

SOUNDS OF SHOREBIRDS 2. EVOLUTION

by Edward H. Miller

In the first article of this series I outlined some methods for analyzing, describing, and depicting sounds of shorebirds (Miller 1983a). In this one I shall discuss how the acoustic repertoires of shorebirds are organized, why different species have unique kinds of sounds, and how acoustic characteristics can be used to trace evolutionary pathways.

REPERTOIRES

The different kinds of sounds used by a species constitute its acoustic repertoire. Describing and understanding repertoires present a major challenge to research on animal communication. How many kinds of sounds characterize a species? Do repertoire size and characteristics vary with social system? Do they change seasonally, or differ among species?

The starting point for these and other questions is physical description coupled with behavioural observations. Sounds commonly are classified simultaneously by physical characteristics and presumed function. Thus one can describe distinctive sounds used in mobbing predators, fighting, copulation, brooding, etc. A major pitfall here is that categories of sounds may be set up or labelled in ways that are unintelligible to other workers (what is a "territorial" call? a "sexual" call? or a "warning" cry?). Even the most anthropomorphic or interpretive names for categories are harmless, however, if adequately detailed physical and behavioural descriptions are given for each category.

Many categories are easy to establish, as for discrete flight notes of wintering sandpipers put to flight by a human observer. By describing many such sounds by their physical properties and the circumstances in which they occur, one can arrive at an estimate of a species' repertoire. A common problem lies in defining the smallest unit within a repertoire: is a curlew's trill or an oystercatcher's piping a natural category, or should each sound element of trilling or piping be our starting point? Consider the "motorboat" sound of male Semipalmated Sandpipers *Calidris pusilla* during nuptial flight displays (Figure 1; Miller 1983b). The sound is a series of elements which are uttered rhythmically and rapidly (about 30-40 per second in long series); here, the

motorboat sound, not its constituents, seems to form a meaningful category at the level of the repertoire. Even though the motorboat sound is composed of physically different kinds of units, these occur in fixed sequence, and the sequence itself occurs in behaviourally meaningful situations.

The correspondence between a particular kind of sound and the contexts in which it occurs is often very poor: sounds with specific "meanings" are very rare, which makes sense when one considers the wealth of things shorebirds must communicate about, and the limitations of their acoustic repertoires. On the one hand, particular call types may be used in diverse situations. Thus Willets *Catoptrophorus semipalmatus* use one kind of call "as a greeting and contact call, an indication of flight intention, and a flight enticement call" (Sordahl 1979, p.563); Whimbrels *Numenius phaeopus* use one when gliding in to land, by incubating birds responding to their mates, and during change-overs at the nest (Skeel 1976, 1978, Cramp 1983). More difficult to understand is the converse situation, when different kinds of calls are used in very similar circumstances: copulating Willets use two call types during copulation attempts (Sordahl 1979); Whimbrels use several kinds of calls in response to predators (Skeel 1976, 1978, Cramp 1983); and many calidridine sandpipers use two different call types in response to humans near the brood (Miller 1984, and see below).

Explanations for the examples just provided can come only from detailed research. In the former case, we must ask whether the diverse situations share some characteristics in common, and whether the calls uttered in them are really physically indistinguishable. In the latter case, we must question whether the precise circumstances really are identical: what is the behaviour of calling Whimbrels toward different classes of predators, and how does this vary with distance from the nest, gender, or stage of nesting, for example? Answers to these questions rely on painstaking observations, such as those reported by Mace (1981) on vocal behaviour of Northern Jacana (*Jacana spinosa*, see next section).

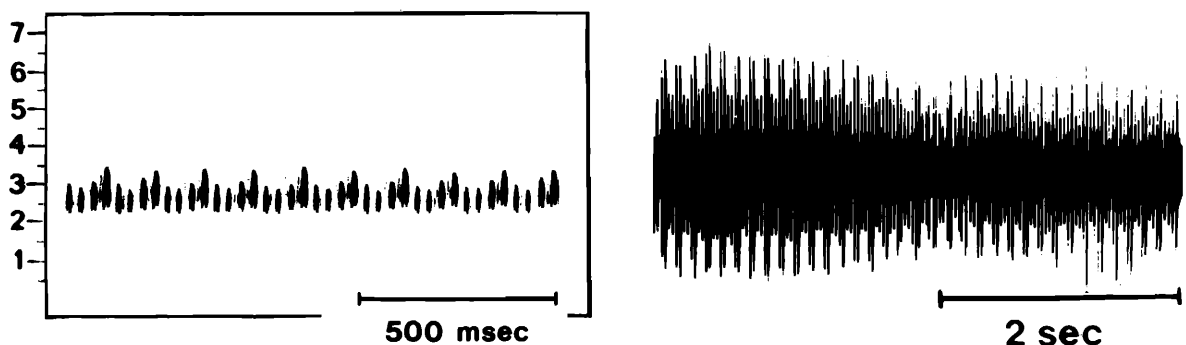


Figure 1. Sound spectrogram (left) and oscillogram (right) of the "motorboat sound" of male Semipalmated Sandpipers *Calidris pusilla*. The spectrogram's vertical scale is in KiloHertz; analyzing filter bandwidth, 300 Hz (see Miller 1983b),

