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Chapter 6

COMMUNICATION IN BREEDING SHOREBIRDS

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I. INTRODUCTION

Shorebirds offer rich opportunities for comparative research because of their wide geographic distribution and their phylogenetic, ecological, and social diversity. There are more than 200 extant species, which occur in all zoogeographic regions of the world. Some species are resident and sedentary year-round, like the Shore Plover (*Charadrius novaeseelandiae*), which exists in small numbers only on the Chatham Islands east of New Zealand; others undertake phenomenal migrations each year, spending only 2 months or even less on the breeding grounds, with the remainder in migration or on wintering areas (e.g., certain Arctic species). Shorebirds inhabit the high mountains of Asia and of North and South America; they dwell in swamps and in hot, arid areas of Africa, Australia, and elsewhere; and they are found on muddy, rocky, or sandy seacoasts around the world (see Burger, this volume; Hale, 1980; Johnsgard, 1981). This wide geographic and ecological scope is paralleled by a great diversity of social systems, both on and off the breeding grounds. All these characteristics make shorebirds a likely group to enhance our understanding of the evolution and ecology of social behavior, a prediction supported by recent studies (e.g., Erckmann, 1981; Myers, 1981; Oring and Lank, 1982; Pitelka *et al.*, 1974; van Rhijn, 1983; Walters, 1980, 1982; and chapters in these volumes).

Studies on communicative behavior in shorebirds have lagged far behind those on social systems, and have contributed little to conceptual advances in the study of animal communication. A major reason for this is the difficulty in studying shorebirds. For example, in contrast to many species of oscines, on which most of our understanding of avian acoustic communication rests, shorebirds typically inhabit areas that are ecologically or geographically remote or difficult to work in, they often nest at low densities, are difficult to approach, offer no simple counterpart to oscine song, can be extremely mobile while in display, and are often hard to maintain or rear in captivity. Thus, though good descriptive studies on communication are possible for many species, few opportunities exist for rigorous field or laboratory experimental work on shorebirds like that routinely carried out on songbirds (e.g., see chapters in Kroodsma and Miller, 1982a).

Considering these facts, why should a chapter on shorebird communication be written, and what research potential do shorebirds offer? There are several answers to this question. First, it is important to begin to draw together our knowledge of shorebird communication, so that we can eventually understand its characteristics and its relationships to habitat, life history, and phylogeny. It is particularly urgent to expand and improve documentation of displays in certain populations and species, because they are uncommon, rare, or susceptible to extinction. The main offering of shorebirds to the study of animal communication lies in improved understanding of evolutionary pattern and process, through descriptive comparative studies, and in providing a data base against which to assess the generality of findings on more experimentally tractable taxa. For example, a major focus in communication research is ontogeny, which has implications for dialect formation, mimicry, duetting, and geographic variation. These areas are under intensive study in oscines, but are essentially unstudied and unknown in shorebirds, a group in which ontogeny of acoustic communication may be very different (see Section II.E.4).

This chapter begins with an overview of some external features of shorebirds that provide certain kinds of information about an individual's characteristics (including gender, age, etc.; see next paragraph). Following that, several studies on the organization and causation of displays are summarized. Acoustic components of displays are then reviewed, and their organization into repertoires, and functioning in several well-studied communication systems are discussed. Display characteristics and use are intimately related to social processes, so the relationship of social structure and ecology to communication is then considered. Finally, geo-

graphic variation and some evolutionary trends in displays, and the significance of displays to systematics, are treated.

Current concepts and theories of animal communication are diverse and divergent (Green and Marler, 1979; Hailman, 1982). As a consequence, there is no simple, single way to discuss communication even within a taxonomic group, without admitting strong conceptual biases. Two examples illustrate this point. Consider first the question of whether animals communicate honestly. A paradigm of honest communication would predict that breeding males of many species would accurately transmit information in their songs about their distance from other males. This could be effected through physical characteristics of song that degrade predictably with distance, thereby permitting listeners to accurately estimate distance from the singer (Richards and Wiley, 1980; Wiley and Richards, 1982). A contrasting paradigm might suggest that a singer could deceive listeners to his advantage by concealing his distance; this might lead to listeners expending time and energy in trying to locate a singer, or might keep them at great distances from him. Song features that undergo little degradation or attenuation over distance would thereby evolve. These simple paradigms provide different explanations for observed song characteristics, and lead to different predictions about evolutionary trends in song structure.

