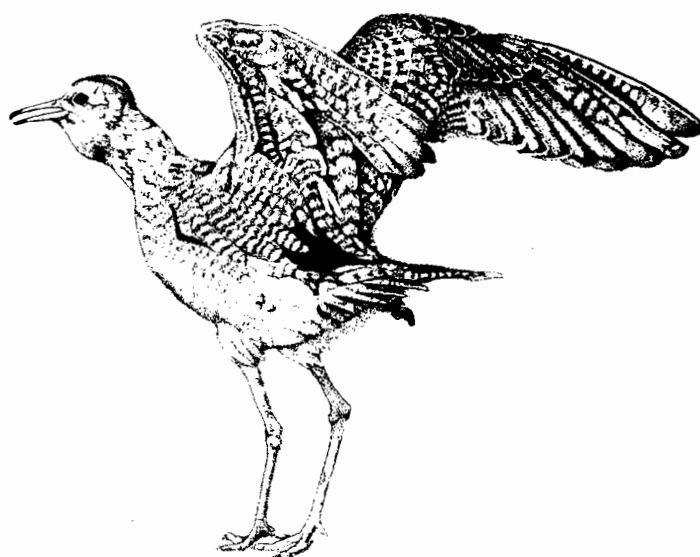




Acoustic Signals of Shorebirds

A Survey and Review of Published Information

Edward H. Miller



A Royal British Columbia Museum Technical Report

A Technical Report

Acoustic Signals of Shorebirds

A Survey and Review of Published Information

Edward H. Miller

**ROYAL
BRITISH
COLUMBIA
MUSEUM**

*Province of British Columbia
Ministry of Tourism and
Ministry Responsible for Culture*

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ABSTRACT

Bioacoustic analyses for 120 of the 218 species of shorebirds (Charadriiformes: Charadrii) have appeared in more than a hundred published papers, books, reports and theses. Most analyses are in the form of sound spectrograms. These cover a small fraction of species' repertoires, and most are accompanied by only scant observations on acoustic signaling behaviour or social interactions. The single best source of information on shorebird sounds is Stanley Cramp's outstanding "The Birds of the Western Palearctic" (Vol. 3; Oxford University Press, 1983). It has technically excellent sound spectrograms for 54 species with clear detailed behavioural notes. Other key references are Glutz *et al.* (1975, 1977), Bergmann and Helb (1982), and Maclean (1985); major additions to our knowledge are anticipated in Marchant and Higgins (in press). Future research on shorebird sounds should feature more detailed physical analyses, observations on sound-signaling behaviour and its social significance, key taxa whose sounds are currently not documented (especially threatened taxa), and applications for conservation and management (e.g., use of sounds in census taking; characterization of sounds in discrete populations).

I. INTRODUCTION

Shorebirds are a fascinating and diverse group of birds, but their communicative behaviour is poorly known (Miller, 1984). This is unfortunate, as shorebirds offer a wealth of contrasts that can reveal important ecological and evolutionary processes while enriching our knowledge of bird behaviour generally. I have prepared this report to facilitate research on shorebird communication. Its aims are to provide a general guide to literature on shorebird acoustics and to recommend research priorities. I try to meet these aims by listing species for which sound analyses have been published or are available in reports or theses, providing references, critically assessing the adequacy of existing analyses and coverage, and recommending directions for future work. The references listed and discussed here are updated and corrected from earlier summaries (Miller, 1984; Miller et al., 1988).

I introduce the report with an account of the physical analysis of bird sounds (Section II, p. 2). There I also discuss how sounds can be described, analysed and prepared as illustrations for publication. As well, I comment on the technical adequacy of published sound analyses for shorebirds, and on ways to describe behaviour that accompanies sound signaling. A critical review of coverage in the taxonomic list follows (Section III, p. 10). That Section includes recommendations for future research. The taxonomic list (Section IV, p. 17) is organized alphabetically by family, and by genus and species within each family. References to sound analyses are listed under each species and are given in full in Section V (p. 37). Illustrations for the report form Section VI (p. 51).

Nomenclature in this report follows that of Hayman et al. (1986), with the addition of Chionididae, Pedionomidae and *Prosobonia ellisi*. Their account differs from certain others in the small number of *Himantopus* species recognized, the large number of *Haematopus* species, the recognition of *Calidris paramelanotos*, and in some other ways.

Many authors of the papers, reports and theses discussed below have helped me greatly in many ways, and I extend my gratitude to them all. I am indebted to Erica Bates for assisting me in the early phases of this project, to Christine Dionne for helping me to complete it, and to Gerry Truscott for overseeing its technical production. Craig Dickson, Don Kroodsma and John Marchant carefully and thoughtfully reviewed drafts of this report, and I have revised it following most of their suggestions. Frederike Verspoor and Carron Nixon have helped me to obtain many articles and books, and Adolf Ceska translated some important Russian papers.

I welcome criticisms and comments from which future revisions of this report or additions to it could benefit.

Edward H. Miller
September 1992

II. DESCRIBING AND ANALYSING BIRD SOUNDS

General remarks

People have long been fascinated by the complexity and beauty of bird sounds, and have written numerous accounts of them. Observers commonly used written descriptions or musical notation before equipment was developed to analyse sounds. Applications of musical notation to bird sounds date to at least three centuries ago, and are occasionally still used (Hooker and Hooker, 1969; Armstrong, 1973; Fig. 1).

Musical notation removes much subjectivity from description but is limited "because birds do not sing by the musical scale, by time, by key, or by any definite pitch" (Arlton, 1949:7). Even so, some useful compilations of bird sounds summarized in musical notation have been published. They enable the reader to distinguish different species and they also provide good characterization of pitch, timing, complexity and diversity of different species' vocalizations (e.g., Mathews, 1904; Saunders, 1921; Arlton, 1949).

Most published descriptions of bird sounds use written descriptions. Detailed descriptions using standard terminology can convey a lot of information but often use words whose meanings can be ambiguous, differ from reader to reader, change over time, vary across cultures, or rely upon comparisons with other species or sound classes (which therefore must be familiar to the reader to be useful).

Variation in how observers transcribe sounds can be illustrated with the song of the Upland Sandpiper (*Bartramia longicauda*). It has been described as "weird windy whistles" (Peterson, 1990:144) and as a "long slurred whistle" (Robbins et al., 1983:122). It has been transcribed as "willa-willa-willa' followed by a vibrant 'rrrrrphleeoo' " (Hayman et al., 1986:322) and as "whooleeeeeee wheelooooooooo" (Peterson, 1990:144). Such descriptions and transcriptions are useful mainly for identifying birds in the field through a process of elimination. Even there they can be troublesome, for adjectives like the ones used above are open to interpretation, and people vary greatly in how they transcribe sounds and how they interpret transcriptions.

Some publications rely heavily on transcriptions (e.g., Hayman et al., 1986; Peterson, 1990), others use them variably (e.g., National Geographic Society, 1987), while others use none (e.g., Robbins et al., 1983). Almost all publications include written descriptions, however, and employ a bewildering variety of adjectives. Consider the following selection from shorebird accounts in Peterson (1990), for example:

accented, clear, emphatic, forceful, high, insistent, liquid, loud, low, mellow, musical, nasal, noisy, piping, plaintive, rapid, rapidly repeated, rasping, rattling, repetitious, sharp, short, slurred, staccato, thin, trilled, variable.

Obviously, adjectives need to be chosen carefully and used with standard meanings as much as possible, especially within single publications. Descriptions of sounds based on comparisons are useful mainly for field identification within a known area or set of species. For example, a common kind of call of wintering Rock Sandpipers (*Calidris ptilocnemis*) has been described as:

"Not known to differ from Purple Sandpiper"
(Hayman et al., 1986:379)

"flicker-like du-du-du"
(Peterson, 1990:142)

"flicker-like"
(Robbins et al., 1983:128)

Almost all descriptive material on shorebird sounds (indeed, on animal sounds generally) thus serves to characterize their general qualities and to facilitate field identification within particular areas, seasons and sets of species that are likely to be encountered. Written descriptions and transcriptions are not intended to provide rigorous physical or behavioural baselines for different species, although in many cases they are so complete and clear that they can be useful in that regard (e.g., Cramp, 1983; Hayman et al., 1986).

To adequately describe sounds so their descriptions can be analysed and compared rigorously, it is necessary to use some form of physical analysis. I describe some technical approaches to such analysis next.

Technical analysis

The sound spectrograph was developed in the late 1940s to analyse human speech. It proved to be nearly ideal for analysing bird sounds, since birds' voices and hearing are similar to humans' in many ways. Thus bird sounds can be displayed graphically as frequency changes over time and over important parts of a species' hearing range, revealing fine structure (Fig. 2). Sound spectrograms (also called audiospectrograms, sonograms or sonagrams) quickly became a standard way to portray bird sounds, and have become mandatory in many kinds of investigations.

Sound spectrograms have many uses in zoology. Because of the fine detail they provide, they have been used to investigate diverse questions in ornithology, such as on respiration, mechanisms of voice production, adaptation for transmission in different habitats, phylogenetic relationships, social recognition, cultural transmission of song, vocal mimicry, learning and geographic variation.

Conventionally, bird sounds have been analysed over a frequency range up to either 4,000

or 8,000 cycles per second (Hertz, or Hz), with an analysing filter bandwidth that provides good temporal resolution. A 300-Hz bandwidth, or "wide-band" setting, over the 8,000 Hz (=8 kiloHertz, or kHz) range has been standard. The frequency scale used has usually been linear rather than logarithmic. Such conventional practices have been a tremendous boon to research in bioacoustics for they have permitted a ready comparison of analyses that have already been made in straightforward repeatable ways. Furthermore, most have been produced on equipment manufactured by a single company (Kay Elemetrics in Pine Brook, New Jersey)!

The widely used "8 kHz, wide-band, linear frequency scale, Kay sound spectrogram" has contributed immensely to the documentation and study of bird sounds. Even so, most investigators have not exploited sound spectrographs fully to analyse the rich structure of bird sounds. To explore fully the structure of bird sounds one can use different settings to "compress" or "stretch" the sound in the frequency and time domains. For example, the scale magnifier function can be used to set lower and upper frequency limits for analysis; the logarithmic frequency scale can portray sounds more like birds hear them; slow tape speed permits exploration of fine details of temporal structure; and different bandwidths emphasize temporal and frequency-related features of interest (Davis, 1964; Watkins, 1967¹; Greenewalt, 1968¹; Marler, 1969¹; Hold, 1970¹; Cramp, 1977; Marshall, 1977; Szöke and Filip, 1977; Gaunt, 1983a; Hall-Craggs, 1979; Beecher, 1988¹, Richard, 1991).

As a simple illustration of the value of analysing sounds over different time scales, consider the song of the Dunlin (*Calidris alpina*). It is evident from Fig. 3 that much hidden detail is revealed even when the song is just temporally "stretched" to double the length seen on a typical 8 kHz representation (note however that the song's overall frequency trends are more apparent in the top figure). Even more detail is revealed as the temporal domain is explored further.

The choice of an appropriate analysing filter bandwidth is extremely important, for this determines the resolution obtained in the frequency and time domains. To reveal details of frequency a narrow bandwidth should be used. Temporal features are seen more sharply in wide-band analyses (technical details and specific recommendations are in the references in footnote 1). The differences are evident in analyses of song of the Short-billed Dowitcher (*Limnodromus griseus*), which shows strong frequency modulation. This is clearest in a narrow-band analysis (Fig. 4).

Kay sound spectrograms have been the most widely used form of analysis to date. Digital analyses, such as through signal-analysis packages for personal computers, are now becoming

¹These are excellent general papers on the subject.

widely available, however². The purposes of digital analyses are similar, but analyses are executed differently and are much more flexible than analog analyses. "Analysing filter bandwidth" is emulated by "bin" or "frame" size, providing variable resolution in the frequency and time domains. A large number of points per bin provides sharp frequency resolution but poor temporal resolution; a small number of points provides sharp temporal resolution but poor frequency resolution. For example, 100 points per bin is equivalent to a 293-Hz analysing filter bandwidth, and they provide comparable spectrograms when analysed over the same frequency range (e.g., 8 kHz). Digital analyses are repeatable and highly flexible, and enable workers to investigate time, amplitude and frequency in great detail, either singly or in combination. Thus, one can investigate easily how a sound's energy is distributed across different frequencies (Fig. 5). Such an analysis is of great value to evolutionary biologists, for different species or geographic areas can be readily compared. Sounds from birds in habitats that differ in propagation characteristics can also be compared: temporal and spectral characteristics of many kinds of sounds (particularly long-distance sounds) are adapted for optimal propagation through a species' environment (Wiley and Richards, 1982).

A third type of analysis shows how amplitude changes over time. Many bird sounds show rapid and complex changes in amplitude; waveform representations such as oscillograms, amplitude profiles, and amplitude envelopes are good ways to illustrate them (Fig. 6). Again, such analyses are valuable in various evolutionary and ecological investigations.

