

13 Acoustic Differentiation and Speciation in Shorebirds

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Shorebirds offer rich opportunities for ecological and evolutionary research because of their high ecological and social diversity, worldwide distribution, and taxonomic richness (Hayman et al. 1986). The group has therefore received much attention from systematists, who have resolved many relationships and revealed many patterns using an array of anatomical, biochemical, and genetic characters (Bock 1958, Jehl 1968, Strauch 1978, C. G. Sibley and Ahlquist 1990, Chu 1994, 1995). To date, behavioral characters have been used little in systematic studies of shorebirds, though behavior (especially communication) has proven to be invaluable in systematic studies of birds and other taxa (R. B. Payne 1986, von Helversen and von Helversen 1994, Bretagnolle, this volume, Martens, this volume). Shorebirds have a great variety of striking optical and acoustic displays, which should prove valuable in exploring species relationships and detailing patterns of evolutionary differentiation (E. H. Miller 1984, 1992, Ward 1992). The purpose of this chapter is to illustrate the usefulness of vocal and nonvocal acoustic displays in resolving species limits and relationships among closely related shorebird species.

Shorebirds include many closely related species that are difficult to distinguish by external features but can be distinguished easily by vocalizations, even by their nonbreeding call notes (Hayman et al. 1986, Paulson 1993). Intriguingly, and paradoxically, shorebirds also seem to exhibit great evolutionary conservatism in the form and use of acoustic displays. Evolutionary conservatism is suggested by several observations. First, only minor geographic variation in shorebird vocalizations has been noted over large distances and between disjunct populations (E. H. Miller and Baker 1980, E. H. Miller 1983a, 1986, E. H. Miller et al. 1983). Second, acoustic displays of closely related species sometimes are extremely similar, even between species that diverged from one another long ago (e.g., Green and Solitary Sandpipers, *Tringa ochropus* and *T. solitaria*: Oring 1968; Long-billed and Short-billed Dowitchers, *Limnodromus scolopaceus* and *L. griseus*: E. H. Miller et al. 1984). Conservatism is suggested also by the unifor-

mity present in acoustic displays across entire higher taxa, such as the oystercatchers (Haematopodidae; A. J. Baker 1974, E. H. Miller and Baker 1980, Cramp 1983, A. J. Baker and Hockey 1984). Evolutionary conservatism seems paradoxical in light of the presumed need for species specificity, which makes shorebirds an especially interesting group for investigating speciation and the origin of isolating mechanisms.

In this chapter, I discuss breeding displays in some related species of shorebirds. I emphasize long-distance nuptial displays for two reasons. First, such displays likely evolve quickly through sexual selection (Mayr 1963, West-Eberhard 1983, Eberhard 1985, Butlin and Ritchie 1994). Indeed, because long-distance nuptial displays simultaneously serve in species recognition and mating competition, sexual selection may actually accelerate speciation (R. B. Payne 1986, Coyne et al. 1988, Andersson 1994, Coyne 1994, von Helversen and von Helversen 1994). Second, long-range displays are not complicated by optical display components and fine acoustic features that commonly evolve for short-range communication (E. H. Miller et al. 1988, Bain 1992). Therefore, long-range displays should be prone to geographic variation and should be sensitive markers of species limits. It is important to note that long-range nuptial displays are not the exclusive domain of males; for example, females of the polyandrous Eurasian Dotterel (*Eudromias morinellus*) “in winnow-glide display flights . . . give rhythmic sequences of *peeps* which act as songs and carry long distances”—a display form strikingly similar to one used by males of most monogamous plover species (Nethersole-Thompson and Nethersole-Thompson 1986, p. 309; Fig. 13.2A, below; see Owens et al. 1994). Such nuptial displays should tell us much about species’ distinctiveness and phylogenetic relationships, regardless of the displaying sex.

Background Accounts: Systematics and Acoustics

Gallinago snipe. There are about 15 species of snipe. The superspecies *Gallinago gallinago* includes the forms *gallinago* (Eurasia) and *delicata* (North America). These forms (usually treated as subspecies of *G. gallinago*) differ in plumage, number of tail feathers, and other features (Tuck 1972, Cramp 1983). Another subspecies, *G. g. faeroensis*, is recognized for Iceland and for the Faeroe, Orkney, and Shetland Islands (Cramp 1983, Hayman et al. 1986). Sometimes other taxa are referred to as subspecies of *G. gallinago*, including South American (*G. paraguaiiae*) and African (*G. nigripennis*) Snipe (Tuck 1972, Devort et al. 1990).

A loud nonvocal display (drumming) is widespread in snipe and was also found in the group’s ancestral species (Miskelly 1987, 1990). Drumming occurs during the repeated dives in males’ spectacular aerial displays during the breeding season (Fig. 13.1; Tuck 1972, Glutz et al. 1977, Reddig 1978, 1981, Cramp 1983, Byrkjedal 1990, Devort et al. 1990). The sound is generated by vibration of the outer