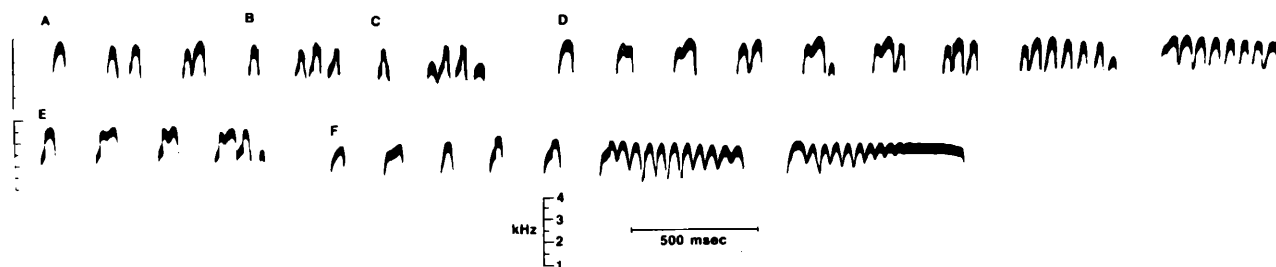


Figure 2. "Alarm" calls by six (lettered A to F) Blackish Oystercatchers *Haematopus ater* disturbed by me near their nests. Analyzing filter bandwidth, 300 Hz.

"GRADED" AND "DISCRETE" SOUNDS

Structure and function of sound signals in shorebirds obviously are not aligned always in a simple way, a fact which cautions us to take careful note of the behaviour of calling birds, and of the circumstances surrounding them. Such care is particularly important with kinds of sounds which are difficult to classify because they are highly variable, and this applies to many shorebird sounds. Consider calls of Blackish Oystercatchers *Haematopus ater* disturbed by me near the nest (Figure 2). The calls varied from brief simple ones to long compound ones with a terminal whistle (e.g. the last call for bird F in Figure 2). I do not know the significance of such variation, but it probably reflects the caller's level of "excitement", and hence the likelihood of behaving in certain ways, information of a sort useful to its mate (and perhaps to other oystercatchers), but not comprehensible to us at present.

Graded sounds like the ones just described occur within repertoires of many species, and even characterize entire sound-signalling systems of others. Calls of undisturbed calidridine sandpipers brooding or tending their chicks vary greatly in loudness, duration, and certain other features, a trend which occurs in short-distance calls of numerous species such as phalaropes (Howe 1972). Almost the whole sound system of the Northern Jacana is built around subtle grading in various features; this may be the most extreme example of grading in shorebird acoustic communication (Jenni *et al.*, 1972, Mace 1981).

The importance of graded (versus *discrete*) acoustic communication to social systems and ecology will be touched on in the next article. Here it is sufficient to note that sound classes within species, and even whole communication systems across species, differ in the extent to which grading occurs. Discrete sound types with obvious functions are very useful in research on evolutionary patterns because they are easy to work with. Consider the difficulties in trying to infer evolutionary relations among the world's oystercatcher species using calls like those in Figure 2! In contrast, stereotyped and discrete call types, like many used in long-distance communication to attract mates or deter competing males, offer good material for such research. These sounds are often conspicuously unique to different species or groups of species. The distinctiveness of sounds (especially those involved in sexual or aggressive encounters) for different but related species commonly has been attributed to the need for species identification in the face of potentially wasteful interbreeding. Thus the loud and beautiful nuptial song of *Pluvialis* plovers and of *Calidris* sandpipers serve as *isolating mechanisms*, in settings where congeners also mate and nest. This explanation is appealing, but current thinking downplays this evolutionary origin for the species-distinctiveness of song. Rather, song structure reflects the need *within* species for efficient and rapid pair-formation, and reflects competition among males (usually) for successful mate-attraction. The function of song (and other prominent types of sounds) in promoting species isolation is thus seen to be a minor side effect.