Preparing illustrations

Beecher (1988) made many thoughtful recommendations for analysing and illustrating sounds according to which features are of particular interest. Here I discuss some practical considerations in illustrating sound analyses for publication. To present graphical summaries of sound analyses effectively requires common sense and the application of fundamental graphic principles (Tufte, 1983, 1990). It also requires a working knowledge of sound analysis, though this is not always evident in publications.

Frequency and time grids overlain on sound spectrograms are often useful. Cramp (1983) used a grid of fine red lines on each sound spectrogram. The faint colour and fine lines of the grid are not distracting, and they provide a quick guide to overall frequency and temporal trends (Fig. 7). Frequency lines are particularly useful when illustrations are small, as in MacLean (1985) and Robbins et al. (1983), or over a logarithmic frequency scale (Fig. 8).

Illustrations should portray multiple examples over the range of sounds being investigated,

²For example: CANARY, developed by the Bioacoustics Research Program, Laboratory of Ornithology, Cornell University, Ithaca, New York, U.S.A. 14853; CSL, developed by Speech Technology Research Ltd., Suite D, 1623 Mackenzie Avenue, Victoria, B.C., Canada V8N 1A6.

not just single examples. This is particularly important where sound classes are indistinct from one another and intergrade (Fig. 9) or where multiple comparisons are being made. In both cases a reader's comprehension is enhanced when the comparisons are facilitated through appropriate layout of the figures (e.g., in some logical progression of intergradation as in Fig. 9, or side-by-side as in Fig. 10).

Illustrations can be extremely effective in summarizing complex temporal sequences or complex inter-relationships of optical and acoustic display components [Fig. 11; see other examples in Miller (1984, 1988, 1991)].

Preparing Kay sound spectrograms for publication is tedious with older types of machines (up to and including the digital sound spectrograph, model 7800) because they use paper with a coating that is easily cracked, chipped, scratched or smudged. To prepare and physically apply frequency and time scales to them can be frustrating and time-consuming, especially when preparing several spectrograms for a composite figure. Furthermore, the grey-to-black tones are difficult to translate into adequately detailed black-and-white prints. One effective and inexpensive way to do it is to reproduce sound spectrograms as photo-mechanical transfers (PMTs) at commercial outlets like engineering/drafting stores. This procedure retains most fine details of shading, even though the prints are nearly black-and-white, so is preferable to the use of pen-and-ink tracings. PMTs can be prepared on a continuous scale of reduction and magnification and the resulting prints can be composed readily into final illustrations for publication.

Recent Kay sound spectrographs (e.g., Kay DSP Sona-Graph 5500, with thermal printer) produce PMT-like prints with all the advantages just mentioned. The growing availability of inexpensive microcomputer-based sound analyses has facilitated the preparation of illustrations, because acceptable illustrations can be printed directly in a form that needs little modification for publication (see footnote 2, p. 5). Some manufacturers (e.g., Mitsubishi) produce "video printers" that make highly detailed photo-quality prints. In fact the prints show more detail than can be reproduced in most publications.

To save time, money and frustration, many workers use pen-and-ink tracings, which are simple to work with and can be reproduced as black-and-white photographs. Such renderings are useful for stressing certain features, particularly for narrow-band sounds. Sound characteristics that can be highlighted usefully with pen-and-ink drawings include duetting, plus general temporal and frequency organization of complex utterances or sequences (e.g., oystercatcher piping; Fig. 12). Tracings prepared as composite illustrations are effective also for summarizing overall variations and trends, and for facilitating comparisons among sound classes or across species (Fig. 13; see also Fig. 10). Tracings are valuable for illustrating sounds that have been recorded with a lot of background noise. Despite these advantages, pen-and-ink tracings are not desirable as a general form of presentation. For one thing, they are inaccurate and insufficiently detailed, especially for broad-band sounds (Fig. 14). Pen-and-ink renderings also obscure many important

attributes, such as relative strengths of harmonics, or modulations in amplitude or frequency (Fig. 15). Finally, observers have different biases in the features they choose to illustrate and emphasize.

It is essential to report accurately and fully on details of analysis (see references in footnote 1, p. 4). Most published papers on shorebird acoustics fail to meet acceptable standards in this regard. Some examples are:

- The make and model of analysing equipment or software used for analysis are not given (e.g., Phillips, 1972; Dowsett et al., 1977).

- Technical details that determine frequency and temporal resolution are not reported (i.e., effective analysing filter bandwidth or bin size; e.g., Baker, 1974; Höglund and Lundberg, 1987).

- The effective analysing filter bandwidth is not corrected for the analysing frequency range used. In analog analyses the most common error is to report a specific analysing filter bandwidth, such as 300 Hz, though this applies only to the 8 kHz range on the most widely used non-digital Kay machines. In fact, the effective analysing filter bandwidth is reduced when drum or tape speed is reduced (e.g., in analysing a sound over the 16 kHz range) and it is increased at higher speeds (e.g., Miller, 1983a, b; Miller et al. 1984; see Fig. 4).

- The "high-shape" setting is used, instead of "flat". The former setting is designed to emphasize those frequencies that are important in the analysis of human speech, so is inappropriate for analyses of bird sounds [e.g., Oring, 1968; Haig, 1992 (Haig, pers. comm.)].

- The analysing frequency range is not given or only a portion of the frequency range is illustrated, thereby making it unclear whether only that portion was analysed (e.g., Terborgh and Weske, 1972; Byrkjedal et al., 1988). A related flaw is when a single frequency marker is shown, with no indication of scale (e.g., Fig. 15a).

- Finally, to be technically correct the frequency scale should be labelled as "frequency", yet most workers simply indicate the unit - namely Hz (e.g., Fig. 12). This is like a growth study showing a plot of "grams" as a function of age, with no indication of what "grams" refer to (kidney? brain? etc.). Also, it is not uncommon for workers to report frequency units as "number of cycles" rather than as "number of cycles per second": Robbins et al. (1966) illustrate frequency in "KC" while Bursian (1971) reports it in "Kilocycles". Other errors in reporting the frequency scale arise [e.g., Walters (1990) labels it "log frequency" but shows actual frequency values on a logarithmic scale]. Without question the most common minor error is in the spelling and abbreviation of Hertz (Hz) and kiloHertz (kHz). The word is derived from the name of the physicist Heinrich Hertz, so by convention only the "H" is capitalized. Yet one commonly encounters hz, khz, KHz, kHz, Khz, etc. (e.g., Dabelsteen, 1978; Warham and Bell, 1979).

Papers that report on shorebird sounds do not all have detailed physical baseline description as their primary goal. Even so, all authors should satisfy the basic research criterion of independent repeatability by other workers. Technical details and graphical presentations that are available for shorebird sound analyses are clearly inadequate in this respect, as indicated in the preceding discussion (and I am as guilty as anyone!). In light of the increasingly widespread availability of inexpensive "user-friendly" software for digital analysis of sounds, and of good critical review papers on signal analysis, there is no longer any reason for such poor reporting.

Behavioural observations

It is difficult to describe behaviour well and in a standard manner that enables comparisons by other workers (Miller, 1988, 1991). Here I discuss some principles of behavioural description that are relevant for describing sounds and sound repertoires.

We can only sample a species' repertoire, not exhaustively describe it. Thus our descriptions are inherently incomplete, both in the number of sound types we recognize and the behavioural contexts they appear in. The notions of "sampling" and "incompleteness" are statistical concepts that are well established in biology: our completeness and understanding improve in step with the more information we compile, through observing birds for more hours, over the 24-hour day, throughout the seasons, and in varied behavioural settings. This is all common sense. The limitations to sampling are rarely mentioned in descriptions, though, or are often just vague or implied. Let me illustrate this point with an example.

The Least Sandpiper (*Calidris minutilla*) breeds from western Alaska to Nova Scotia (Miller, 1986). It winters along both eastern and western coasts of North America, south to the Caribbean and northern half of South America (Hayman et al., 1986; Heinonen and Chebez, 1988). Most North American observers therefore encounter this species on migration or during winter, as is clearly implied for the following descriptions of the species' calls: "shrill, high *kreee*" (National Geographic Society, 1987:130); "thin *krreet*, *kree-eet*" (Peterson, 1990:148); and "high *breep*" (Robbins et al., 1983:132). These brief descriptions refer to one class of sound. In fact this species produces at least 20 classes, mainly on the nesting grounds (E.H. Miller, unpublished observations). In this example, then, a simple but substantial improvement to the descriptions would be to just indicate the call type's seasonal context. [For sound spectrograms of calls by migrants, and parental "alarm" calls, see Cramp (1983) and Miller (1984, 1985).]

Details on the behavioural circumstances in which sounds are used are also essential to good descriptions. Behavioural contexts are hard to describe, though, because people tend to be interpretive or anthropomorphic. Words like "alarm", "distraction" and "threat" appear frequently in published descriptions of bird behaviour yet reflect human behavioural categories, not necessarily those of birds. A description such as "the alarm call is 'pip-wheet'" (Hayman et al., 1986:311) assumes that we have a common understanding of

what "alarm" is to a Magellanic Plover (*Pluvianellus socialis*)! Some straightforward simple notes on gender, breeding status, age, behaviour, etc., would clarify what is meant (standing? running? flying? And, if the latter, is the flight circling around, away from, or towards the observer? etc.). The same authors' description for the Tawny-throated Dotterel (*Oreopholus ruficollis*) is exemplary: "Generally silent on the ground, but calls loudly when flushed, a distinctive, tremulous, reedy note with a falling inflexion, often repeated (frequently heard from flocks flying overhead)..." (op. cit.:310).

The last topic I will discuss is that of behavioural categories. Humans tend to impose categories on nature that reflect human views and preconceptions, rather than how nature is organized. For example, people often distinguish bird "calls" from "songs", with the latter typically referring to complex loud vocalizations of males. The world of bird sounds cannot be broken down so easily, for bird sounds range from simple to complex, loud to soft, vocal to instrumental, and harsh to pleasing. Thus a first step in describing sounds is to describe their properties, rather than to erect categories. The properties themselves may be the important element of communication: a sandpiper brooding its chick may use a range of soft, calming sounds, for example: it may not matter which particular type of sound is employed (e.g., Gyger et al., 1987). In many cases, discrete classes of sounds do exist, of course. I discuss these matters more completely elsewhere, with special reference to variable signal types that intergrade with one another (Miller, 1988, 1991).

Behavioural observations: recommendations

Describe sounds by their properties. When using categories, characterize them fully in terms of their properties. Describe the general behaviour and attributes of calling birds, including locomotion, social circumstances, breeding status, apparent eliciting stimuli, proximity to important environmental features (e.g., predators, nest, other bird), and so on. Cramp (1983) and Hayman et al. (1986) are good models for such descriptions. Finally, describe what you see, not what you think the bird is feeling or trying to do. But use common sense: an observer's intuition and overall familiarity with a species are vitally important elements in attributing function to behaviour.

III. REMARKS ON AVAILABLE ANALYSES

In this Section I comment on published analyses of shorebirds from two perspectives. First, I survey the completeness of existing taxonomic coverage (Section IV, p. 17) and make recommendations for future research. I summarize these recommendations and suggest some areas where research on shorebird acoustics is badly needed or can make substantial contributions (p. 14).

Burhinidae (p. 17)

Nine species of stone-curlews and thick-knees are recognized, two in the genus *Esacus* and seven in *Burhinus*. Of these, calls of four *Burhinus* species have been analysed. Cramp (1983) provides a superb summary of social behaviour and calls in the widely distributed *B. oedicnemus*, based mainly on European accounts, and including five sound spectrograms. Voice in the other three species is poorly known by comparison. There has been no dedicated research on acoustic communication in any species of burhinid, but Cramp (1983) and Bergmann and Helb (1982) provide an adequate benchmark for the family. It would be valuable to extend those treatments with a focussed study on acoustic signaling in *B. oedicnemus* and to provide a general account for *Esacus*.

Charadriidae (p. 17)

Sixty-five species of plovers are recognized, forming a diverse group with a world-wide distribution. Calls of 33 species have been analysed: 17 species in the complex *Charadrius* group (including *Anarhynchus*); all four *Pluvialis* species; and 12 of 24 *Vanellus* species. Some good studies have been carried out on the abundant and widespread *Ch. vociferus* plus four New Zealand species (including the unusual *Anarhynchus* and *Ch. novaeseelandiae*). Other very good descriptive papers are on *Ch. montanus* and *wilsonia*. Good baseline descriptions also exist for *Ch. alexandrinus*, *Ch. bicinctus*, *Ch. dubius*, *Ch. hiaticula*, *Ch. morinellus*, *P. apricaria*, *V. spinosus* and *V. vanellus*. Nuptial displays in the latter species have been analysed in detail by Dabelsteen (1978). In many respects *V. vanellus* is atypical of the genus, so it would be desirable to have a descriptive study for a more typical species. The odd *V. cayanus* deserves separate study. A baseline account for a sandplover species is needed. Particularly distinct charadriids that merit research are the South American *Ch. modestus*, *Phegornis* and *Oreopholus*; the Australian *Ch. cinctus*, *Ch. melanops*, *Ch. rubricollis* and *Peltohyas*; and the African *Ch. forbesi* or *tricoloris*.