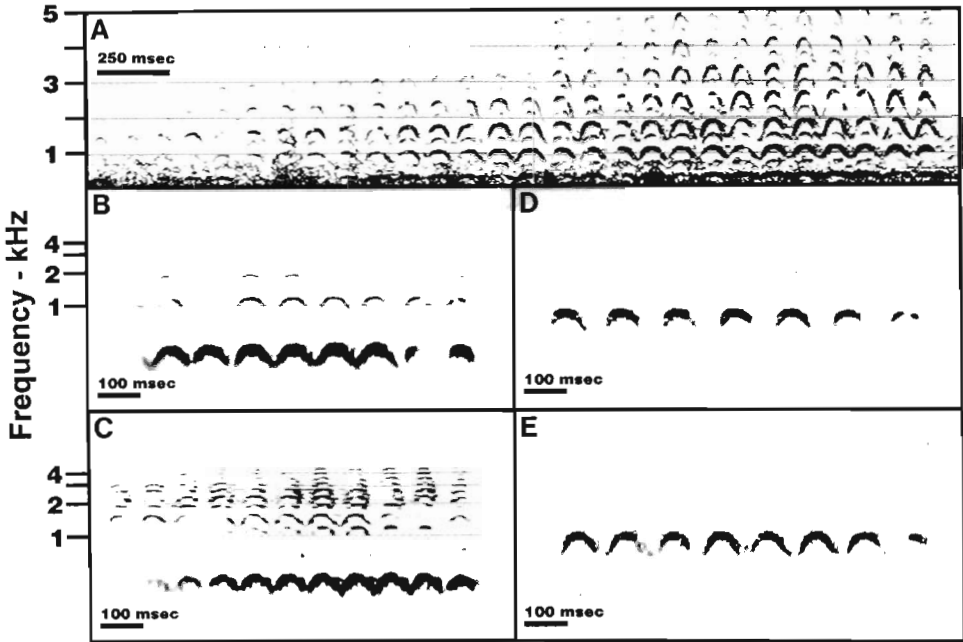


Fig. 13.1. The nonvocal drumming display of Common Snipe differs strongly between the disjunct forms *G. g. gallinago* and *G. g. delicata*. (A) Entire drum from *G. g. gallinago* (Iceland). (B) Last second of A, on a different time scale. (C) Last second of drum from *G. g. gallinago* (Russia). (D, E) Last second of drums from *G. g. delicata* in British Columbia (D) and Manitoba (E). Analyzing filter bandwidth, approximately 50 Hz. Analyses were done over the frequency range 100–5000 Hz (note that a logarithmic frequency scale was used for parts B–E). *Sources:* All recordings except C are by E. H. Miller; A, B, near Raularhöfn, Iceland; C, Veprintsev 1982, recorded by B. N. Veprintsev and V. Leonovitch, Semzha, Kanin Peninsula, White Sea, Russia; D, near Creston, British Columbia; E, near Churchill, Manitoba.

rectrices in the airstream modified by the set wings. Breeding males also utter several kinds of loud vocalizations in the air and on the ground (Tuck 1972, Grudzien 1976, Glutz et al. 1977, Bergmann and Helb 1982, Cramp 1983, Nakamura and Shigemori 1990). Drumming in *gallinago* and *delicata* is a long, eerie sound. It begins softly and increases in loudness and frequency as a dive progresses, reaching a crescendo just before a dive ends (Fig. 13.1A). Each drum is several seconds long and is pulsed and rich in harmonics.

Charadrius plovers. Plovers are a large and diverse family (Charadriidae) with many interesting systematic puzzles. One such puzzle concerns Common Ringed (*Charadrius hiaticula*) and Semipalmated (*Ch. semipalmatus*) Plovers, sibling species whose relationship to one another is unresolved. They are treated as separate species in most accounts, although they do hybridize (N. G. Smith 1969). The Common Ringed Plover has a Holarctic distribution that includes Canadian high-arctic populations. The Semipalmated Plover is confined to North America; it has a generally subarctic distribution (locally sympatric in places with Common

Ringed Plover; C. G. Sibley and Monroe 1990), although it breeds south as far as Oregon (Paulson 1993).

Breeding males of many *Charadrius* species engage in conspicuous display flights that include striking optical signals (slow exaggerated wingbeats, lateral rocking, etc.) and loud vocalizations. Common Ringed and Semipalmated Plovers utter several kinds of vocalizations in their display flights, including a loud, rhythmically repeated call (RRC). A more complex vocalization (song) is sometimes given during display flights and invariably given at the end of a display.

Calidris sandpipers. Calidridine sandpipers (24 species) are a monophyletic group within the Scolopacidae. They have diverse mating systems, and their breeding biology has been studied extensively (Pitelka et al. 1974). Several species complexes exist, including one (referred to as "AMP" hereafter) that comprises Dunlin (*Calidris alpina*), Purple Sandpiper (*C. maritima*), and Rock Sandpiper (*C. ptilocnemis*). It is widely assumed that *maritima* is most closely related to *ptilocnemis* (e.g., Cramp 1983, C. G. Sibley and Monroe 1990). The three species show extensive geographic variation in size and plumage (Todd 1953, S. F. MacLean and Holmes 1971, Browning 1977, Greenwood 1979, 1986, Cramp 1983, Wenink et al. 1993, 1994, 1996, Wenink and Baker 1996).

Many calidridine species have aerial displays that are convergent with those of *Charadrius* plovers (Cramp 1983, E. H. Miller 1984, 1992), and they have two call types that are given in similar circumstances. For descriptive purposes the two types are referred to as RRCs and songs, though they almost certainly are not homologous between the Charadriidae and Scolopacidae.

Pluvialis plovers. Four species of *Pluvialis* are recognized: *apricaria*, *dominica*, *fulva*, and *squatarola*. The Grey Plover (*P. squatarola*) is sometimes placed in its own genus (*Squatarola*). The American Golden-Plover (*P. dominica*) and Pacific Golden-Plover (*P. fulva*) are closely related and often are considered conspecific (C. G. Sibley and Monroe 1990). They differ greatly in habitat, distribution, migration, and vocalization, however, and should be considered separate species (Connors et al. 1993; sonograms in Greenewalt 1968, Tikhonov and Fokin 1981, E. H. Miller 1984, G. L. MacLean 1985, Connors et al. 1993, Marchant and Higgins 1993, and Johnson and Connors 1996). The phylogeny of *Pluvialis* is only partly known. The Grey Plover is the least derived *Pluvialis* species, but it is not known whether *P. apricaria* diverged before or after the sibling species *P. dominica* and *P. fulva* (A. J. Baker pers. comm.).

Male *Pluvialis* engage in dramatic aerial displays during the breeding period (Drury 1961, E. G. F. Sauer 1962, Cramp 1983, E. H. Miller 1984, 1992, Byrkjedal 1996) that serve both to attract mates and to proclaim territory occupancy. As in *Charadrius*, the displays include conspicuous optical signals (slow exaggerated wingbeats, lateral rocking, etc.) and loud vocalizations. As in *Charadrius* and the calidridines mentioned, there are two major classes of vocalizations: RRCs and song. These probably are homologous to the same classes recognized for *Charadrius*, but not scolopacids.

Homologous Features

Background. Phylogenetic analysis requires the identification of homologous features. Methods for selecting homologous features and deciding whether they are ancestral (plesiomorphous) or derived (apomorphous) for a group have been treated extensively (Eldredge and Cracraft 1980, E. O. Wiley 1981, D. R. Brooks and McLennan 1991). The concept of homology is best developed for anatomical characters because most phylogenetic analyses have been based on them (Hall 1994). In light of early ethological interest in the phylogeny of display behavior, however, it seems surprising that ethological characters have been used so little in phylogenetic analyses (R. B. Payne 1986, D. R. Brooks and McLennan 1991, Wenzel 1992, Gittleman and Decker 1994).