A second example deals with the kinds of information encoded in signals, assuming honest communication. Smith (1977) proposes that the messages encoded in signals are fixed in number and in what they refer to; a signal's meaning to a receiver results from his appraisal of many external circumstances in the immediate context of signaling, plus his prior experience, the signaler's identity and characteristics, etc. A converse view has been expressed by Beer (1975): why can't a particular type of display have a variety of messages, at different times and in different contexts?

The above contrasts serve to illustrate the current lack of wide acceptance of any particular paradigm for animal communication. In this chapter, I follow Smith (1977) in treating displays as though they make various kinds of information available about a signaler's behavioral and nonbehavioral states, even though there is often no evidence that such information is communicatively significant. This approach has the virtue of specifying the potential range of information available to receivers, and the important parts of that range can be narrowed through observation or experiment. Further, I consider that displays and display behavior cannot be viewed just from an adaptationist perspective, for their char-

acteristics arise or are influenced also by other factors (notably phylogeny).

II. COMMUNICATION IN BREEDING SHOREBIRDS

A. External Characteristics and Appearance

In this section, I outline some important attributes of shorebirds that are apparent from external features: gender, population origin, individuality, age, and physiological state.

Many shorebird species are cryptically patterned and colored, and follow a widespread trend in being darker above than below (counter-shading), and in having the dorsal plumage approximate substrate color (chromatic matching) (see Graul, 1973a; Hailman, 1977). However, even the most unassuming species have distinctive features of potential communicative significance. For example, the Least Sandpiper (*Calidris minutilla*), the smallest of the 24 species in the Calidridini, is inconspicuously colored and patterned in the breeding season. Notable features are the yellowish legs and fairly dark appearance, especially on the breast (Fig. 1a; see Prater *et al.*, 1977). As in other monogamous species of calidridines, males are smaller than females (see Jehl, 1970). Male nuptial plumage is dark and gray, in contrast to the warmer, browner tones of females, and it is easy to distinguish the sexes by this plumage difference when paired birds are together, often even when in flight. This sexual difference is paralleled in the White-rumped Sandpiper (*Calidris fuscicollis*; Sutton, 1932) and the Upland Sandpiper (*Bartramia longicauda*; E. H. Miller and D. R. M. Hatch, unpublished observations). Jehl (1973) reports that ventral barring in male Stilt Sandpipers (*Calidris himantopus*) tends to be darker than in females. In brightly colored subspecies of the Dunlin (*Calidris alpina*), the hindneck of males "appears as a pale whitish collar," but in females is spotted, streaked, and only "slightly lighter in tone than . . . the crown and mantle" (Ferns, 1981, p. 94). Also, the upper breast of females has a more intense buffy wash (Ferns, 1981). These observations could be multiplied, but suffice to emphasize that a broad trend exists even in drab species of Scolopacidae for strong plumage differences that reliably signal gender. Sexual differences characterize many other taxa, of course, particularly those with extensive black in the plumage like *Vanellus* and *Pluvialis*. Similarly, males and females in many *Charadrius* species and in the Least Seedsnipe (*Thinocorus rumicivorus*) differ in the extent and intensity of black coloration in facial markings