Chionididae (p. 21)

Only two species, *Chionis alba* and *minor*, constitute this remarkable family. Ironically, no analyses of their sounds have been done, though their social behaviour, social structure, and optical signals are among the best known of all shorebirds (Burger 1979, 1980, 1981, 1984; Burger and Millar, 1980; Peter et al., 1988; Verheyden, 1988; Verheyden and Jouventin,

1991)!

Dromadidae (p. 21)

A single species, *Dromas ardeola*, is recognized. It has a remarkable colonial social system, with the use of nesting burrows, but details of social behaviour are scanty and no sound analyses are available.

Glareolidae (p. 21)

This family comprises eight species of coursers (four each of *Cursorius* and *Rhinoptilus*), eight of pratincoles (seven *Glareola* plus *Stiltia*), and the odd *Pluvianus*, which is allied to the coursers. Acoustic signals and signaling behaviour are well described for *Pluvianus*. A few prominent kinds of vocalizations have been analysed for two *Cursorius*, three *Glareola*, and one *Rhinoptilus* species. No dedicated research on acoustic communication has been done on any species of glareolid except *Pluvianus*, so benchmark descriptions and analyses are needed for species that represent the family better.

Haematopodidae (p. 22)

There are reasonably good published accounts of acoustic signals in five of the 11 species of *Haematopus*. Sounds of the distinctive *bachmani* and *fuliginosus* are undescribed. Those of the rare endemic species *chathamensis* should be re-described. A detailed physical and behavioural study on at least one oystercatcher species is long overdue; Cramp's (1983) account of European *ostralegus* is a good starting point.

Ibidorhynchidae (p. 22)

Ibidorhyncha struthersii is the sole member of this odd family, which is allied to the Haematopodidae. Its sounds are undescribed.

Jacanidae (p. 22)

There are eight species of jacanas in six genera: *Actophilornis* (2), *Hydrophasianus* (1), *Irediparra* (1), *Jacana* (2), *Metopidius* (1) and *Microparra* (1). Detailed analyses have been published only for *J. spinosa*, which has a complex structurally graded system of vocal signals. Because of the high number of genera, the accounts for *J. spinosa* may not be representative. Therefore, even general analyses for the other genera are desirable.

Pedionomidae (p. 23)

One kind of sound signal of the remarkable *Pedionomus torquatus* has been well described. The phylogenetic and ecological distinctiveness of this species, and its possibly precarious status, give high priority to more extensive research on its sound signals.

Pluvianellidae (p. 23)

Behaviour and displays of *Pluvianellus socialis* have been described meticulously by Jehl (1975). No sound analyses have been undertaken, however. As for the preceding family, because of the species' phylogenetic importance and unknown, but possibly threatened status, high priority should be placed on adequate coverage of its sound-signaling system.

Recurvirostridae (p. 23)

This family contains four species of *Recurvirostra* and two of *Himantopus*. It also contains the unique *Cladorhynchus leucocephalus*. *H. himantopus* is taxonomically complex and comprises three major groups (Hayman et al., 1986); the basic structure of the acoustic repertoire is well described. Descriptions and analyses for *R. avosetta* by Adret (1982) are outstanding. A detailed study of acoustic communication in *H. himantopus* would be easy to do, and would usefully extend and improve existing descriptions [those in Sordahl (1980), for example, are very good but are illustrated by sound spectrograms of poor quality]. *Cladorhynchus* is ecologically, behaviourally and evolutionarily unique in the family, and deserves separate study. If any "pure" *H. novaehollandiae* remain, their vocalizations should be documented too.

Rostratulidae (p. 23)

This small family contains two monotypic genera, *Nycticryphes* and *Rostratula*. Two call types of the latter have been published as small sound spectrograms. The species are behaviourally and ecologically interesting, and are different enough from one another that effort should be put into documenting the acoustic signaling systems of each.

Scolopacidae (p. 24)

This large and complex family includes 89 species in 23 genera. Sounds have been analysed for 62 species in 21 genera. Effective coverage is not as good as these figures suggest, however:

1. Arenariini: Sounds of *Arenaria interpres* are well described. Those of the interesting and narrowly distributed derivative species *melanocephala* are undescribed.
2. Calidridini: The Calidridini include 25 species, 19 in the genus *Calidris* and the others

in monotypic genera. The best repertoire descriptions are for *C. alba*, *alpina*, *canutus*, *maritima*, *minuta*, *minutilla* and *temminckii*. These descriptions are all available only as composites, however, as no species has been subjected to dedicated study. Male nuptial vocalizations have been studied in considerable detail for many species. Key species in the tribe are virtually or completely unknown acoustically, including *C. acuminata*, *C. paramelanotos*, *C. ptilocnemis*, *C. tenuirostris*, *Eurynorhynchus*, *Philomachus* and *Tryngites*.

3. Gallinagonini: This tribe is diverse and poorly known acoustically. It comprises *Coenocorypha* (two species), *Lyminocryptes* (one species) and *Gallinago* (15 species). Reasonably good coverage of *G. gallinago* exists and is a good reference point for study of the other species in the genus. *Gallinago* species meriting particular attention are those with restricted distributions, for such species are of both biogeographic interest and conservation concern (*hardwickii*, *imperialis*, *jamesoni*, *macrodactyla*, *megala*, *nemoricola*, *nobilis* and *stricklandii*). As a group, *Gallinago* species also need particular attention paid to questions of the number and distinctiveness of species, for the boundaries are not clear in many cases. Sound signals, particularly mating signals, may prove to be useful in this regard. The other genera need to have coverage of their repertoires expanded, especially the uncommon and localized New Zealand endemic species *Coenocorypha*.

4. Limnodromini: A few male nuptial vocalizations of the three *Limnodromus* species have been analysed. There are two clear research priorities for this group: to establish a repertoire description for *griseus* or *scolopaceus*, and to substantially improve documentation of sound signals in the localized (threatened?) *semipalmatus*.

5. Limosini: Four species of godwit (*Limosa*) are recognized. Sounds of *lapponica* and *limosa* are well described; those of the North American species are undescribed.

6. Numeniini: Seven of the nine curlew species have been studied to varying degrees. The best known are *Numenius americanus*, *arquata*, *minutus* and *phaeopus*. Together these provide a firm baseline for the tribe. More comprehensive descriptions for *Bartramia* are needed, and the rare and endangered *N. borealis*, *tahitiensis* and *tenuirostris* should receive high priority for study.

7. Phalaropodini: There are three species of *Phalaropus*. All have had their sounds well analysed. Howe's (1972) study of social behaviour and communication in *tricolor* is excellent. However, that species is so distinct phylogenetically that a comparable study of one of the others is needed too (Dittmann et al., 1989; Dittmann and Zink, 1991).

8. Prosoboniini: Three recent species form this unique group, but only one (*Prosobonia cancellata*) is extant (Walters, 1991). Its range is now restricted to the Tuamotu Archipelago in French Polynesia. Its sounds are undescribed and have high priority for study.

9. Scolopacini: The woodcocks (*Scolopax*, six species) are a fascinating and poorly known

group. I located 23 references, almost all of which concern male "roding" (*rusticola*) or "peent" calls (*minor*), with reference to their applicability in census taking of these two game species. The M.S. thesis on *minor* by Beightol (1972; Samuel and Beightol, 1973) includes a fair repertoire description. Research priorities are to document the repertoire of *rusticola*, which differs greatly from *minor*, and to analyse representative sounds of the remaining species, all of which have extremely localized distributions and may be threatened.

10. Tringini: Good comprehensive descriptions exist for *Actitis hypoleucos*. *A. macularia* is a widely distributed common species that is one of the best known shorebird species in the world, thanks to research by Oring (Oring et al. 1983; Oring, 1984). Astonishingly, only a single (experimental) study has been done on its acoustic signals, so this species' repertoire remains superficially described. The western subspecies of *Catoptrophorus* has been studied in detail. Sounds of the distinctive *Xenus cinereus* and *Heteroscelus* are essentially undescribed. Remaining tringines are in the genus *Tringa* (10 species). Of these, good descriptions are available for *erythropus*, *glareola*, *nebularia*, *ochropus*, *solitaria*, *stagnatilis* and *totanus*; the extensive descriptions of *nebularia* vocalizations by Nethersole-Thompson and Nethersole-Thompson (1979) make this species' repertoire the best known for any shorebird species. Priorities for bioacoustic research on this tribe are *Actitis macularia*, *Heteroscelus* and *Xenus*.

Thinocoridae (p. 35)

The four species of seedsnipe are split equally between *Attagis* and *Thinocorus*. No sound analyses have been published. The species are not threatened but they represent an interesting adaptive shift to herbivory in dry open country, so are of interest ecologically and behaviourally. *Th. orbignyianus* and *rumicivorus* are parapatric over an extensive area (ca. 2,000 km), so isolating mechanisms between them are of evolutionary interest (Vuilleumier, 1991). Repertoires of both genera should be documented.

Summary of recommendations

Based on the preceding survey I suggest that top priority for sound recording and analysis be assigned to species that are of conservation concern and are also of particular interest behaviourally, ecologically, evolutionarily or taxonomically. Using these criteria, highest priority goes to: *Charadrius sanctaehelenae*, *rubricollis* and *thoracicus*; *Coenocorypha*; *Haematopus chathamensis*; *Himantopus novaezelandiae*; *Limnodromus semipalmatus*; *Numenius borealis*, *tahitiensis* and *tenuirostris*; *Pedionomus*; *Pluvianellus*; *Prosobonia*; *Rhinoptilus bitorquatus*; *Tringa guttifer*; and *Vanellus gregarius*. As well, poorly known tropical species with localized distributions may be at risk, including many *Gallinago* and *Scolopax* species; these deserve immediate attention.

Many taxa that are not of immediate conservation concern are of great scientific interest because of their phylogenetic positions. Families for which repertoires should be described

are: Chionidae; Dromadidae; Ibisornithidae; Pluvianellidae; Rostratulidae; and Thinocoridae. Many lower taxa are also of interest because their phylogenetic relationships are unclear, including: *Bartramia*; *Oreopholus*; *Peltohyas*; *Phegornis*; *Rhinoptilus*; *Cladorhynchus*; *Esacus*; *Gallinago* except *gallinago*; *Glareola*; *Heteroscelus*; Jacanidae except *Jacana*; *Scolopax rusticola*; *Stiltia*; *Vanellus cayanus*; other *Vanellus* species except *vanellus*; and *Xenus*.

Shorebird acoustics offer good models for much research on behaviour, ecology and evolution, apart from any interest in shorebirds *per se*. For example, the adaptation of sounds and signaling behaviour for long-distance transmission could be studied easily in shorebirds: some species advertise at night, others during the day, and yet others are crepuscular; some advertise aerially, others from the ground, and others from prominences; and species that signal over long distances inhabit diverse habitats, ranging over open flat terrain from sea level to high elevations, swamps, dense forest, sea coasts, and torrential rivers. Shorebird sounds must encode individuality in many circumstances, such as in permanent residents, species with prolonged care of offspring, and colonial species. Geographic variation in shorebird sounds is virtually unstudied but is an exciting area for investigation because they appear to be shaped little by learning. The distributional characteristics of related shorebird species offer numerous natural experiments and contrasts for such research: localized vs. widespread, fragmented vs. continuous, resident vs. migrant, one- vs. two-dimensional, etc. Differences in sounds between sibling species may reveal the origin of isolating mechanisms and the origin of species; good material is offered by several taxa, including the species complexes of *Gallinago gallinago*, *Himantopus himantopus* and *Charadrius hiaticula/semipalmatus*.

There are many reasons for recording and analysing shorebird sounds aside from their scholarly interest to comparative biologists, of course. Some practical considerations for conservation are the identification of unique taxa that may need protection. This is particularly true for species that have discontinuous distributions; that include marginal, isolated or island populations; and that include both resident and migratory populations. Such features of species or species groups suggest that genetically distinctive components may exist that deserve formal recognition as subspecies or species. Available evidence suggests that shorebird sounds are not imitated as are many oscine sounds (i.e., are evolutionarily conservative) so where they differ across populations there is good reason to suspect that different taxa are involved³. All investigations of which I am aware have been on the Scolopacidae; only the brief report on *Gallinago gallinago* by Thönen (1969) suggests that substantial geographic differences exist (in this case between Europe and North America). Other groups of scolopacids, and other families of shorebirds, should be examined for geographic variation. Representative situations in other families that would be worth investigating, to establish whether geographic variation exists and can characterize

³Some vocal classes of oscines exhibit little intraspecific variation, however (e.g., Kroodsma et al., 1984). For suboscines see Kroodsma (1984, 1985) and Kroodsma et al. (1987).

different populations, are resident populations of: *Burhinus oedicephalus* (Burhinidae); *Charadrius alexandrinus* (Charadriidae); *Chionis minor* (Chionidae); *Cursorius temminckii* (Glareolidae); *Haematopus palliatus* (Haematopodidae); *Himantopus himantopus* (Recurvirostridae); *Rostratula* (Rostratulidae); and *Attagis gayi* or *Thinocoris orbignyianus* (Thinocoridae). Classes of sounds that are used to attract mates or deter competing conspecific individuals should be chosen for study for these are the ones that diverge most dramatically during early stages of population differentiation (West-Eberhard, 1983; Eberhard, 1985). In certain of the families that I've just listed, this kind of signal is absent or at least not clearly present, so other types would have to be examined (Chionidae, Haematopodidae, Recurvirostridae).