Adolf Remane proposed three criteria for recognizing homologous characters: "(1) similarity of position in an organ system, (2) special quality (e.g., commonalities in fine structure or development), and (3) continuity through intermediate forms" (D. R. Brooks and McLennan, 1991, p. 7). These criteria are a useful starting point for considering homologous features of shorebird sounds. Examples for the first two follow; the intermediate forms (item 3) are straightforward and are not discussed here.

Remane's criterion of position. This criterion has a natural extension in the sequential structuring of many sounds. The sequence of song parts in *Pluvialis* plovers provides an example. The brief part ("y" in Fig. 13.4B, C, below) in the song of American and Pacific Golden-Plovers differs structurally but can be judged as homologous based on its position between the two parts (x, z) that precede and follow it. Other examples are in the RRCs of *Charadrius* and the song of dowitchers, Least Sandpiper (*Calidris minutilla*), and Purple Sandpiper (described below).

Remane's criterion of special quality. Slight continuous changes in the acoustic domains of time, frequency, and amplitude presumably can evolve easily, hence continuous quantitative measures of them (e.g., modulation rate, vocalization duration) are likeliest to be phylogenetically informative around the species level. Categorical variables (e.g., harmonic structure, pure tone) hold more promise for phylogenetic analysis at higher levels. The closely related American and Pacific Golden-Plovers differ greatly in RRC duration, for example, yet the calls are organized identically as sequences of homologous parts (Fig. 13.3C–F, below). Because the parts can be distinguished qualitatively, Remane's criterion of special quality can be applied. Examples include (1) the harmonic richness (pulsing) in the first part of RRCs in Semipalmated Plover, Common Ringed Plover, American Golden-Plover, and Pacific Golden-Plover (marked in Figs. 13.2C, F, 13.3E, F); (2) the rhythmic and quasi-rhythmic frequency modulation (FM) in the long element of song in American and Pacific Golden-Plovers (marked in Fig. 13.4); and (3) the crescendo near the end of snipe drums (Fig. 13.1A).

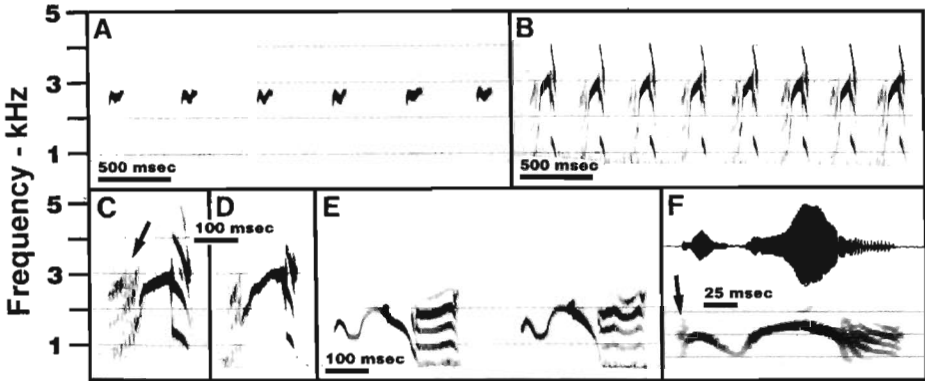


Fig. 13.2. Aerial display calls (rhythmically repeated calls, or RRCs) occur widely in plovers, regardless of their mating system, and show both strong similarities and distinctive differences between related species. (A) Part of long sequence of calls by female Eurasian Dotterel in nuptial display flight. (B) The same as A, but for male Semipalmated Plover (British Columbia). (C) Single call from B. (D) Single call from long sequence by male Semipalmated Plover (Alaska). (E) Two successive calls from long sequence by male Common Ringed Plover (Spitzbergen). (F) Amplitude envelope (upper) and corresponding sonogram (lower) of a single call from a long sequence by a male Common Ringed Plover (Russia). The introductory harmonically rich (pulsed) parts are marked by arrows in C and F (compare Fig. 13.3E, F). Analyzing filter bandwidth, 100–115 Hz. Analyses were done over the frequency ranges 100–5000 Hz (A–E) and 100–8000 Hz (F). *Sources:* A, Veprintsev (1982), Maria Pronchishcheva Bay, Taimyr Peninsula, Russia; B, C, recorded by E. H. Miller, "Haines Triangle," British Columbia, between Haines, Alaska, and Haines Junction, Yukon; D, recorded by P. G. Connors, Penny River, Alaska; E, recorded by E. H. Miller, Longyearbyen, Svalbard, Norway; F, Veprintsev (1982), recorded by B. N. Veprintsev and V. Leonovitch, Krest Bay and Eul'kal', Chukotka, Russia (note that this calling sequence on Veprintsev's record appears to be at the twice the correct speed; the analyses shown in part F are based on this assumption).

Because of their complexity and consequent resistance to rapid evolutionary change, *relationships* among acoustic features should prove to be particularly informative in phylogenetic analysis at levels above the species. Relationships can be characterized in quantitative measures of covariation or in more general terms such as AM-FM coupling. Relationships can also be manifest as emergent properties (e.g., sequential organization). A simple form of sequential organization is directional change over time, as illustrated by "sequential grading" in amplitude, frequency, and duration of elements in snipe drums. More complex sequential organization is the ordering of homologous parts within RRCs (e.g., of *Charadrius* and *Pluvialis*; Figs. 13.2, 13.3), and of song parts in dowitchers and Least Sandpiper (Fig. 13.5). Complex relational properties occur at higher hierarchical levels, too; for example, "embedded grading," with graded sequences nested within other graded sequences. An example is the song of Dunlin and Rock Sandpiper, which shows grading both within each song unit and over an entire song. Another example is the long pulsed elements in the song of dowitchers, Least Sandpiper, and Purple Sandpiper, which decline in frequency successively both within and across song units (Fig. 13.5; see p. 253).

