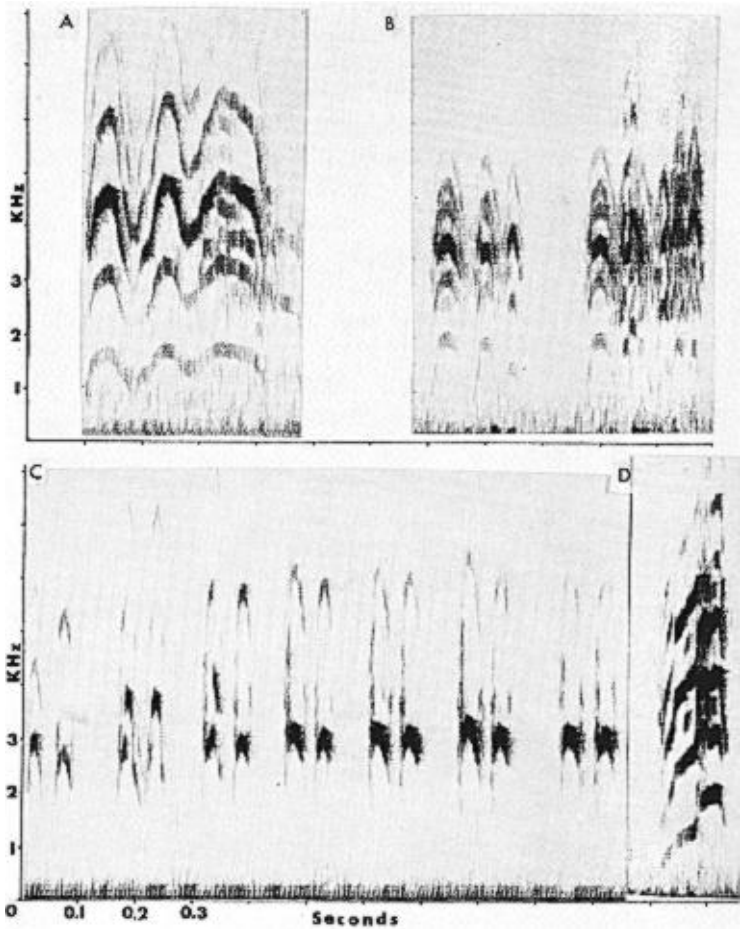


Fig. 4. Sex-specific female call of: a, *antillarum*; b, *albifrons*; c, sex-specific male call, *antillarum*; d, fishing call, *albifrons*.

The male Least Tern utters a call that appears to have no counterpart in the Little Tern's vocabulary (Fig. 4c). A repeated staccato note, almost without overtones, it is heard frequently but not invariably following courtship feeding. After the male feeds his mate he flies off making the fly-away call, as I dubbed it in my field notes. When the chicks hatch, the male transfers his feeding activity to them and stops using the call. He may sound it after the first few feedings of chicks on the first post-hatching day, but not thereafter.

Crooning call.—The call made by parents talking to their chicks (not

TABLE 2
COMPARATIVE MEASUREMENTS OF LITTLE TERN AND TWO POPULATIONS OF
LEAST TERNS

	<i>S. a. albigrons</i>	<i>S. a. antillarum</i>	<i>S. a. "browni"</i>
Culmen length (mm)			
N	41	13	19
\bar{x}	29.7	27.8	27.6
Range	23.5-35.0	26.0-30.7	26-30
SD	2.10	1.77	1.22
Wing length (mm)			
N	41	19	20
\bar{x}	170.8	165.8	168.8
Range	160-179	161-171	164-176
SD	5.49	3.61	3.31
Tail length			
N	36	-	17
\bar{x}	87.1	-	89.9
Range	71-107	-	84-102
SD	10.04	-	5.07

illustrated) has been previously described and shown spectrographically to be a variant of the basic call of the Least Tern (Massey 1974). Little Terns also talk to their chicks, using vocalizations that sound as if derived from their basic call.