Many migratory shorebird species have widespread or disjunct breeding ranges where nuptial sound population "markers" can be sought. Taxa that are worth investigating are: *Calidris alba* and *canutus*; western and eastern subspecies of *Catoptrophorus*; *Ch. alexandrinus*, *nivosus* and *melodus*; and *Limosa fedoa* and *limosa*. Obviously there are many other situations that are worthy of study as well.

In contrast to the state of knowledge about breeding vocalizations, almost nothing is known about acoustic communication outside the breeding season: structural characteristics, functions, variability, species-specificity, etc. Better documentation of sounds at these critical seasons could aid census taking and identification of difficult species, such as small calidridines [see Dierschke (1989) and Piersma et al. (1990, 1991)]. Some species are widespread on both breeding and wintering grounds, and may show geographic variation in wintering calls. Such calls would be easy to record, and such an investigation may reveal geographic variation that is valuable in management.

Finally, research on physical characteristics, social significance, ecological influences, and behavioural rhythms can aid in estimating size and density of breeding and resident populations, and in monitoring population status over time. Such studies are particularly important for species that are hard to enumerate visually. To my knowledge, such work has only been carried out on *Scolopax minor* and *rusticola*.

IV. TAXONOMIC SUMMARY OF ANALYSES

In the following list I have indicated by asterisks those species whose sound repertoires are documented with sound spectrograms that cover at least five structurally different sound types. Major references (i.e., those covering at least five sound classes) are marked with two asterisks. Other references, that document sound classes not in the major references, or that provide other important information (e.g., on individuality), are marked with single asterisks. Single major references do not exist for some species that meet the criterion of five sound classes (e.g., *Glareola pratincola*). I have marked graduate theses only if data have not been formally published (e.g., Howe, 1972; Mace, 1981).

For each family I have indicated in brackets the number of species for which analyses are available and the number of species in the family; the latter includes recently extinct species (e.g., "4/9"). In addition to the species included in Hayman et al. (1986), are Chionididae (two species), Pedionomidae (one species), and *Prosobonia ellisi* (Walters, 1991).

Most sound spectrograms in Robbins et al. (1966) are identical to those in Robbins et al. (1983), so reference to the latter also applies to the former. Exceptions are noted.

Burhinidae (4/9)

BURHINIDAE

Burhinus capensis

MacLean (1985)

Burhinus

* *Burhinus oedicnemus*

** Bergmann and Helb (1982)

** Cramp (1983)

Burhinus senegalensis

Cramp (1983)

Burhinus vermiculatus

MacLean (1985)

Charadriidae (33/65)

CHARADRIIDAE

* *Anarhynchus frontalis*

** Phillips (1980)

Anarhynchus

CHARADRIIDAE

Charadrius

- * *Charadrius alexandrinus*
 - ** Bergmann and Helb (1982)⁴
 - ** Cramp (1983)
 - Glutz et al. (1975)⁴
 - ** Krey (1991)
- * *Charadrius bicinctus*
 - ** Phillips (1980)
- * *Charadrius dubius*
 - ** Bergmann and Helb (1982)
 - ** Cramp (1983)
 - ** Glutz et al. (1975)
 - * Tikhonov and Fokin (1980)
- * *Charadrius hiaticula*
 - ** Bergmann and Helb (1982)
 - ** Cramp (1983)
 - * Glutz et al. (1975)
 - * MacLean (1985)
 - * Tikhonov and Fokin (1979)
 - * Tikhonov and Fokin (1981b)
 - * Tikhonov and Fokin (1982)
- Charadrius leschenaultii*
 - Nadler and Königstedt (1986)
- Charadrius melodus*
 - Haig (1992)
- Charadrius mongolus*
 - MacLean (1985)
 - Nadler and Königstedt (1986)
- * *Charadrius montanus*
 - ** Graul (1974)
 - Miller (1984a)
- * *Charadrius morinellus*
 - * Bergmann and Helb (1982)
 - ** Cramp (1983)
- * *Charadrius novaeseelandiae*
 - ** Phillips (1977)

Charadrius...

⁴The lowest of the three sound spectrograms shown on p. 214 of Glutz et al. (1975) and that on p. 132 (part a) of Bergmann and Helb (1982) are mis-labelled: they illustrate *Calidris alpina* song (Krey, 1991).

CHARADRIIDAE

...*Charadrius*

- Charadrius obscurus*
Phillips (1980)
- Charadrius pecuarius*
MacLean (1985)
- Charadrius semipalmatus*
Miller (1984a)
- Charadrius tricollaris*
MacLean (1985)
- * *Charadrius vociferus*
Borror (1970)
** Bursian (1971)
Cramp (1983)
* Gaunt (1983b)
* Heckenlively (1972)
* Nol (1980)
** Phillips (1972)
Robbins et al. (1983)
- * *Charadrius wilsonia*
** Bergstrom (1988)
Robbins et al. (1983)
- * *Pluvialis apricaria*
** Bergmann and Helb (1982)
** Cramp (1983)
** Nethersole-Thompson and Nethersole-Thompson (1986)
Richard (1991)
- Pluvialis dominica*
Greenewalt (1968)
Miller (1984a)
Robbins et al. (1983)
- Pluvialis fulva*
MacLean (1985)
Tikhonov and Fokin (1981b)
- * *Pluvialis squatarola*
** Bergmann and Helb (1982)
* Cramp (1983)
* MacLean (1985)
* Miller (1984a)
Robbins et al. (1983)
* Tikhonov and Fokin (1980)

Pluvialis

CHARADRIIDAE

Vanellus

Vanellus albiceps

MacLean (1985)

Vanellus armatus

Maclean (1985)

Walters (1990)

Ward (1987a)

Ward (1987b)

Ward and Maclean (1988)

Vanellus chilensis

Miller (1984a)

Walters (1990)

Vanellus coronatus

MacLean (1985)

Ward (1987a)

Ward (1987b)

Ward (1989)⁵

Ward and Maclean (1988)

Vanellus crassirostris

MacLean (1985)

Walters (1990)

Vanellus gregarius

Cramp (1983)

Vanellus leucurus

Cramp (1983)

Vanellus lugubris

Ward (1987a)

Ward (1987b)

Ward (1989)⁵

Ward and Maclean (1988)⁶

Vanellus melanopterus

MacLean (1985)

Ward (1987a)

Ward (1987b)

Ward (1989)

Ward and Maclean (1988)

Vanellus...

⁵The captions for Fig. 1d and e are transposed: d = *V. lugubris* "alarm" call (not "territorial"); e = *V. coronatus* (D. Ward, *in litt.*).

⁶The last two elements in Fig. 7 are "rarely included in alarm" (D. Ward, *in litt.*; see also preceding footnote).

CHARADRIIDAE**...*Vanellus****Vanellus senegallus*

Maclean (1985)

Ward (1987a)

Ward (1987b)

Ward and Maclean (1988)

* *Vanellus spinosus*

** Bergmann and Helb (1982)

Cramp (1983)

* *Vanellus vanellus*

** Bergmann and Helb (1982)

** Cramp (1983)

** Dabelsteen (1978)

* Nethersole-Thompson and Nethersole-Thompson (1986)

Robisson (1987)

Wollemann and Olszky (1977)

Chionididae (0/2)**CHIONIDIDAE****Dromadidae (0/1)****DROMADIDAE****Glareolidae (7/17)****GLAREOLIDAE***Cursorius cursor*

Bergmann and Helb (1982)

Cramp (1983)

Cursorius rufus

MacLean (1985)

*Cursorius**Glareola nordmanni*

Cramp (1983)

MacLean (1985)

Glareola nuchalis

MacLean (1985)

* *Glareola pratincola*

* Bergmann and Helb (1982)

* Cramp (1983)

* MacLean (1985)

*Glareola** *Pluvianus aegyptius*

** Cramp (1983)

** Howell (1979)

Pluvianus

Rhinoptilus cinctus
Dowsett et al. (1977)
MacLean (1985)

GLAREOLIDAE
Rhinoptilus

Haematopodidae (7/11)

HAEMATOPODIDAE

- * *Haematopus ater*
Miller (1979c)
Miller (1984a)
Miller (1984b)
** Miller and Baker (1980)
Haematopus chathamensis
Baker (1974)
* *Haematopus leucopodus*
** Miller and Baker (1980)
* *Haematopus moquini*
** Baker and Hockey (1984)
MacLean (1985)
* *Haematopus ostralegus*
Baker (1974)
** Bergmann and Helb (1982)
** Cramp (1983)
MacLean (1985)
Nethersole-Thompson and Nethersole-Thompson (1986)
* Tikhonov and Fokin (1979)
* Tikhonov and Fokin (1980)
Tikhonov and Fokin (1981a)
* Tikhonov and Fokin (1982)
* *Haematopus palliatus*
Miller (1984a)
** Miller and Baker (1980)
Haematopus unicolor
Baker (1974)

Haematopus

Ibidorhynchidae (0/1)

IBIDORHYNCHIDAE

Jacaniidae (2/8)

JACANIDAE

Actophilornis africanus
MacLean (1985)

Actophilornis

	JACANIDAE
* <i>Jacana spinosa</i>	<i>Jacana</i>
** Jenni et al. (1974)	
** Mace (1981)	
Pedionomidae (1/1)	PEDIONOMIDAE
<i>Pedionomus torquatus</i>	
Pettigrew and Larsen (1990)	
Pluvianellidae (0/1)	PLUVIANELLIDAE
Recurvirostridae (3/7)	RECURVIROSTRIDAE
* <i>Himantopus himantopus</i>	<i>Himantopus</i>
Bergmann and Helb (1982)	
** Cramp (1983)	
MacLean (1985)	
Robbins et al. (1983)	
** Sordahl (1980) ⁷	
Sordahl (1986) ⁷	
* Wollemann (1978)	
* <i>Recurvirostra americana</i>	<i>Recurvirostra</i>
** Sordahl (1980) ⁷	
Sordahl (1986) ⁷	
* <i>Recurvirostra avosetta</i>	
** Adret (1982)	
* Cramp (1983)	
MacLean (1985)	
* Tikhonov and Fokin (1979)	
* Tikhonov and Fokin (1980)	
Tikhonov and Fokin (1982)	
Wollemann and Olaszy (1977)	
Rostratulidae (1/2)	ROSTRATULIDAE
<i>Rostratula benghalensis</i>	<i>Rostratula</i>
MacLean (1985)	

⁷Some sound spectrograms in Sordahl (1980) are shown also in Sordahl (1986), where they are of much better quality.

Scolopacidae (62/89)

SCOLOPACIDAE

Arenariini

* *Arenaria interpres*

Arenaria

- ** Bergmann and Helb (1982)
- * Cramp (1983)
- * Maclean (1985)
- * Nadler and Königstedt (1986)
- Robbins et al. (1983) (not in 1966 edition)
- * Tikhonov and Fokin (1979)
- * Tikhonov and Fokin (1980)
- * Tikhonov and Fokin (1981a)
- Tikhonov and Fokin (1982)

Calidridini

* *Aphriza virgata*

Aphriza

- ** Miller, Gunn and MacLean (1987)
- Miller, Gunn and Veprintsev (1988)
- * Robbins et al. (1983) (not in 1966 edition)

* *Calidris alba*

Calidris

- * Bergmann and Helb (1982)
- ** Cramp (1983)
- Glutz et al. (1975)
- MacLean (1985)
- * Miller, Gunn and Veprintsev (1988)
- Robbins et al. (1983)

Calidris...