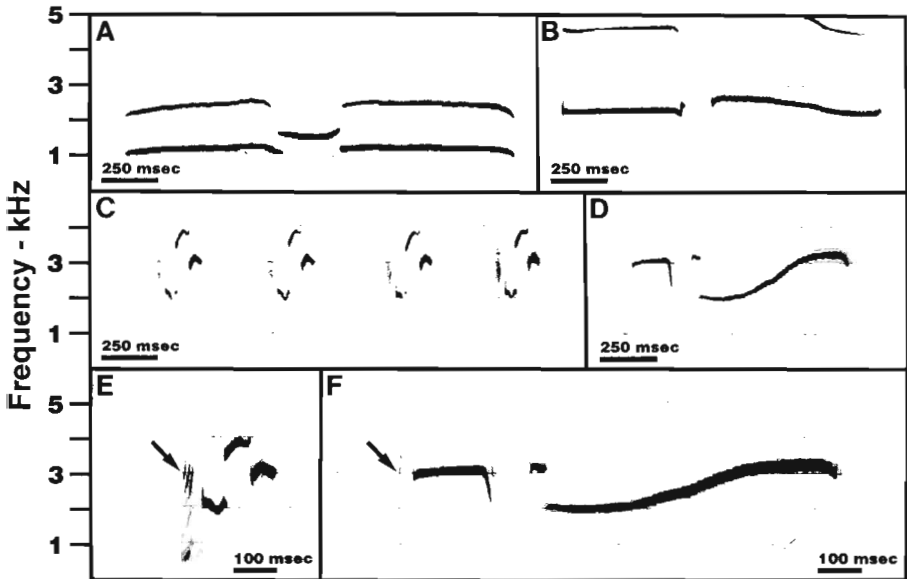


Fig. 13.3. Differences and similarities between RRCs of *Pluvialis* plovers; note the large species differences in fine frequency and temporal characteristics. (A) Single RRC by Grey Plover (Russia). (B) Single RRC by Eurasian Golden-Plover (Russia). (C) Four RRCs by American Golden-Plover (Alaska). (D) Single RRC by Pacific Golden-Plover (Alaska). (E) Single RRC by Lesser Golden-Plover (last RRC in C, on different time scale). (F) Single RRC by Pacific Golden-Plover (RRC in D, on different time scale). Analyzing filter bandwidth, 57 Hz. Analyses were done over the frequency range 100–5000 Hz. *Sources:* A, recorded by I. Byrkjedal, near Sabettayakha River, Yamal, Russia; B, recorded by B. Veprintsev and V. Leonovitch, Semzha, Kanin Peninsula, Russia; C, recorded by E. H. Miller, Canning River delta, Alaska; D, recorded by P. G. Connors, Seward Peninsula, Alaska.

Microevolutionary Processes and Patterns

Transmission distance. Long-distance displays must be physically adapted to withstand various forms of degradation and attenuation to reach and be perceived accurately by receivers; hence they should be simpler than short-distance displays, all else being equal (Bain 1992). This principle is well illustrated by acoustic displays of shorebirds that inhabit open, windy environments. These displays show two common adaptations: narrow bandwidth and rhythmic repetition (Schleidt 1973a, E. H. Miller 1984). Many shorebird displays do not conform to this pattern, however, and are extremely complex; examples are shown in Figs. 13.2–13.6. Problems with transmitting complex sounds over long distances can be reduced through frequent repetition, especially rhythmic repetition, and especially if the display form varies little across repetitions. Exceptions to this generalization occur too, however. An example is the Least Seedsnipe (*Thinocorus rumicivorus*), males of which rise infrequently in flight display, then utter a single complex song as they glide to the ground (G. L. Maclean 1969, E. H. Miller 1996). It can be concluded that adaptations for long-range transmission do not

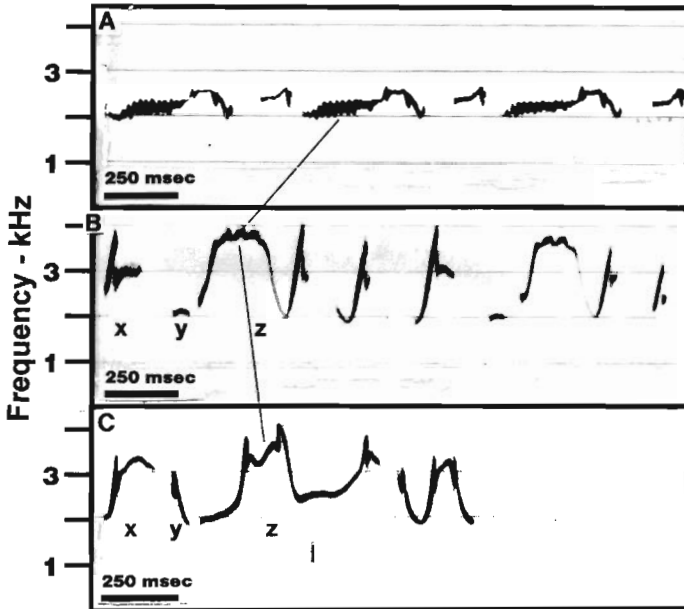


Fig. 13.4. Differences and structural correspondences in song of different species of *Pluvialis* plovers. (A) Eurasian Golden-Plover (Russia). (B) American Golden-Plover (Alaska). (C) Pacific Golden-Plover (Alaska). Corresponding elements in B and C are marked as x, y, and z; the thin lines between panels connect corresponding frequency-modulated regions in song of the three species. Analyzing filter bandwidth, 58 Hz. Analyses were done over the frequency range 100–5000 Hz. Sources: A, recorded by B. Veprintsev and V. Leonovitch, Semzha, Kanin Peninsula, Russia; B, recorded by P. G. Connors, Seward Peninsula, Alaska; C, recorded by E. H. Miller, Nunivak Island, Alaska.

account for physical complexity or most specific physical attributes of shorebird nuptial sounds. The principal evolutionary constraint set by long transmission distance presumably is on acoustic variability, not complexity. This generalization appears to apply even at the level of syntax (e.g., in RRC and Song organization), as long- and short-range vocalizations do not differ appreciably in syntactic complexity (such a comparison is confounded by the multidimensionality of short-range communication, however; Bain 1992).

Geographic variation. Many shorebird species are widely distributed, have disjunct populations, or are permanent residents—attributes that seem ideal for promoting geographic differentiation in displays. Again, shorebirds do not conform to expectation. Parental alarm and piping vocalizations of the nonmigratory American Oystercatcher (*Haematopus palliatus*) are similar in disjunct populations in Argentina and Massachusetts (E. H. Miller and Baker 1980). Nuptial flight song of male Short-billed Dowitchers is essentially identical in disjunct breeding populations in northwestern North America and Labrador (E. H. Miller et al. 1983). RRCs and song of Dunlin, Semipalmated Sandpiper (*Calidris pusilla*), and American Golden-Plover are extremely similar in Alaska and Manitoba