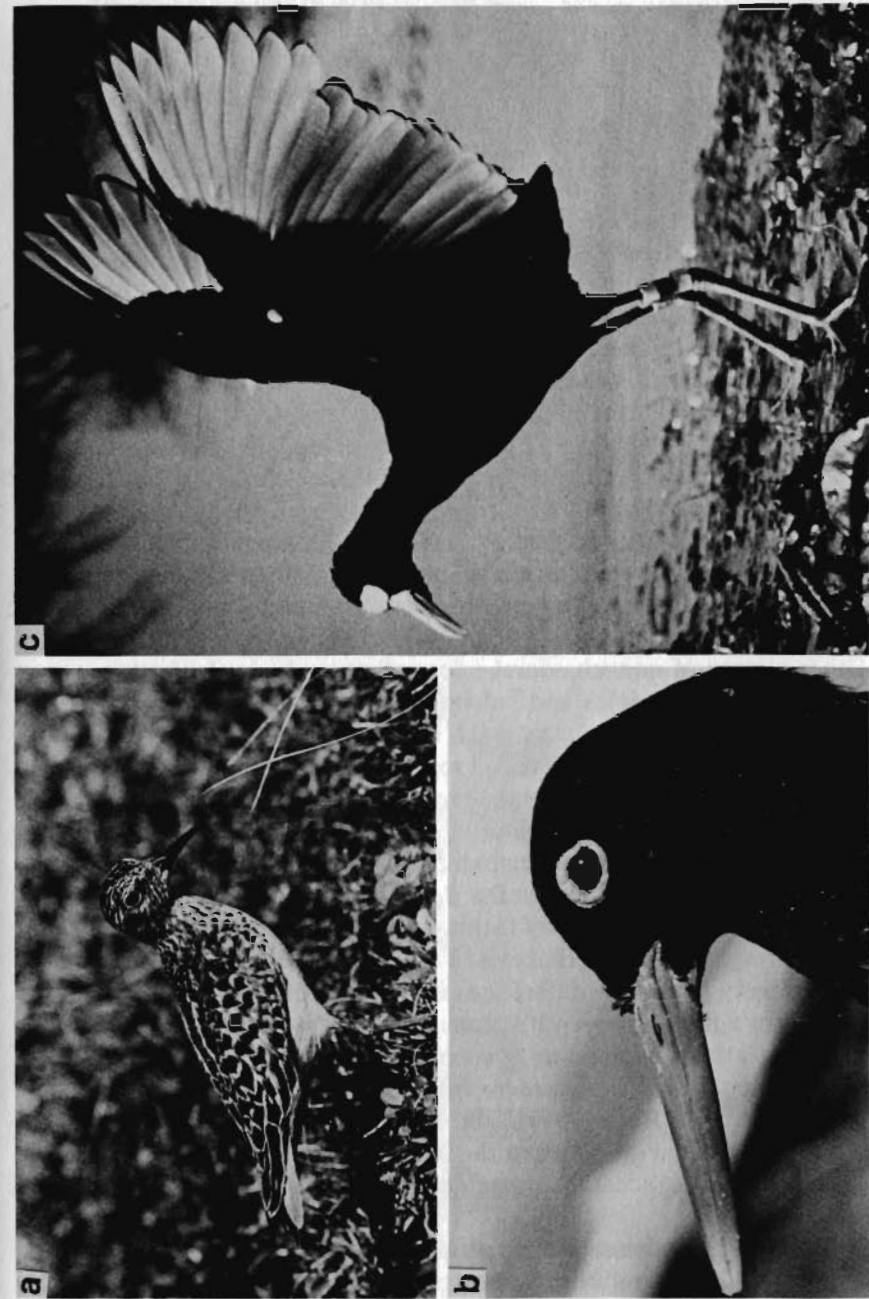


Fig. 1. (a) Least Sandpiper (*Calidris minutilla*) in nuptial plumage [photograph by P. A. Johnsgard]. (b) African Black Oystercatcher (*Haematopus moquini*) showing the distended naked eye-ring [photograph by A. E. Burger]. (c) Northern Jacana (*Jacana spinosa*) in a display in which the striking primaries and carpal spurs are exposed [photograph by T. R. Mace].

and breast bands. Polyandrous species are typified by females being brighter, darker, or more intensively/contrastingly marked than males (e.g., *Phalaropus*, Rostratulidae). In general, it is likely that sexual dimorphism in nuptial plumage of most shorebird species is probably great enough to be a reliable and communicatively significant static-optical indicator of gender.