-
- * *Calidris alpina*
 - Baker (1982)
 - ** Bergmann and Helb (1982)
 - ** Cramp (1983)
 - Glutz et al. (1975) (see also footnote 4, p. 18)
 - * Krey (1991)
 - MacLean (1985)
 - Miller (1983b)
 - Miller (1984a)
 - Miller (1984b)
 - * Miller, Gunn and Veprintsev (1988)
 - Nethersole-Thompson and Nethersole-Thompson (1986)
 - Richard (1991)
 - Robbins et al. (1983)
 - Stiefel and Scheufler (1989)
 - * *Calidris bairdii*
 - * MacLean (1985)
 - * Miller, Gunn and Veprintsev (1988)
 - * Robbins et al. (1983) (not in 1966 edition)
 - * *Calidris canutus*
 - * Bergmann and Helb (1982)
 - ** Cramp (1983)
 - * Glutz et al. (1975)
 - * MacLean (1985)
 - Miller, Gunn and Veprintsev (1988)
 - * *Calidris ferruginea*
 - * Bergmann and Helb (1982)
 - ** Cramp (1983)
 - Glutz et al. (1975)
 - * MacLean (1985)
 - Miller, Gunn and Veprintsev (1988)
 - Calidris fuscicollis*
 - Glutz et al. (1975)
 - Miller (1984a)
 - Miller, Gunn and Veprintsev (1988)
 - Robbins et al. (1983) (not in 1966 edition)

Calidris...

SCOLOPACIDAE

...*Calidris*

* *Calidris maritima*

Bergmann and Helb (1982)⁸

- * Cramp (1983)
- Glutz et al. (1975)
- * Miller (1984a)
- Miller (1984b)

Calidris mauri

Holmes (1973)
Robbins et al. (1983)

Calidris melanotos

Glutz et al. (1975)
MacLean (1985)
Miller, Gunn and Veprintsev (1988)
Myers (1982)
Robbins et al. (1983)
Tikhonov and Fokin (1980)

* *Calidris minuta*

- * Bergmann and Helb (1982)
- * Cramp (1983)
- Glutz et al. (1975)
- * MacLean (1985)
- * Tikhonov and Fokin (1981a)⁹
- * Tikhonov and Fokin (1981b)

Calidris...

⁸The sound spectrograms attributed to this species on pp. 25 and 141 (part a) of Bergmann and Helb (1982) are mis-labelled; they illustrate *C. temminckii* flight song (W. Krey, *in litt.*).

⁹The sound spectrogram (tracing) attributed to this species in Fig. 1E of Tikhonov and Fokin (1981a) is mis-labelled; it illustrates *C. temminckii* flight song. Fig. 1E is correctly referred to *C. temminckii* in the text of that paper, however (P. Tomkovich, *in litt.*).

-
- * *Calidris minutilla*
 - * Cramp (1983)
 - Kroodsma and Miller (1982)
 - Miller (1977)
 - Miller (1979a)
 - Miller (1979b)
 - Miller (1979c)
 - * Miller (1983a)
 - Miller (1983b)
 - Miller (1983c)
 - Miller (1984a)
 - Miller (1984b)
 - * Miller (1985)
 - * Miller (1986)
 - Miller, Gunn and Veprintsev (1988)
 - Robbins et al. (1983)
 - Calidris ptilocnemis*
 - Miller, Gunn and Veprintsev (1988)
 - * *Calidris pusilla*
 - * Miller (1983b)
 - * Miller (1984a)
 - Miller (1984b)
 - * Robbins et al. (1983)
 - Calidris ruficollis*
 - MacLean (1985)
 - Miller, Gunn and Veprintsev (1988)
 - Calidris subminuta*
 - Maclean (1985)
 - Miller, Gunn and Veprintsev (1988)
 - * *Calidris temminckii*
 - * Bergmann and Helb (1982) (see also footnote 7, p. 23)
 - ** Cramp (1983)
 - * Glutz et al. (1975)
 - MacLean (1985)
 - Nethersole-Thompson and Nethersole-Thompson (1986)
 - * Tikhonov and Fokin (1980)
 - Tikhonov and Fokin (1981a)
 - * Tikhonov and Fokin (1981b)
 - ** Tomkovich and Fokin (1984)

SCOLOPACIDAE

- Limicola falcinellus*
 Bergmann and Helb (1982)
 Cramp (1983)
 Glutz et al. (1975)
 Miller, Gunn and Veprintsev (1988)
 Svensson (1987)
- Philomachus pugnax*
 Bergmann and Helb (1982)
 Cramp (1983)
 Tikhonov and Fokin (1981b)
- Micropalama himantopus*
 Kroodsmma and Miller (1982)
 Miller (1983b)
 Miller, Gunn and Veprintsev (1988)
 Robbins et al. (1983)
- Tryngites subruficollis*
 MacLean (1985)
 Miller, Gunn and Veprintsev (1988)
- Gallinagonini**
- Coenocorypha aucklandica*
 Warham and Bell (1979)
- Coenocorypha pusilla*
 Miskelly (1987)
 Miskelly (1990)
- * *Gallinago gallinago*
 Bergmann and Helb (1982)
 ** Cramp (1983)
 * Glutz et al. (1977)
 Grudzien (1976)
 Nethersole-Thompson and Nethersole-Thompson (1986)
 Reddig (1978)
 ** Reddig (1981)
 Robbins et al. (1966)
 Robbins et al. (1983)
 Thielcke (1976)
 Thönen (1968)

Limicola

Philomachus

Micropalama

Tryngites

Coenocorypha

Gallinago

Gallinago...

SCOLOPACIDAE

...*Gallinago*

- * *Gallinago hardwickii*
** Nakamura and Shigemori (1990)

Gallinago imperialis
Terborgh and Weske (1972)

Gallinago media
Bergmann and Helb (1982)
Cramp (1983)
Ferdinand (1966)
Glutz et al. (1977)
Höglund (1989)
Höglund and Lundberg (1987)
Lemnell (1978)
MacLean (1985)

Gallinago nigripennis
MacLean (1985)

Gallinago stenura
Byrkjedal (1990)
Cramp (1983)
Labutin et al. (1982)

Lymnocyptes minimus
Bergmann and Helb (1982)
Cramp (1983)

Lymnocyptes

Limnodromini

Limnodromus griseus
Greenewalt (1968)
Miller (1983c)
Miller, Gunn and Harris (1983)
Miller, Gunn, Myers and Veprintsev (1984)
Robbins et al. (1983)

Limnodromus

Limnodromus scolopaceus
Miller, Gunn, Myers and Veprintsev (1984)
Robbins et al. (1983)

Limnodromus semipalmatus
Fiebig and Jander (1985)

SCOLOPACIDAE

Limosini

- * *Limosa lapponica*
 - ** Bergmann and Helb (1982)
 - ** Cramp (1983)
Glutz et al. (1977)
 - ** Byrkjedal et al. (1989)
- * *Limosa limosa*
 - ** Bergmann and Helb (1982)
 - ** Cramp (1983)
Glutz et al. (1977)
MacLean (1985)
 - * Richard (1991)
Wollemann and Olaszy (1977)

Limosa

Numeniini

- Bartramia longicauda*
 - Ailes (1976)
 - Cramp (1983)
 - Glutz et al. (1977)
 - Miller (1984a)
 - Robbins et al. (1983)
- * *Numenius americanus*
 - Forsythe (1967)
 - ** Forsythe (1970)
Greenewalt (1968)
Robbins et al. (1983)
Sordahl (1979)
- * *Numenius arquata*
 - ** Bergmann and Helb (1982)
 - ** Cramp (1983)
 - ** Glutz et al. (1977)
Gretton (1991)
MacLean (1985)
Nethersole-Thompson and Nethersole-Thompson (1986)
- * *Numenius minutus*
 - ** Boswall and Veprintsev (1985)
 - ** Labutin et al. (1982)
 - ** Veprintsev and Zablotskaya (1982)

Bartramia

Numenius

Numenius...

SCOLOPACIDAE

...*Numenius*

- * *Numenius phaeopus*
 - * Bergmann and Helb (1982)
 - ** Cramp (1983)
 - Glutz et al. (1977)
 - MacLean (1985)
 - Nethersole-Thompson and Nethersole-Thompson (1986)
 - Robbins et al. (1983) (not in 1966 edition)
 - Skeel (1976)
 - ** Skeel (1978)
- Numenius tahitiensis*
 - Robbins et al. (1983) (not in 1966 edition)
- Numenius tenuirostris*
 - Gretton (1991)

Phalaropodini

- * *Phalaropus fulicarius*
 - * Bergmann and Helb (1982)
 - ** Cramp (1983)
 - Miller (1984)
- * *Phalaropus lobatus*
 - * Bergmann and Helb (1982)
 - ** Cramp (1983)
 - MacLean (1985)
- * *Phalaropus tricolor*
 - ** Howe (1972)
 - * MacLean (1985)

Phalaropus

SCOLOPACIDAE

Scolopacini

- * *Scolopax minor* *Scolopax*
Beightol (1972)
* Beightol and Samuel (1973)
Borrer (1970)
* Bourgeois (1977)
* Bourgeois and Couture (1977)
Greenewalt (1968)
Miller (1982)
Robbins et al. (1983)
Samuel and Beightol (1972)
** Samuel and Beightol (1973)
Weir (1979)
Weir and Graves (1982)
- * *Scolopax rusticola* *Scolopax*
* Bergmann and Helb (1982)
* Cramp (1983)
Ferrand (1983)
* Ferrand (1987)
* Glutz et al. (1977)
* Hirons (1977a)
Hirons (1977b)
* Mal'chevskii (1981)
* Mal'chevskii (1982)
Marcstrom (1974)
Nemetschek (1977)

Tringini

- * *Actitis hypoleucos* *Actitis*
* Bergmann and Helb (1982)
** Cramp (1983)
* Glutz et al. (1977)
MacLean (1985)
** Nethersole-Thompson and Nethersole-Thompson (1986)
Tikhonov and Fokin (1981a)
Tikhonov and Fokin (1981b) *Actitis...*

SCOLOPACIDAE

- * *Actitis macularia* ...*Actitis*
* Cramp (1983)
* Heidemann and Oring (1976)
Knudsen (1972)
* Miller (1984a)
* Robbins et al. (1983)
- * *Catoptrophorus semipalmatus* *Catoptrophorus*
Robbins et al. (1983) (not in 1966 edition)
** Sordahl (1979)
- Heteroscelus incanus* *Heteroscelus*
Miller (1984a)
Robbins et al. (1983)
- * *Tringa erythropus* *Tringa*
Bergmann and Helb (1982)
* Byrkjedal et al. (1988)
** Cramp (1983)
Glutz et al. (1977)
MacLean (1985)
- Tringa flavipes*
Cramp (1983)
Greenewalt (1968)
Miller (1984a)
Robbins et al. (1983)
- * *Tringa glareola*
Bergmann and Helb (1982)
** Cramp (1983)
Glutz et al. (1977)
* MacLean (1985)
Nethersole-Thompson and Nethersole-Thompson (1986)
* Tikhonov and Fokin (1980)
Tikhonov and Fokin (1981b)
- Tringa melanoleuca*
Nethersole-Thompson and Nethersole-Thompson (1986)
Greenewalt (1968)
Robbins et al. (1983) *Tringa...*

SCOLOPACIDAE

...*Tringa*

- * *Tringa nebularia*
 - Bergmann and Helb (1982)
 - ** Cramp (1983)
 - Glutz et al. (1977)
 - MacLean (1985)
 - Miller (1984a)
 - ** Nethersole-Thompson and Nethersole-Thompson (1979)
 - ** Nethersole-Thompson and Nethersole-Thompson (1986)
 - Tikhonov and Fokin (1981a)
 - Tikhonov and Fokin (1981b)
 - Zvonov and Tikhonov (1981)
- * *Tringa ochropus*
 - ** Bergmann and Helb (1982)
 - ** Cramp (1983)
 - ** Glutz et al. (1977)
 - MacLean (1985)
 - Nethersole-Thompson and Nethersole-Thompson (1986)
 - ** Oring (1968)
 - Tikhonov and Fokin (1981a)
 - Tikhonov and Fokin (1981b)
- * *Tringa solitaria*
 - Cramp (1983)
 - ** Oring (1968)
 - Robbins et al. (1983)
- * *Tringa stagnatilis*
 - * Bergmann and Helb (1982)
 - ** Cramp (1983)
 - Glutz et al. (1977)
 - * MacLean (1985)
- * *Tringa totanus*
 - ** Bergmann and Helb (1982)
 - ** Cramp (1983)
 - ** Glutz et al. (1977)
 - MacLean (1985)
 - ** Nethersole-Thompson and Nethersole-Thompson (1986)
 - Wollemann and Olsazy (1977)

Xenus cinereus

- Bergmann and Helb (1982)
- Cramp (1983)
- MacLean (1985)

Xenus

Thinocoridae (0/4)

THINOCORIDAE

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VI. ILLUSTRATIONS

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FIGURE 1. "Song" of the Spotted Sandpiper (*Actitis macularia*) expressed in musical notation. [From Arlton (1949:33).]



FIGURE 2. A typical sound spectrogram showing a portion of song by Temminck's Stint (*Calidris temminckii*). The vertical dimension is frequency (related to a bird's perception of pitch) and the horizontal dimension is time. [From an original sound spectrogram used to prepare those in Cramp (1983:316); courtesy of Joan Hall-Craggs.]