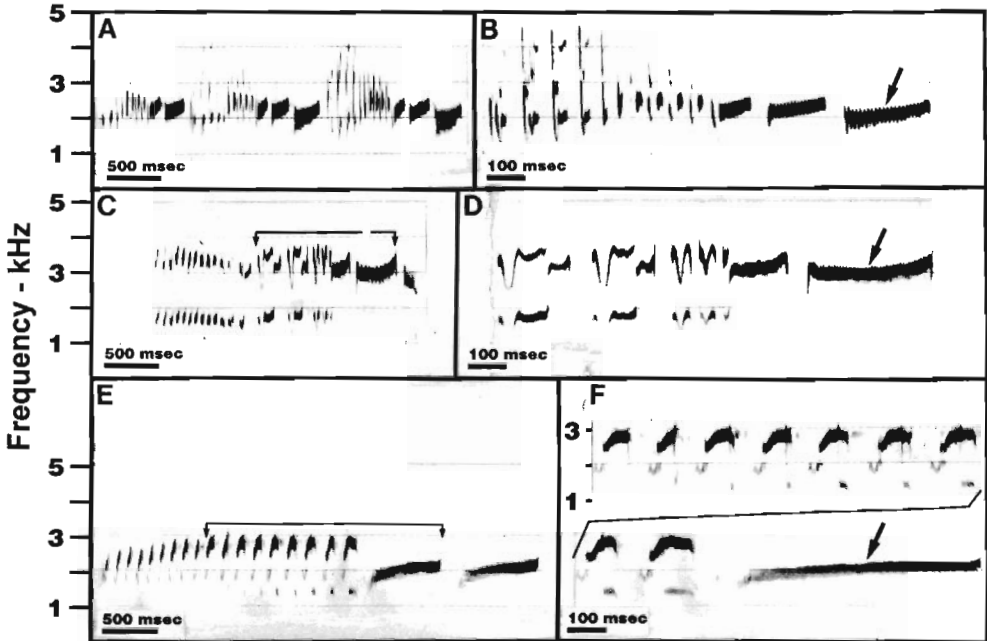


Fig. 13.5. Evolutionarily ancient song organization in Scolopacidae, showing structural similarities judged to be plesiomorphous (see text). (A) Short-billed Dowitcher (British Columbia), last three song units in five-unit sequence. (B) Central of part A, shown on a different time scale. (C) Least Sandpiper (Manitoba), single song unit with introductory trill (a variable feature; the part between arrows is shown in D). (D) Marked part of C, shown on a different time scale. (E) Purple Sandpiper (Iceland), single song (The part between arrows is shown in F). (F) Marked part of E, shown on a different time scale. The terminal long pulsed elements are judged to be homologous across species; one example for each species is marked in B, D, and F (compare Fig. 13.6). Analyzing filter bandwidth, 115 Hz. Analyses were done over the frequency range 100–5000 Hz. *Sources:* All recordings are by E. H. Miller; A, B, "Haines Triangle," British Columbia, between Haines, Alaska, and Haines Junction, Yukon; C, D, near Churchill, Manitoba; E, F, near Raufarhöfn, Iceland.

populations (E. H. Miller 1983a, Connors et al. 1993), and those of the Least Sandpiper show only weak frequency differences between Alaska and Nova Scotia, paralleling differences in body size (E. H. Miller 1986). Drumming of the snipe *G. g. gallinago* and *G. g. delicata* likewise is uniform throughout the vast breeding range of each form (see next section). By itself, the lack of geographic variation in shorebird nuptial displays does not weaken the prediction that sexually selected traits will vary geographically. That prediction is a comparative one and needs to be tested by comparing sexually selected displays (e.g., RRCs and song) with display types that are not sexually selected (e.g., parental alarm) within a species. This matter is discussed further below.

The low geographic variation in shorebird acoustic displays suggests that little vocal "learning" takes place. Thus, acoustic displays should reflect historical patterns and phylogeny fairly clearly, and should be useful in resolving systematic problems such as those involving sibling species.

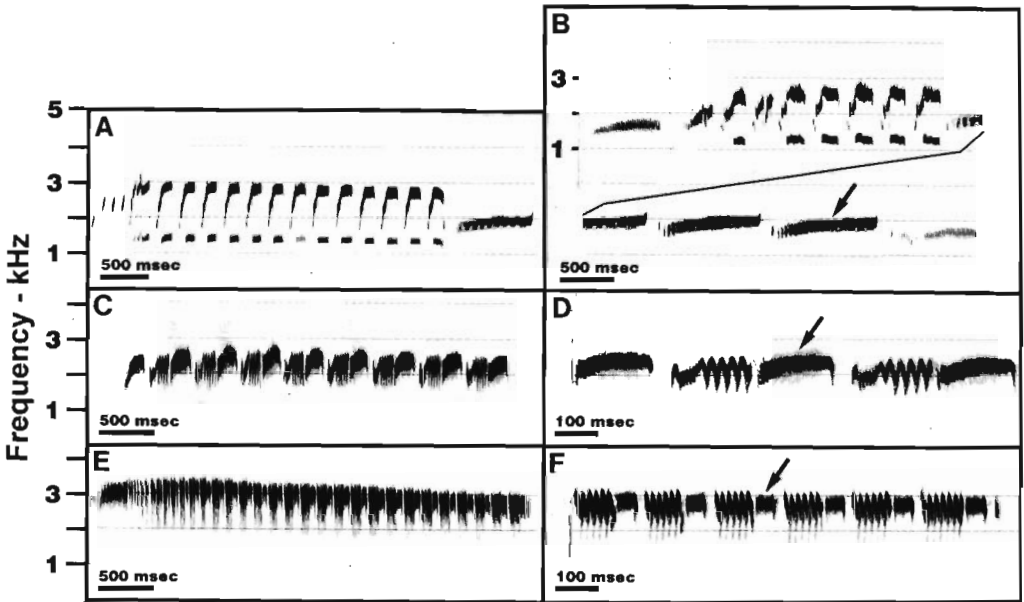


Fig. 13.6. Song structure within a species complex of calidridine sandpipers. (A) Purple Sandpiper (Iceland), single song with introductory trill (a variable feature). (B) Purple Sandpiper (Spitzbergen), single song embedded in long series of RRCs (single RRCs are shown before and after the song). (C) Rock Sandpiper (Alaska). (D) Last second of C, shown on different time scale. (E) Dunlin (Alaska). (F) Last second of E, shown on a different time scale. The terminal long pulsed elements in B (one is marked) are judged to be homologous to those marked in D and F (compare Fig. 13.5). Analyzing filter bandwidth, 115 Hz. Analyses were done over the frequency range 100–5000 Hz. Sources: All recordings are by E. H. Miller; A, near Raufarhöfn, Iceland; B, Longyearbyen, Svalbard, Norway; C, D, St. Paul Island, Pribilof Islands, Alaska; E, F, Nunivak Island, Alaska.