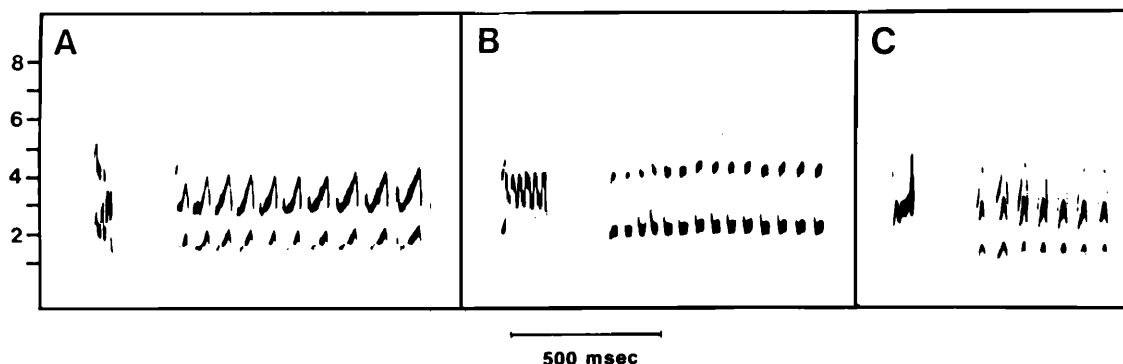


Figure 3. Sound spectrograms of calls by calidridine sandpipers disturbed by me near their young. A - Semipalmated Sandpiper *Calidris pusilla*; B - Least Sandpiper *C. minutilla*; C - Purple Sandpiper *C. maritima*. Analyzing filter bandwidth, 300 Hz.

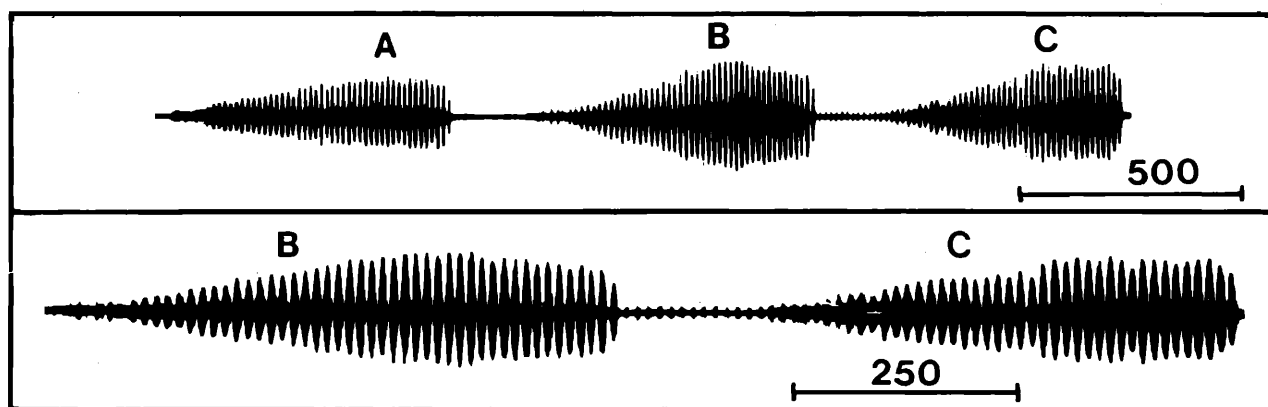


Figure 4. Oscillograms of nuptial calls of North American Dunlin *Calidris alpina*, to illustrate their pulsed nature; this gives them a "buzzy" quality. Calls B and C are shown at two different time scales, indicated in milliseconds.

SYSTEMATICS AND GEOGRAPHIC VARIATION

Sound signals are likely to provide valuable insight into evolutionary patterns of shorebirds. Discrete call types, like those uttered by parent calidridines when approached by humans, offer an example (Figure 3). Most species I am familiar with have two distinct kinds of calls in such a circumstance: a brief frequency-modulated call, and a trill. These call types are readily accepted as "equivalent" across species in an evolutionary sense (*i.e.* able to be judged as homologous), and it should be possible to draw conclusions about evolutionary relationships among calidridines based on call characteristics. In general, call types which are subject to strong selective pressure (as through sexual selection) offer the best material for studying population differentiation or species relationships; more conservative kinds of calls, like those used by migrants or wintering birds, should be more useful in studying relationships at higher levels (*e.g.* genera).

Little use has been made of acoustic characteristics in shorebird systematics. However, some colleagues (W.W.H. Gunn, S.F. Maclean, Jr., J.P. Myers, and B.N. Veprintsev) and I have been studying nuptial calls of male calidridine sandpipers, and have noted some consistent and potentially useful differences among certain groups of species. One call type, the simple, rhythmically-repeated call uttered by males over their "territory", differs strongly between Dunlin *Calidris alpina*, Baird's Sandpiper *C. bairdii*, and Sanderling *C. alba*, on the one hand, and Least Sandpiper *C. minutilla*, Long-toed Stint *C. subminuta*, Stilt Sandpiper *C. himantopus*, and Surf-bird *Aphriza virgata*, on the other. The former species have a pulsed "frog call"; the latter have an unpulsed tonal call which may have some introductory elements (Miller 1983b; Figure 4). To make sense of such features in evaluating species' affinities, it is necessary to distinguish ancestral features from those which evolved later; only the latter kind can help us sort things out. Our study of the Calidridini is in progress. We feel that other groups of species whose sounds may be usefully studied for taxonomic purposes are *Charadrius* plovers, tringine sandpipers, curlews, snipe, and woodcock.

Geographic variation in shorebird sounds has been studied very little (Miller 1984), which is surprising when one considers the potential practical values such work may have in distinguishing different migrating or wintering birds. I shall discuss potential applications, ecology, and social systems in the next and final article.

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