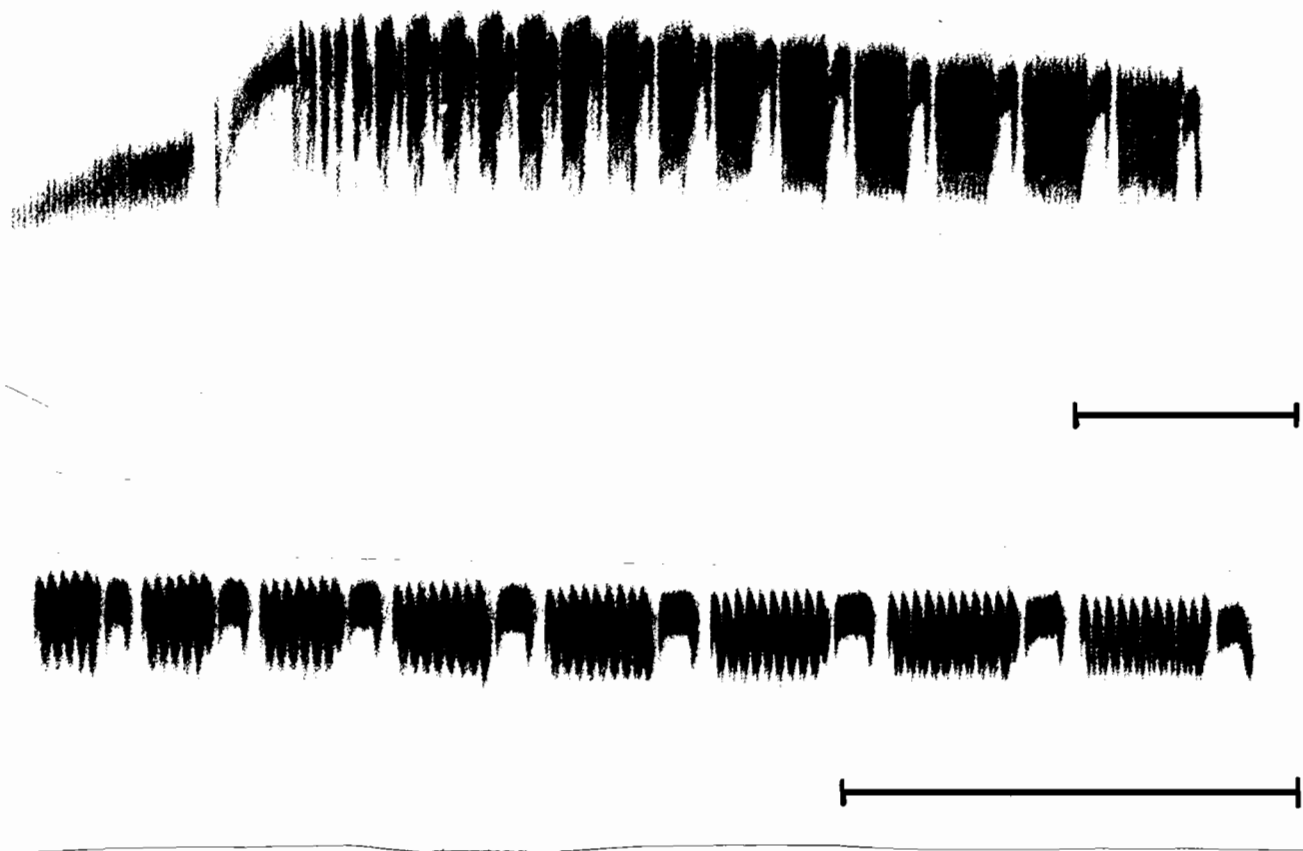


FIGURE 3. "Stretching" the temporal scale can dramatically reveal physical details of bird sounds. Here, an introductory call followed by song of the Dunlin (*Calidris alpina*) (above), and the last eight couplets of the song (below), are shown as sound spectrograms over time scales differing by a factor of two. Greater detail is apparent in the bottom illustration. Time markers, 250 msec. [After Miller (1983a:Fig. 5).]

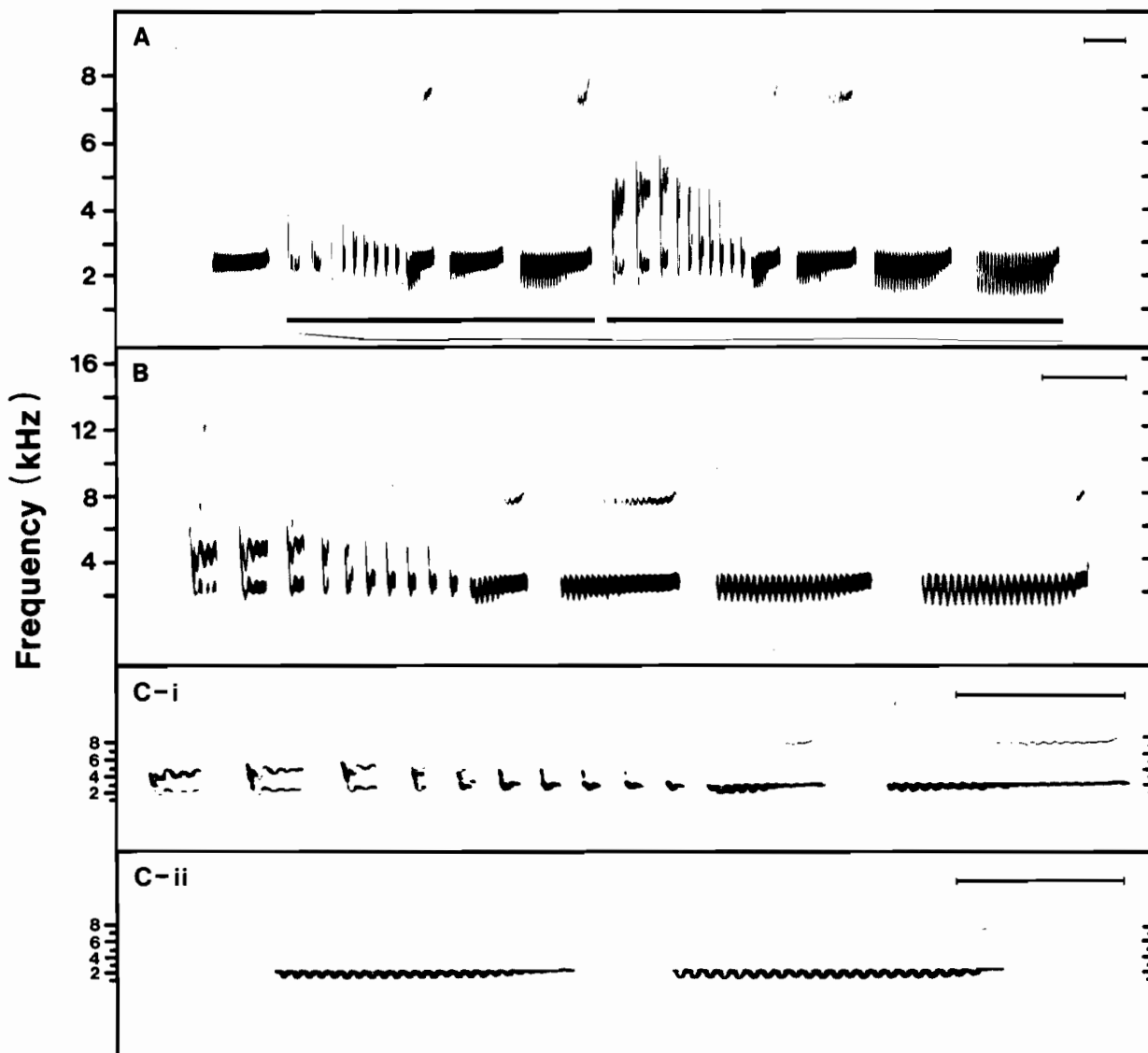


FIGURE 4. Sound spectrograms of song in the Short-billed Dowitcher (*Limnodromus griseus*). A - Buzzy element followed by two song units (underlined; analysing filter bandwidth, 300 Hz). B - Second song unit shown in panel A, on a different time scale (analysing filter bandwidth, 150 Hz). C (two parts) - Same song unit as in B, on different frequency and time scales (analysing filter bandwidth, 11.25 Hz). Time markers, 125 msec. [From Miller et al. (1984:Fig. 2); in the original publication the analysing filter bandwidths were incorrectly reported for all frequency ranges except 80-8000 Hz; see remarks, pp. 7-8.]

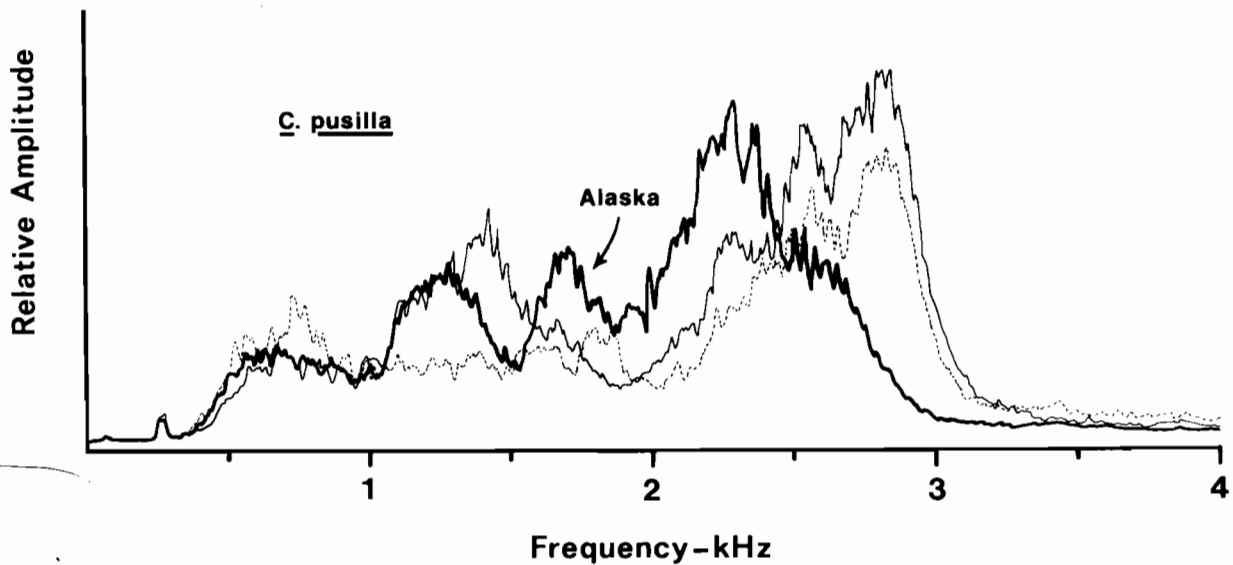


FIGURE 5. Frequency spectra of male aerial advertising calls in the Semipalmated Sandpiper (*Calidris pusilla*). Geographic variation is suggested in this example: Alaskan birds have lower-frequency calls than those from northern Manitoba (two unmarked spectra from near Churchill, Manitoba are shown). [After Miller (1983a:Fig. 4).]



FIGURE 6. Oscillogram of introductory call followed by song in the Dunlin (*Calidris alpina*), showing characteristics of amplitude (vertical dimension) over time (horizontal dimension). Sound spectrograms of this sound sample are shown in Fig. 3. Note the changes in amplitude over the song, the changing temporal patterning, etc. [After original oscillogram used to prepare Miller (1983a:Fig. 6).]

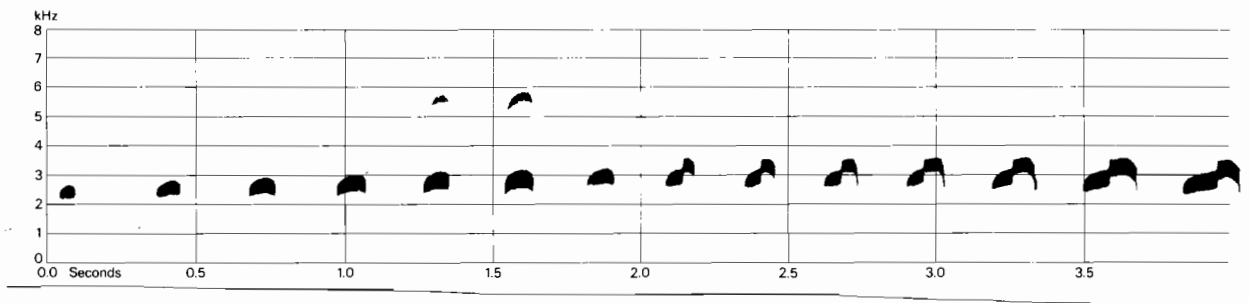


FIGURE 7. Sound spectrogram of call sequence in the Senegal Thick-knee (*Burhinus senegalensis*), showing effective use of an overlain grid to highlight frequency and temporal trends (analysing filter bandwidth, 300 Hz). In the original illustration the grid is faint red so does not distract visually from the sound spectrogram. [After Cramp (1983:82).]