Fishing call.—The Little Tern usually makes a 1-figure call while fishing (Fig. 4d). It is not a separate call, but sounds and looks like the mildest of the alarm calls (Fig. 3c). The Least Tern is an habitually silent fisherman. If it vocalizes at all during fishing, it sounds a 2-figure call that is half the basic call, then expands to the full 4-figure call on catching a fish and flying off to feed a female or chick.

TAXONOMY

Alleged morphological differences between *antillarum* and "*browni*" (Mearns 1916) were not substantiated by Burleigh and Lowery (1942) when they reviewed variation in the Least Tern. They concluded that *antillarum* and "*browni*" were the same race, despite their geographic discontinuity. My own examination of specimens bears out their findings. No plumage characters are consistently different. The number of dark outer primaries, a trait used by Mearns and later discounted by Burleigh and Lowery, varies from 1 to 3 in both cases. Nor do measurements differ. Bill and wing lengths are compared in Table 2. The *t*-test for comparing two groups with unequal population variances shows no significant differences between the races in terms of culmen length ($P = 0.680$) or wing length ($P = 0.791$).

The interior race *athalassos* was separated from *antillarum* on the basis of much darker coloration of the upper parts as well as geographic discontinuity (Burleigh and Lowery 1942). I have seen too few specimens of *athalassos* to make a contribution on this point, nor have I examined the two Mexican subspecies, *mexicana* and *staebleri*, both upheld as valid races by Burleigh and Lowery (1942). For the present, I must limit discussion to the three races I have been able to examine carefully.

Between European and American birds I found several consistent morphological differences. American birds have shorter bills and wings (Table 2). The *t*-test shows a significant difference in culmen length between *albifrons* and "browni" ($P = 0.001$) and *albifrons* and *antillarum* ($P = 0.004$). In terms of wing length the difference is significant between *albifrons* and "browni" ($P = 0.0001$) although not quite between *albifrons* and *antillarum* ($P = 0.07$). Tail lengths are variable and not significantly different.

One plumage difference stands up to scrutiny; the rump and tail of the European bird are white or very pale gray, where the American bird is a darker gray. The number of dark outer primaries is variable, ranging from 1 to 3, as in the American birds.

DISCUSSION

Among colonial nesting gulls and terns, vocalizations play a major role in recognition. In situations where visually similar species nest together, calls probably are a major factor in maintaining the isolation of species. In comparing Arctic Terns (*Sterna paradisaea*) with Common Terns (*S. hirundo*), Cullen (1956) emphasized the advertising call of the male as an isolating mechanism against hybridization. These closely related species often nest together. They have homologous vocal repertoires as well as almost identical behavioral patterns. Although several of the calls show minor differences in tone quality, the only one that is markedly different—in rhythm and pattern as well as in tone quality—is the advertising call of the male (Cullen 1956).

Individual recognition in gull, tern, and seabird colonies is facilitated by vocal as well as visual clues. The din of a nesting colony is a collection of individual calls. In the Sandwich Tern (*Thalasseus sandvicensis*), recordings have been made of fish calls of single birds flying toward the breeding grounds. Spectrograms revealed that no two individuals made calls that were exactly alike, although the basic 3-segment pattern of the call was the same for all. Repeated calls by the same bird were almost identical (Hutchinson et al. 1968).

One particular call is usually identified with recognition. Tinbergen (1960) noted that the Herring Gull (*Larus argentatus*) responded to the

recorded mew call of its mate but not to that of other adults. Working with Gannets (*Morus bassanus*), Nelson (1965) noted that one member of a pair recognized its mate by the landing call of the incoming bird. Recently it has been determined that only the first portion of the Gannet's call is needed for recognition of the individual. The rest of the call is apparently coding other information (White and White 1970).

Recognition of their parents' voices by chicks has been documented in Arctic Terns (Cullen 1956) and Common Terns (Palmer 1941, Stevenson et al. 1970). Experiments with Laughing Gull chicks (*Larus atricilla*) showed that they are able to discern the calls of their own parents (Beer 1969). Black-billed Gull chicks (*L. bulleri*) recognize and respond to the mew call of their parents (Evans 1970). This call is used in courtship feeding, at nest exchange and during feeding of the young, as is the basic call of the Little and Least Tern. In the colonial nesting Common Murre (*Uria aalge*), the young learn to distinguish their own parents' voices and do not beg food from other adults (Tschanz 1959). In all these instances, as with *Sterna albifrons*, the chick learns the basic call used for species recognition early in life by hearing and identifying the individual calls of its parents in association with feeding.