Sexual dimorphism in shorebirds is also pronounced in other morphological features: males of the Ruff (*Philomachus pugnax*) are adorned with ruffs and naked patches on the face, lacking in females (Fig. 2c; Glutz von Blotzheim *et al.*, 1975; Hogan-Warburg, 1966); male oystercatchers have bright, pink bills, in contrast to the dull, orange bills of females (Miller and Baker, 1980); the iris of female Eurasian Avocets (*Recurvirostra avosetta*) tends to be brown, that of the male red-brown (Witherby *et al.*, 1941); the bill of female American Avocets (*R. americana*) is much shorter and more strongly upcurved than that of males (Hamilton, 1975); and so on. Many sexual differences in morphology have resulted from selective pressures surrounding feeding ecology; energetics of egg-laying, incubation, and display; intersexual competition; etc. Such differences have not always arisen or been modified to signal a bird's gender; nevertheless, they often make that important information reliably available to receivers.

Other classes of nonbehavioral information made available through morphology include species and subspecies status. Species differences need not be discussed here; most such differences are obvious, but are not reinforced or accentuated through reproductive interactions between species (see Miller, 1982). An example for shorebirds concerns two sibling species of plovers (*Pluvialis dominica*, *P. fulva*) which breed sympatrically in northwestern Alaska; they exhibit no divergent shift in plumage characters there, despite their similar appearance (Connors, 1983). Differences between subspecies may facilitate segregation during late winter and early spring, and Ferns (1981) and Ferns and Green (1979) document many potentially important differences in plumage of Dunlin subspecies at that season. Subspecies identity is unambiguous in the Masked Plovers (*Vanellus miles miles* and *V. m. novaehollandiae*) of Australia, because of their strongly differing plumages and facial characteristics (van Tets *et al.*, 1967; see also Bock, 1958). The extent to which this information is used in social behavior between the subspecies is not known, though they interbreed in a recently formed overlap zone in Queensland (van Tets *et al.*, 1967).

Individual distinctiveness is not obvious in the plumage and soft parts of many species of shorebirds. Some species show great interindividual variation, however. In the Ruddy Turnstone (*Arenaria interpres*), the