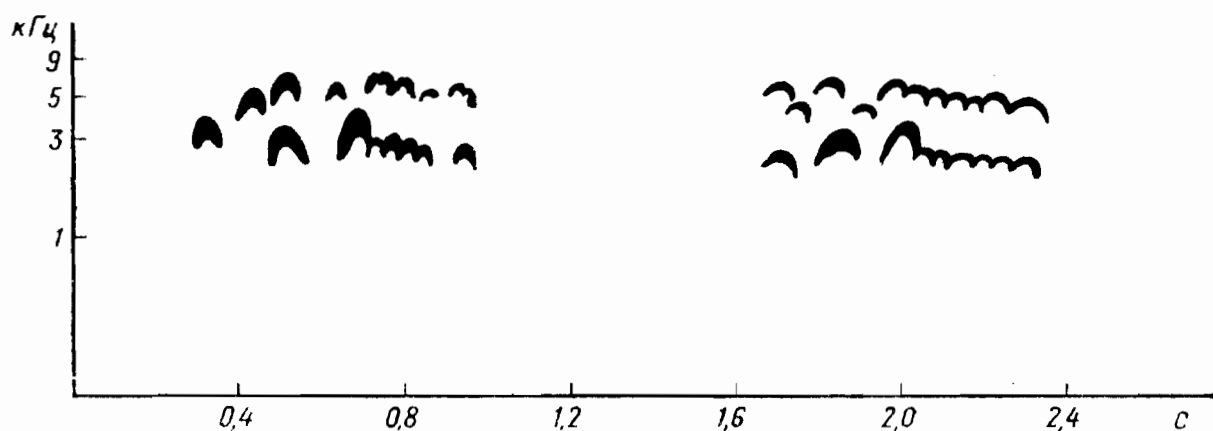


FIGURE 8. Pen-and-ink tracing of sound spectrogram of calls in the Temminck's Stint (*Calidris temminckii*). The frequency scale is logarithmic, so high frequencies are crowded. The presentation could have been improved with thin frequency lines, as in Fig. 7, and by restricting the frequency range for analysis. No details of analysis given. Scales are in kHz and sec. [After Tikhonov and Fokin (1981:Fig. 2).]

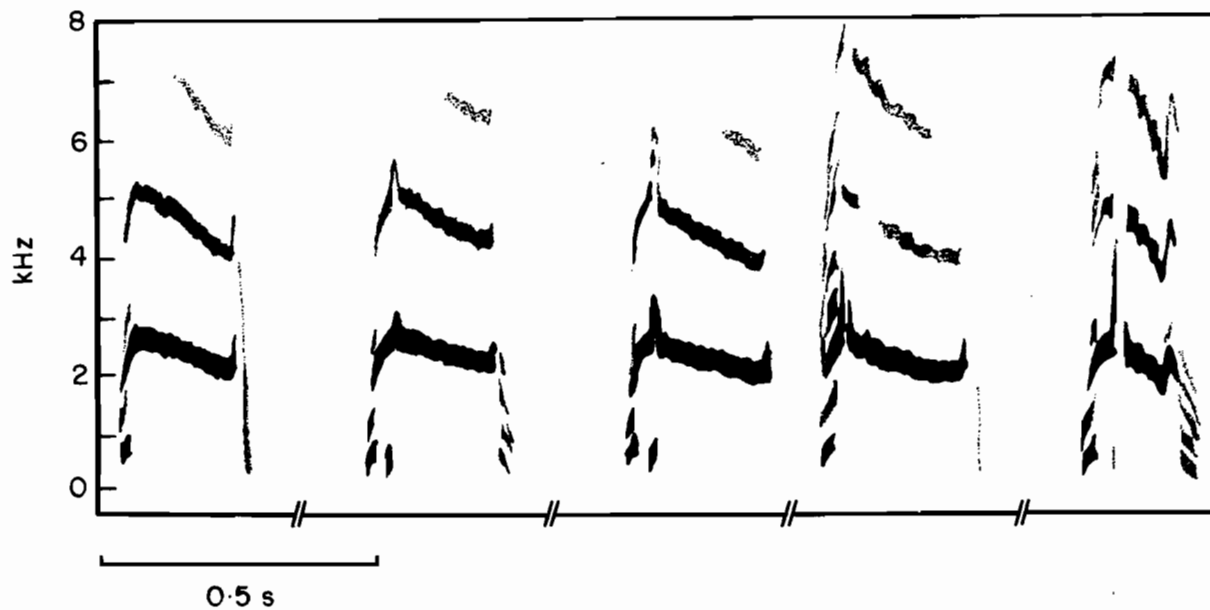


FIGURE 9. Sound spectrogram of calls in the Eurasian Avocet (*Recurvirostra avosetta*), showing effective illustration of structural intergradation by adjacent placement of calls (analysing filter bandwidth, 300 Hz). [From Adret (1982:Fig. 4).]

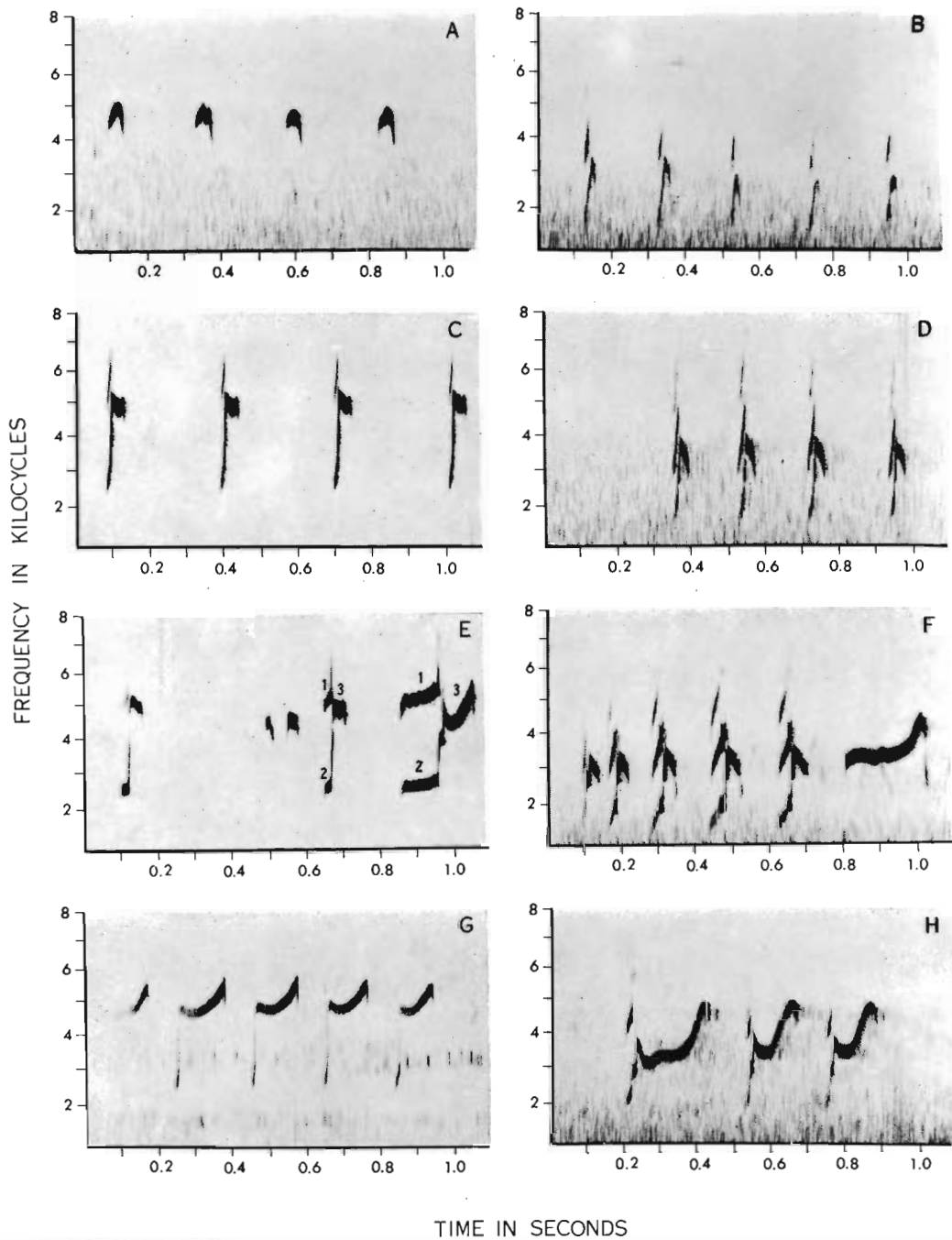


FIGURE 10. Sound spectrograms of calls of Solitary and Green Sandpipers (*Tringa solitaria* and *T. ochropus*), showing effective illustration of species comparisons by placement of homologous call types side-by-side. Sound spectrograms were produced at "H-S (= high shape) and wide band settings" (Oring, 1968:396). [From Oring (1968:Fig. 5).]

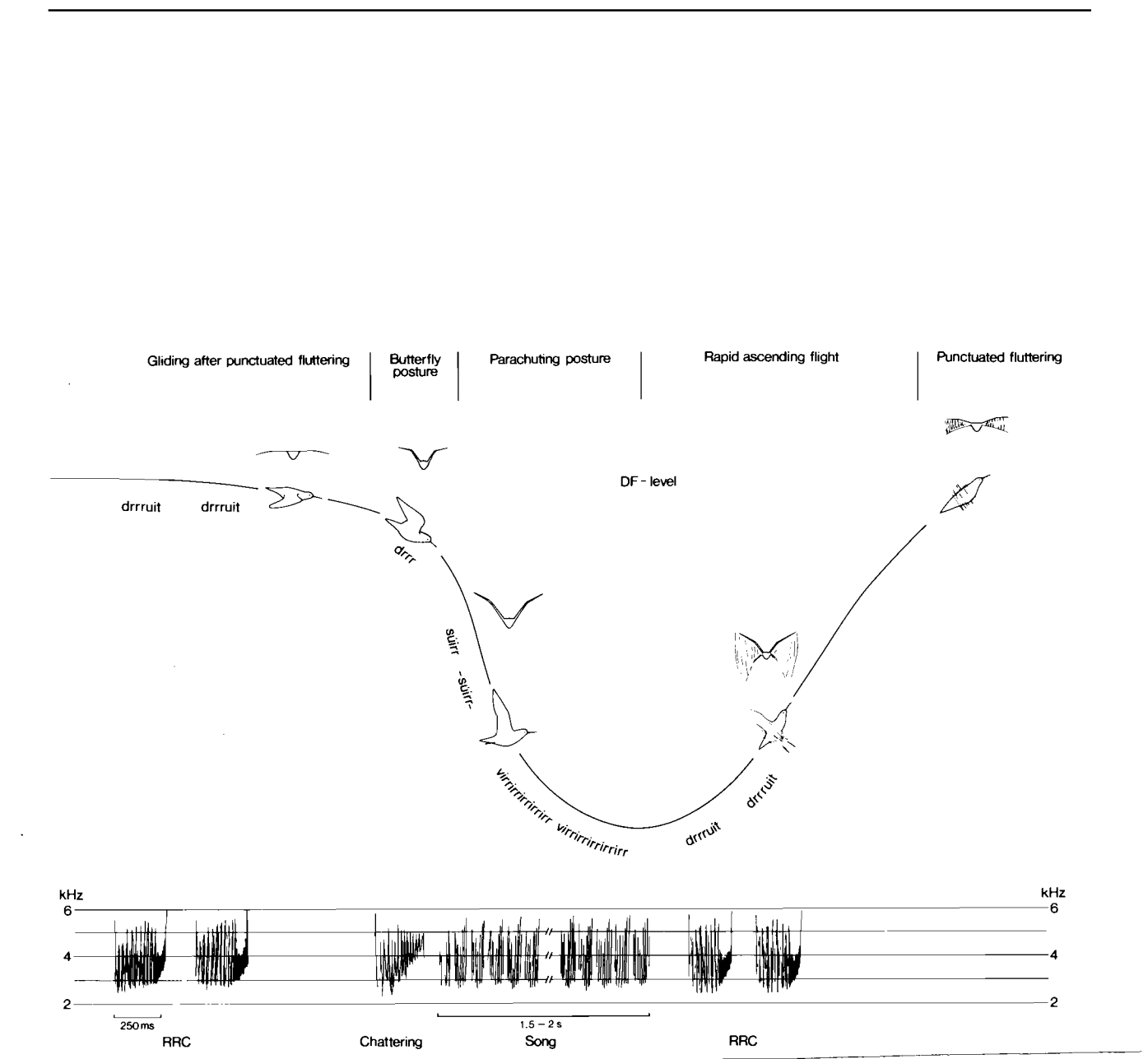


FIGURE 11. Effective illustration of sequencing and of simultaneous optical and acoustic signaling in aerial display of Broad-billed Sandpiper (*Limicola falcinellus*). [From Svensson (1987:Fig. 1).]