Sibling species. Nuptial displays are sensitive indicators of population differentiation and speciation at the level of sibling species, as the following examples make clear. The snipe forms *G. g. gallinago* and *G. g. delicata* usually are treated as subspecies of the species *G. gallinago*, as mentioned above. Thönen (1968) noted a striking difference in snipe drumming between north-coastal Alaska (*delicata*) and western Europe (*gallinago*), being lower in both frequency and modulation rate in the latter.¹ In *gallinago*, the fundamental frequency is approximately 350–400 Hz around the drum's crescendo, and there is a rich frequency spectrum with strong emphasis on odd harmonics (Fig. 13.1B, C). The fundamental frequency in *delicata* is about twice as high, and energy simply falls off progressively with frequency (Fig. 13.1D, E). In *gallinago*, the pulse (modulation) rate is much higher and pulses are correspondingly briefer.

The differences between *gallinago* and *delicata* drumming are strong, involve

¹Other sonograms are in Grudzien (1976), Thielcke (1976), Glutz et al. (1977), Jellis (1977), Reddig (1978, 1981), Bergmann and Helb (1982), Cramp (1983), and Nethersole-Thompson and Nethersole-Thompson (1986).

several prominent acoustic characteristics, and are consistent throughout the vast breeding ranges of the two forms. Therefore it seems reasonable to view *gallinago* and *delicata* as separate species, pending information on nuptial vocalizations, playback experiments, and breeding in areas of local sympatry (western Aleutian Islands? D. D. Gibson pers. comm.).

The closely related Common Ringed and Semipalmated Plovers occasionally are treated as conspecific, yet their nuptial vocalizations differ greatly. RRCs of the Common Ringed Plover are approximately 230–240 milliseconds long and are repeated about every 120–130 milliseconds (Fig. 13.2). RRCs begin with a brief pulsed portion (not visible in many sonograms: compare Fig. 13.2E, F), followed by a frequency-modulated nonharmonic section, and end with a harmonically rich section (Fig. 13.2E, F). The pulsing that corresponds to the harmonic richness of the final call part is evident in the waveform (Fig. 13.2F, upper; see Watkins 1967).²

RRC elements in the Semipalmated Plover correspond exactly to those just described, though they differ in structure. RRCs of this species are briefer and uttered more quickly (Fig. 13.2B). Each RRC is introduced by a rapidly pulsed section followed by two tonal parts (Fig. 13.2C, D). The first of these (the call's central part) rises in frequency from approximately 1500 to 3400 Hz (high values from Queen Charlotte Islands, British Columbia), then declines to the starting frequency of the last part of the call. The frequency contour of this middle part varies geographically but is always characterized by having no harmonics. In contrast, the terminal part is always harmonically rich.

The RRCs of Common Ringed and Semipalmated Plovers differ in call duration, call-part duration, interval between calls, frequency, and frequency contour of the central part. These multiple differences, taken together with the minor geographic variation in RRCs over the extensive breeding range of each form, suggest that the forms should be treated as separate species. This view is strengthened by the observation that even flight calls by nonbreeding birds on migration or wintering grounds “are . . . sufficiently distinct . . . to allow confident identification on call alone” (Hayman et al. 1986, p. 283, Paulson 1993). As for snipe, song structure and areas of local sympatry need to be investigated; song seems to differ greatly between the two forms (E. H. Miller pers. obs.).

Phylogenetic Analysis

It is useful to begin phylogenetic analyses at low levels, where relationships are likeliest to be expressed. Such a conservative approach seems called for in the present case, as differences are apparent even between sibling species.

²For other sonograms of this call type, see Glutz et al. (1975, p. 103, figs. b, c), Bergmann and Helb (1982, p. 130, fig. b), and Cramp (1983, p. 138, figs. IV, V, and VII). The call type may be variable in this species, as some published sonograms do not show the terminal harmonically rich portion (e.g. compare the first two calls in fig. IV with others there, and with those in figs. V and VII in Cramp 1983).

Gallinago snipe. Drumming seems to be a sensitive indicator of differentiation between closely related taxa, but it also offers promise for investigating phylogenetic relationships and evolutionary patterns more generally. Evolutionary divergence above the level of sibling species is surprisingly great. For example, *G. paraguaiiae* exhibits differentiation of elements within each drum, with alternating pulse couplets and singlets (E. H. Miller pers. obs.). Drumming in several other snipe species also has become elaborated beyond a simple series of pulses. In the Pintail (*G. stenura*) and Swinhoe's (*G. megala*) Snipe, each drum ends distinctively with changed intervals between pulses and a long terminal element (Labutin et al. 1982, Veprintsev 1982, Cramp 1983, Byrkjedal 1990). Other striking species differences in drumming occur, though published analyses do not permit detailed comparisons (Terborgh and Weske 1972, G. L. Maclean 1985, Nakamura and Shigemori 1990). Species differences in drumming probably reflect (in part) species differences in number, shape, and size of rectrices, and in how the rectrices are used in drumming—for example, in the temporal pattern and extent of tail spreading (Byrkjedal 1990).

Charadrius plovers. Close relatives of the Common Ringed and Semipalmated Plovers are the Little Ringed Plover (*Ch. dubius*), Killdeer (*Ch. vociferus*), Long-billed Plover (*Ch. placidus*), Wilson's Plover (*Ch. wilsonia*), and Piping Plover (*Ch. melodus*; Bock 1958, Taylor 1978). Published sonograms for the Little Ringed Plover reveal acoustic features astonishingly similar to those described above, and these are likely homologous: calls have a tripartite structure, and the parts have the attributes described above and occur in the same sequence (Glutz et al. 1975, p. 153, fig. 13.E, Bergmann and Helb 1982, p. 131, fig a, Cramp 1983, p. 126, fig. 13.IX). Homologous calls in the Killdeer may correspond only to the central call part recognized here, but more detailed sonograms are needed to confirm this possibility (Bursian 1971, R. E. Phillips 1972). No sonograms of this call type have been published for Wilson's or Piping Plovers, and no sonograms of Long-billed Plover vocalizations have been published at all (E. H. Miller 1992).

The direction of evolutionary change in acoustic characters can be deduced because *Ch. semipalmatus* was derived from one stock of the widespread *Ch. hiaticula* (Taylor 1978). Acoustic changes that occurred during the differentiation of *Ch. semipalmatus* can be summarized as follows: calls became briefer, were uttered more slowly, and became higher in frequency; the pulsed introductory portion of calls became longer and more pronounced; central and terminal call parts became briefer; and the central call part became simpler. Aside from these general patterns and relationships, little can be said because of the dearth of published material. As with *Gallinago*, however, acoustic characters seem to have great potential for resolving species relationships at various levels, and also for tracing the nature of evolutionary change.