It is apparent that vocal divergence has occurred between Least and Little Terns. Differences are noted throughout the repertoire. The basic call shows fundamental changes in structure—rhythm, phrasing, accented figures, and duration of call. Experiments with playbacks of songs in passerines (where the song has been altered) indicate that duration of a figure, timing, and pitch can all be factors in promoting recognition (Emlen 1972). If terns employ the same kinds of aural clues as do songbirds, then the differences in the basic call could preclude recognition between Least and Little Terns. This would effectively prevent interbreeding, should sympatry occur. Playbacks have not yet been tried and might yield interesting results. *S. albifrons* is not, however, an ideal subject for playbacks, and an experimental model would be difficult to devise.

On evidence presented here of morphological, vocal, and behavioral identity, and after review of the taxonomy, I suggest that *antillarum* and "*browni*" are not separate subspecies but the same taxon. Geographic separation of these two groups of birds during the breeding season is the only basis for considering them different races. The status of *athalassos* must remain in question pending further study, including vocalizations. On the other hand, differences between *albifrons* and its American relatives are pronounced enough to merit considering them separate species.

The superspecies concept may well apply to the Little-Least Tern complex. As defined by Amadon (1966) a superspecies is "A group of

entirely or essentially allopatric taxa that were once races of a single species but which now have achieved species status." This is a reasonable explanation for what has occurred between the European and American races of *S. albifrons*. Further exploration of this theory would necessarily include study of two closely related South American species, the Peruvian Tern (*S. lorata*) and the Yellow-billed Tern (*S. superciliaris*), as well as the Fairy Tern (*S. nereis*) of Australia-New Zealand, all of which may be members of this superspecies.

The question arises as to which subspecies of *S. albifrons* has undergone divergence, or if there has been concomitant divergence. A study of the vocalizations of other races might clarify this question. *S. a. sinensis* (Australia and Indochina), *guineae* (West Africa), and *saundersi* (Red Sea) are allopatric races that may all sound completely different, be more like one or the other of those analyzed here, or form a gradient. The fact that two of the American populations are morphologically, behaviorally, and vocally indistinguishable from each other suggests that their separation as breeding populations has been fairly recent in evolutionary time; certainly more recent than the isolation of American from European races. The same phenomenon may be apparent between other subspecies. Whatever the findings, a comparison of vocalizations within this cosmopolitan species would add to our knowledge of the origin and divergence of species.

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SUMMARY

A comparative study was made of three populations of terns currently considered to be subspecies of *Sterna albifrons*.

Behaviorally and vocally, the east coast (*antillarum*) and west coast ("browni") races of the Least Tern in the United States are indistinguishable. Between American Least Terns and the nominate race (*albifrons*), the European Little Tern, subtle behavioral and marked vocal differences occur. In general calls are homologous with one important exception, the male Least Tern has a call that seems to have no counterpart in the Little Tern's repertoire. When spectrograms of homologous calls are compared, divergence is apparent throughout the repertoire. The basic calls of Least and Little Terns differ fundamentally in structure, including rhythm, phrasing, accented figures, repetition of figures, and duration of call.

The taxonomy of the three subspecies is reviewed. No consistent morphological differences separate the two American races. As they are also alike behaviorally and vocally, it is probable that they are one taxon. Between European and American birds several differences are measurable, the latter having shorter bills and wings, and also one consistent difference in plumage color.

The importance of vocalizations in the breeding cycles of *Sterna albifrons* and other colonial nesting species is discussed. Marked differences in the basic call of Little and Least Terns would presumably create a strong barrier against interbreeding, should sympatry occur. Divergence in these allopatric populations has apparently progressed beyond the subspecies stage; the European Little Tern and the American Least Tern may well be discrete species.

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