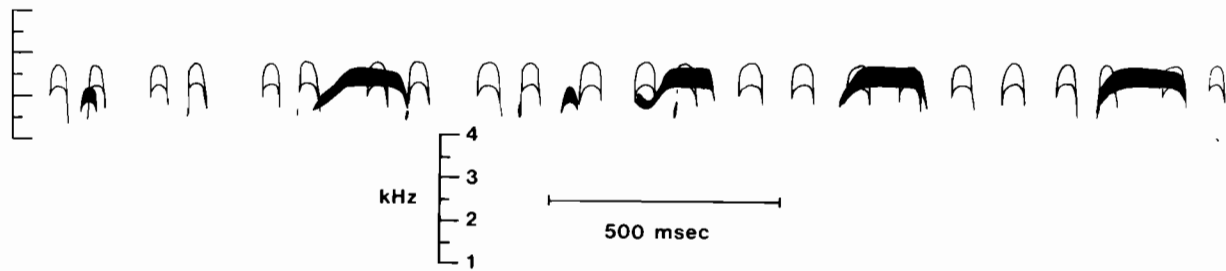


FIGURE 12. Pen-and-ink tracing of a portion of piping sequence in the American Oystercatcher (*Haematopus palliatus*), illustrating calls by two different birds. Original sound spectrograms were produced over an 8 kHz range; analysing filter bandwidth, 300 Hz. [After Miller and Baker (1980:Fig. 10).]

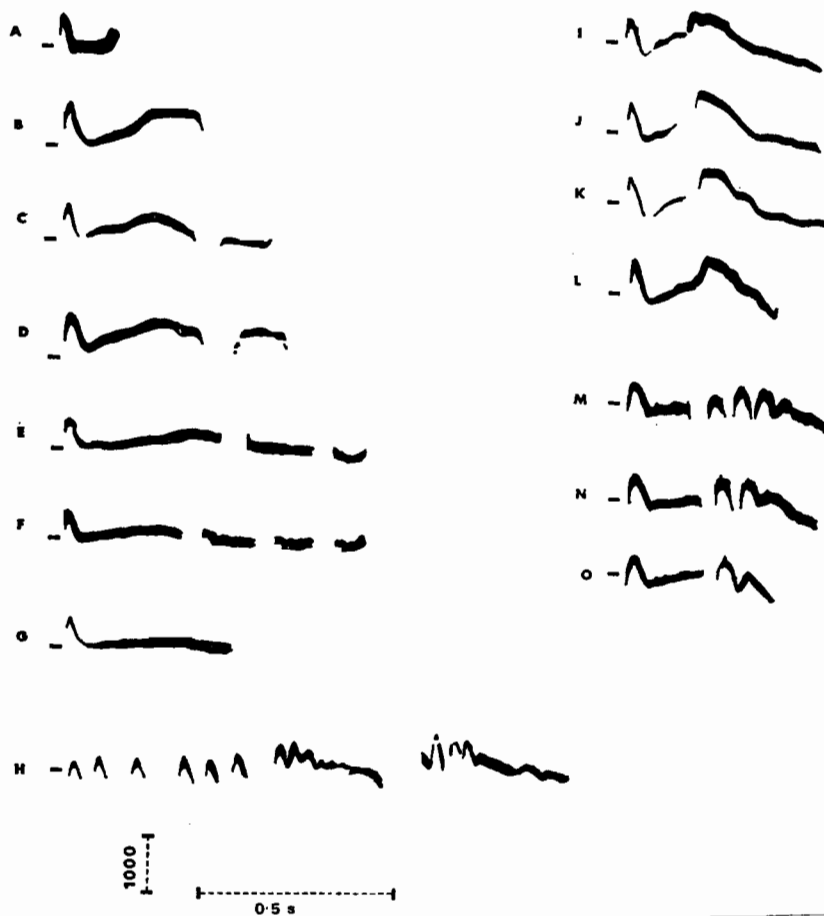


FIGURE 13. Composite illustration using pen-and-ink tracings to show several classes of vocalization, and variation within them, for the Killdeer (*Charadrius vociferus*). The dashes indicate the 4 kHz level; the frequency marker is at 100 Hz. No details of analysis given. [After Phillips (1972:Fig. 1).]

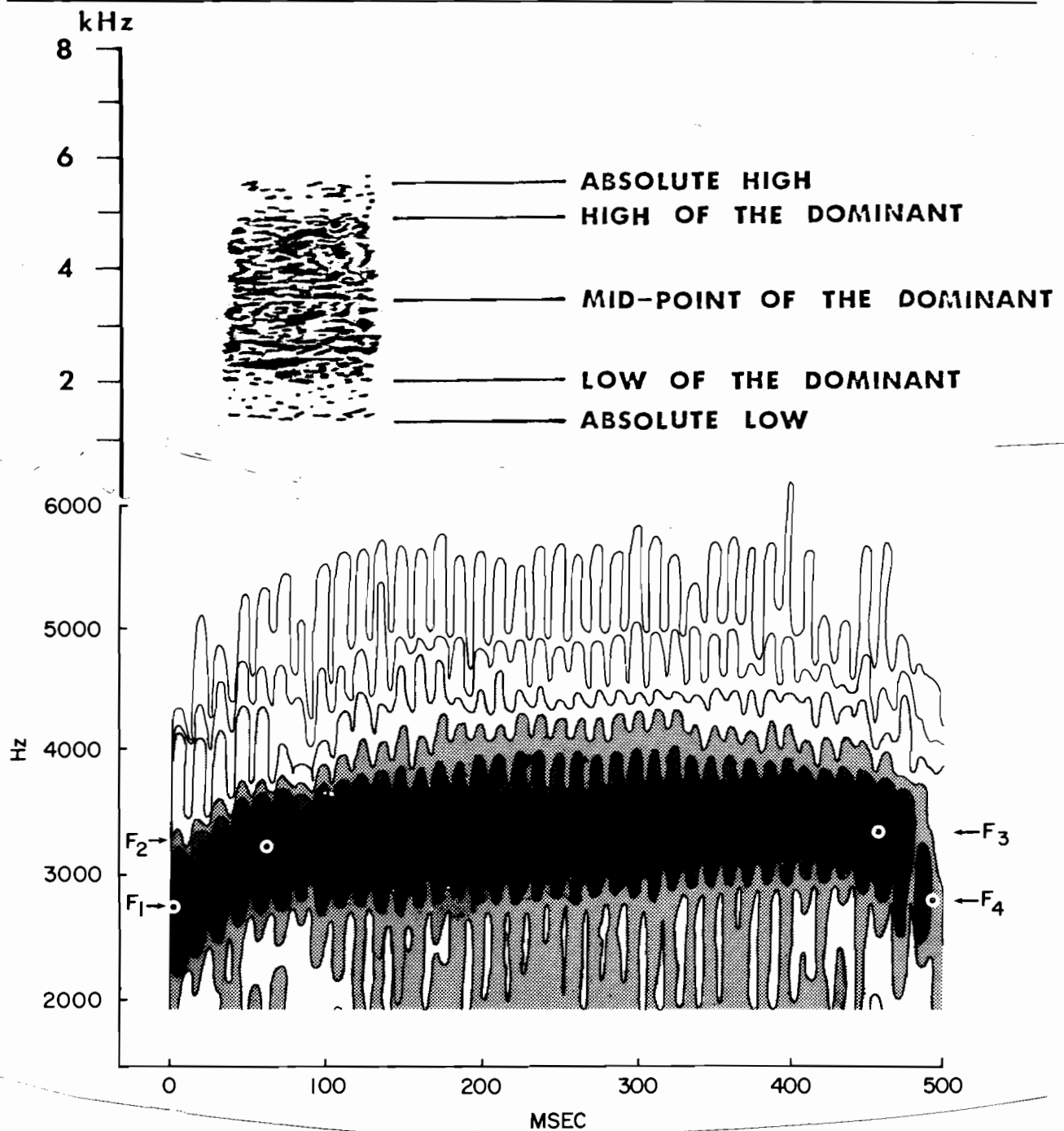


FIGURE 14. Pen-and-ink tracings of sounds of the Northern Jacana (*Jacana spinosa*; above) and American Woodcock (*Scolopax minor*; below), highlighting the difficulty in depicting and estimating frequency characteristics of broad-band sounds accurately, particularly when analysed with a wide-band filter. For *Jacana*, original sound spectrograms were produced over an 8 kHz range; analysing filter bandwidth not given. For details of analysis for *Scolopax* see Weir and Graves (1982). [After Mace (1981:Fig. 2) and Weir and Graves (1982:Fig. 1).]

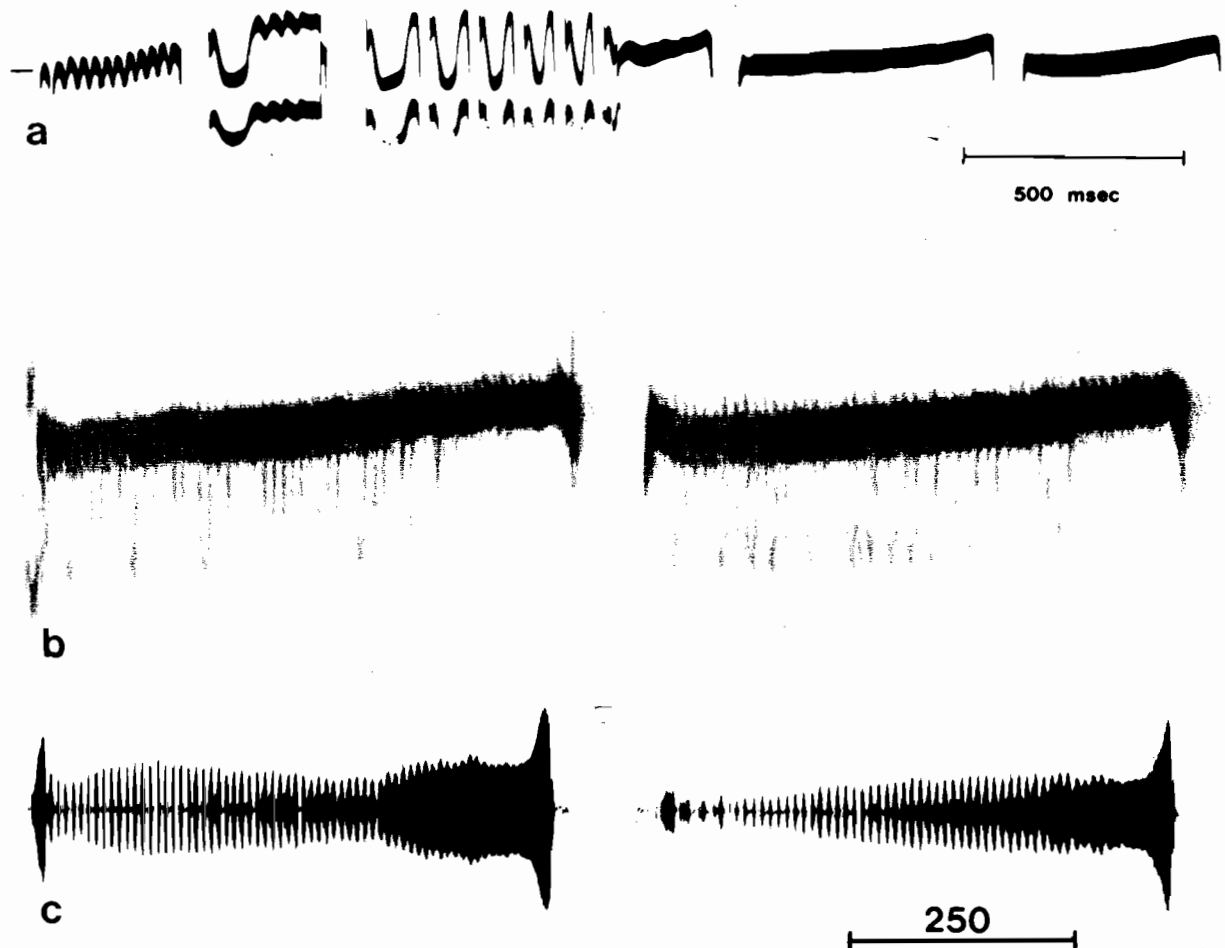


FIGURE 15. Pen-and-ink tracing of song in the Least Sandpiper (*Calidris minutilla*; a). The strong amplitude modulation (pulsing) in the long terminal elements is obscured in this rendering, but is clear in an original sound spectrogram (b) and oscillogram (c). Sound spectrograms were produced over an 8 kHz range; analysing filter bandwidth, 300 Hz. Note that a frequency marker is given in part (a) but there is no indication of scale. The time scale of 250 msec applies to parts (b) and (c). [After Miller (1983b:Figs. 13, 12 and 14-16, respectively).]