Calidris sandpipers. Rhythmically repeated calls differ strongly among the AMP complex species in quantitative features, but those features are uninforma-

tive regarding the species' relationships to one another (E. H. Miller pers. obs.). Other vocal classes must be used to explore relationships.

Ancestral and derived features of AMP song can be deduced by considering song structure in two other scolopacids, the Short-billed Dowitcher and the Least Sandpiper.³ Dowitcher song consists of several rapidly repeated units (Fig. 13.5A). Each song unit begins with a complex trill and concludes with several long frequency-modulated elements. The long terminal elements increase successively in duration, and they decrease in carrier frequency successively both within and across song units (Fig. 13.5B). Least Sandpiper song is extremely similar to this: each of the repeated song units starts with a trill and ends with several frequency-modulated (pulsed) elements. As in dowitchers, the terminal song unit elements increase successively in duration, and they decline successively in carrier frequency both within (Fig. 13.5D) and across song units. Other similarities are suggested in fine features of trill elements. Finally, consider the song of the Purple Sandpiper, which also begins with a trill and ends with several long frequency-modulated (pulsed) elements (Figs. 13.5E, F, 13.6A, B). The song (unit) is rarely repeated in succession, however, as it is in the other two species.⁴ Furthermore, the introductory trill and terminal pulsed elements often are uttered in isolation from one another (Cramp 1983, p. 352, figs. V, VI), lending confusion as to what constitutes song (Cramp 1983). Trill elements in Purple Sandpiper song start at a low frequency and shift to higher frequency, as in the songs of the Short-billed Dowitcher and Least Sandpiper (Fig. 13.5B, D, F). If these structural and organizational (syntactical) similarities of song are interpreted as ancient homologies, then Purple Sandpiper song is ancestral within the AMP complex.

Song structure within AMP has two forms: (1) the form found in the song of the Purple Sandpiper (Figs. 13.5E, F, 13.6A, B), and (2) the form found in Dunlin and Rock Sandpiper song. The song of the latter two species is a long series of repeated, complex units incorporating slow and fast FM (Fig. 13.6C–F). The units are temporally separated from one another and show progressive changes in duration, frequency, and other characteristics over a song. The units of Rock Sandpiper song are about 350–550 milliseconds long and have several distinct parts: an initial pulse, brief rapid FM followed by some long slow pulses, and a long terminal part with rapid FM. The terminal part is remarkably similar to the long FM elements that terminate song in the Short-billed Dowitcher and the Least and Purple Sandpipers described above (Fig. 13.6D). Dunlin song is very similar, but its elements are briefer, more rapid, and higher in frequency. Dunlin song units have only two parts, one corresponding to the slowly pulsed part of Rock Sand-

³For references to published sonograms of Least Sandpiper vocalizations, see E. H. Miller (1984, 1992, 1995). For dowitcher vocalizations, see Greenewalt (1968) and E. H. Miller et al. (1983, 1984).

⁴In my detailed description of Least Sandpiper song, I overlooked its routinely compound nature and referred to each song unit (as recognized here) as song (E. H. Miller 1983b). This feature of song organization became apparent only through comparison with dowitchers (E. H. Miller et al. 1983, 1984).

pipper song elements, the other corresponding to the terminal part with rapid FM (Fig. 13.6F).

Several interpretations can now be made:

1. Purple Sandpiper song is homologous to the repeated unit in Short-billed Dowitcher and Least Sandpiper song.
2. The repeated unit in Rock Sandpiper and Dunlin song is homologous to the entire song of Purple Sandpiper (hence to the repeated song units of Short-billed Dowitcher and Least Sandpiper).
3. The long terminal part with rapid FM in Rock Sandpiper and Dunlin song units corresponds to the long terminal element with rapid FM in song of the other species.
4. Purple Sandpiper song has a uniquely derived condition of loose association of parts, with song trills and song FM elements often occurring by themselves.
5. Song of Rock Sandpiper and Dunlin is derived relative to that of Purple Sandpiper.

A third class of vocalization resolves the relationship between Rock Sandpiper and Dunlin. The cricket vocalization is a distinctive call given on the ground, mainly by males (E. H. Miller pers. obs.). It is uttered rhythmically in bouts or long sequences and may be audible for tens of meters. Sometimes calling males stand on a hummock and give this call for long periods, usually while the mate (or prospective mate) is nearby. The cricket call is used also in various kinds of short-range communication, as during nest-scraping displays. The cricket call has a similar two-part structure in Purple and Rock Sandpipers but is distinctive in having only one part (and in other ways) in Dunlin (E. H. Miller pers. obs.). The cricket call's structure therefore suggests that the Dunlin is the most highly derived species within the AMP complex.

The preceding analysis established that the Purple Sandpiper is the least derived species within AMP, and the Dunlin is the most derived. Furthermore, Rock Sandpiper vocalizations are distinctively different from those of the Purple Sandpiper. In light of these observations, it is untenable to consider Rock and Purple Sandpipers conspecific, and it may be unreasonable even to view them as parts of a superspecies (Cramp 1983, p. 355, C. G. Sibley and Monroe 1990, p. 241).

Pluvialis plovers. The RRCs and song of *Pluvialis* show a range of differentiation that illustrates both extreme evolutionary conservatism and rapid evolutionary change. *Charadrius* can serve as an outgroup for deducing ancestral and derived features of *Pluvialis*. *Charadrius* RRCs exhibit variable harmonic richness, a multipartite structure, sudden frequency shifts, and pulsing. The last three attributes all appear in *Pluvialis* RRCs, so they can be considered ancestral to the genus and must be very old (Fig. 13.3; Connors et al. 1993).

The RRCs of the Grey Plover are uttered very slowly (approx. 5–6 per minute), and those of the Eurasian Golden-Plover (*P. apricaria*) fairly rapidly (approx. 30 per minute; Fig. 13.3). The absence of an introductory pulsed element is a derived condition (Fig. 13.3A, B). The RRC of the Grey Plover has three tonal elements,

which presumably is the ancestral state; that of the Eurasian Golden-Plover has only two, which therefore is derived. In the American Golden-Plover, RRCs are brief (approx. 200 milliseconds) and uttered very rapidly (about 2 per *second*)—about 20 times as fast as in the Grey Plover (Fig. 13.3C)! They begin with a brief pulsed element—the “twisted rope” note of Connors et al. (1993)—that is followed by several brief tonal parts at different frequencies (Fig. 13.3C, E). The RRCs of the Pacific Golden-Plover are much longer (about 1 second) and are uttered much more slowly (some 15–25 per minute). However, they are identical in structure: a brief introductory pulsed element followed by three tonal elements at different frequencies (Fig. 13.3D, F). (Note that the introductory element in both species, and the middle tonal element in *P. fulva* RRCs, are not apparent in most published sonograms.)

Its song structure underscores the uniqueness of the Grey Plover. The song is extremely long and includes an introductory trill followed by a series of long tonal notes with some sudden frequency shifts (Byrkjedal 1996, E. H. Miller pers. obs.). No structural correspondences with the song of the other species are apparent. In contrast, homologous song features seem obvious in the other species, particularly between the American and Pacific Golden-Plovers (Fig. 13.3).

In summary, *Pluvialis* RRCs have differentiated greatly in temporal properties, and this is a prevalent trend (E. H. Miller 1986). Homologous parts of RRCs are readily identifiable, however, and part sequences have been conserved. Fewer homologies in song can be identified; some are attributes (e.g., quasi-rhythmic FM) and others lie in the sequential structure.

Evolutionary rates. The preceding examples all suggest strong evolutionary conservatism in some attributes of acoustic structure. It is of interest to estimate the rate at which some of those attributes evolved. To do this, divergence times and acoustic attributes must be known. Dowitchers can serve as an example.

Long-billed and Short-billed Dowitchers diverged from one another approximately 4 million years (MY) ago (Awise and Zink 1988). On various measures, song differences between them average 22% (E. H. Miller et al. 1984, table 1). Assume, then, that the two species have diverged equally from their common ancestor (i.e., each has diverged 11% over 4 MY). Rate of evolutionary change in song can be judged relative to a factor of e per million years (= 1 darwin; Futuyma 1986). Thus, dowitcher song has changed at a rate of $(0.11/4/2.718)$, or about 10 millidarwins—roughly 1% per million years! This figure is comparable with low average rates of morphological evolution based on the fossil record (e.g., 40 millidarwins for molar height in Tertiary horses), and contrasts with high rates routinely found for colonizing species and laboratory populations (Futuyma 1986). Rates of evolutionary change must have been much slower for other properties of shorebird displays, such as the frequency modulation, harmonic richness, and sequential ordering in the examples provided above.

West-Eberhard's (1983) scenario for speciation and the evolution of sexually selected characters leads to the prediction that displays with different functions

will evolve at different rates. Insufficient evidence exists to judge whether differences in evolutionary rates like those just noted can be explained in that way. Some supportive evidence comes from parental alarm calls versus song and RRCs in calidridine sandpipers. Most calidridine species have two forms of parental alarm—a trill and a single note (E. H. Miller 1984, 1985b, 1992). Alarm call forms are immediately recognizable in species as distantly related as the Surf-bird (*Aphriza virgata*), Baird's Sandpiper (*Calidris bairdii*), and the Least Sandpiper, though they differ in simple quantitative features (E. H. Miller 1985b, E. H. Miller et al. 1987, 1988). In contrast, the songs of those species—though they occur in extremely similar contexts—are so different in structure that homologous features cannot even be identified. A similar contrast between similar alarm calls and dissimilar nuptial vocalizations occurs between the American and Pacific Golden-Plovers (Connors et al. 1993, Johnson and Connors 1996).

Conclusions

Sexual selection has acted on shorebirds to produce nuptial sounds of great complexity, even for sounds used principally over long distances. Many of these sounds are similar in related species, but others are so different that homologous characters cannot be detected. Display types with different functions (e.g., parental alarm) show greater similarities, and hence evolved more slowly (E. H. Miller 1984). This range of variation underscores the importance of sexual selection in effecting species-distinctive mating displays, and also points to a wealth of material for systematics research on shorebirds. Several lines of investigation may be particularly fruitful.

Like passerines, many shorebirds show strong interspecific differences in their displays; in fact, this characteristic led workers to suggest that the usefulness of vocalizations in passerine systematics is limited to species-level questions (W. E. Lanyon 1969, R. B. Payne 1986). In contrast, numerous features of nuptial acoustic displays in shorebirds are evolutionarily conservative and should be useful in revealing relationships well above the species level. Examples include entire display classes, such as drumming in *Gallinago* and semisnipe (*Coenocorypha*); high-level organizational properties, such as embedded grading in dowitcher and calidridine song; sequential organization, as in plover RRCs and calidridine song; individual elements, as illustrated by corresponding parts of plover RRCs and calidridine song; and specific attributes such as pulsing in the terminal elements of calidridine song and tonality in parts of plover RRCs. If nonnuptial acoustic displays are examined together with nuptial ones, it seems likely that some shorebird relationships can be resolved even well above the genus level. In particular, descriptions of vocalizations from outside the breeding period, and from chicks and females, should be sought (Saether 1994).

Vocal characters frequently are vital for resolving the systematic status of cryptic or sibling bird species (W. E. Lanyon 1969, R. B. Payne 1986, N. K.

Johnson 1994), and the same applies to nuptial acoustic displays of shorebirds, despite the evolutionary conservatism just outlined. At higher levels of phylogenetic analysis, it should prove valuable to couple behavioral and genetic analyses. Such an approach will permit evolutionary trends to be traced and evolutionary rates to be estimated—rates of change both in different display classes and in different levels of acoustic structure. The resulting information should reveal a great deal about the action of sexual selection in speciation and about behavioral evolution generally (e.g., regarding evolutionary constraints; McKittrick 1993, von Helversen and von Helversen 1994).

Information and research needs for shorebird communication are similar to needs in other areas of field biology. Better and more extensive information is needed about display characteristics, when displays occur seasonally and during the day, the ecological settings of displays, and the meanings and functions of displays. Such information is needed simply for developing techniques to detect and enumerate shorebirds. Some groups of shorebirds are still essentially unknown yet likely are of conservation concern; examples are woodcock and snipe (E. H. Miller 1992, 1995). It is crucial to determine which members of these groups are distinct species, and knowledge of acoustic display structure is essential to accomplish this (R. B. Payne 1986, N. K. Johnson 1994). The evidence presented above on snipe underscores how little we know about species distinctiveness even in widely distributed and seemingly well-known taxa. Thus, research on the systematics of taxonomically poorly known groups for which such information is of practical conservation concern should have the highest priority.

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