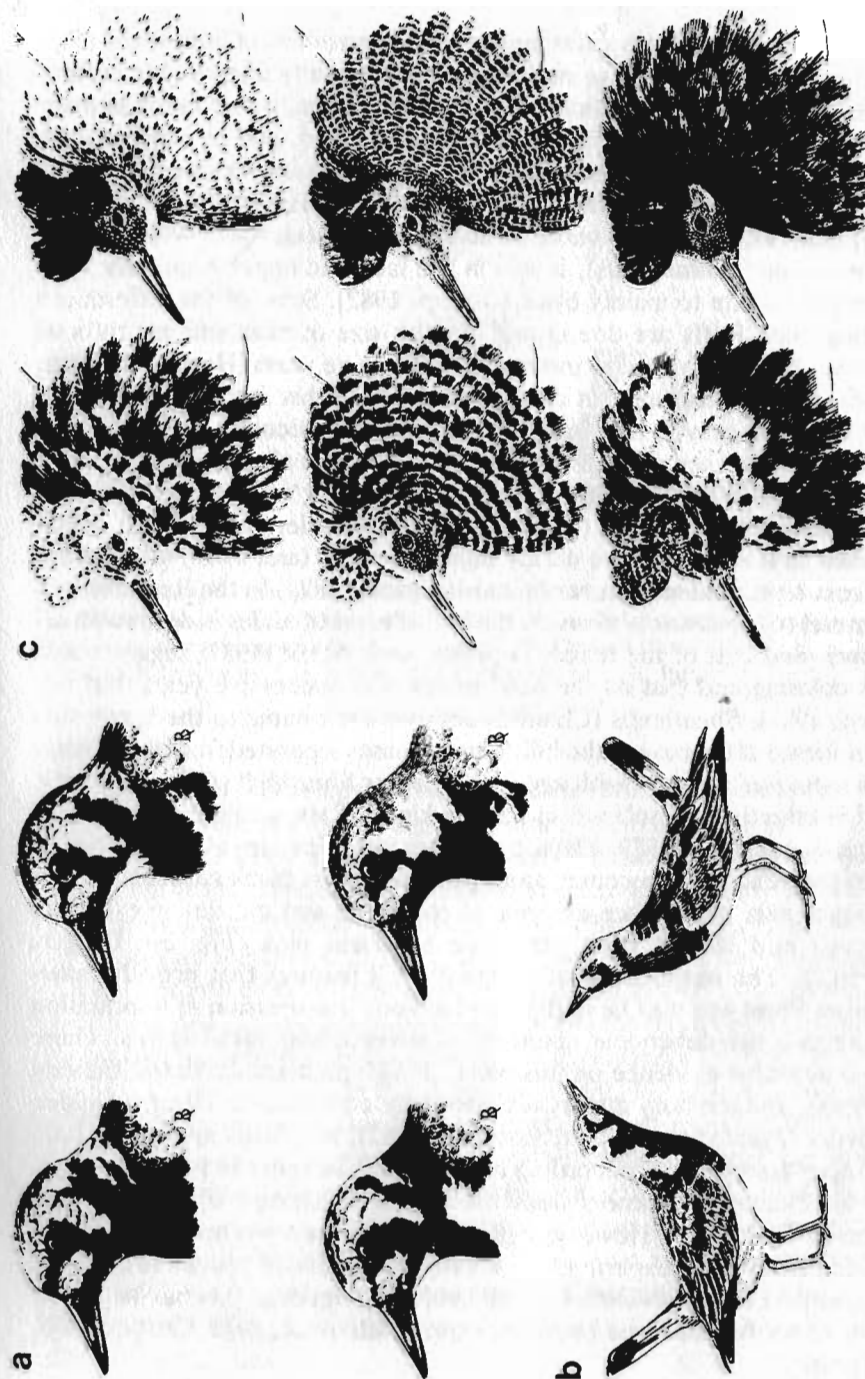


Fig. 2. (a) Variation of facial markings in the nuptial plumage of four male Ruddy Turnstones (*Arenaria interpres*) [after Fig. 1 of Ferns (1978)]. (b) Threat display between breeding male Ruddy Turnstones [after Fig. 117 of Glutz von Blotzheim *et al.* (1977) and Fig. A of Cramp *et al.* (1983)]. (c) Variation of wattles and ruffs in the nuptial plumage of six male Ruffs (*Philomachus pugnax*) [after Fig. 94 of Glutz von Blotzheim *et al.* (1975)].

complex facial markings differ greatly among members of both sexes (Fig. 2a; Ferns, 1978), and these markings are prominently displayed in certain kinds of aggressive encounters (Fig. 2b). Similarly, wattle color in male Ruffs occurs in various shades of yellow and red, and in concert with color and markings of the ruff, allows individuals on lekking hills to be easily distinguished by human observers (Fig. 2c; Hogan-Warburg, 1966; Shepard, 1975). Extreme variation also occurs among Black-winged Stilts (*Himantopus himantopus*), in which the face and upper neck may vary from pure white to mainly black (Goriup, 1982). Some of the differences among male Ruffs are due to age, for the size of ruffs and ear tufts of captives has been noted to increase in successive years (Hogan-Warburg, 1966). Another feature that changes with age in this species is leg color, which is lead-gray in nestlings, and successively becomes greenish-gray, reddish-green, then reddish or orange, in the course of seasons (Andersen, 1951; Hogan-Warburg, 1966). Changes in leg color with age also occur in the American Woodcock (*Scolopax minor*; Shissler *et al.*, 1982). Birds in their first summer have darkly pigmented legs (and bills), while those at least 1 year old tend toward pinkish legs and bills. In the Red-breasted Dotterel (*Charadrius obscurus*), the breast band of males is deep reddish-brown, and that of the female is pinkish-red; Stead (1932) suggests that this coloring and that on the head increase in successive years (but see Reed, 1981). Sheathbills (Chionidae) owe their name to the horny culmen sheath at the base of the bill. This becomes separated from the culmen and increases in depth with age in the Lesser Sheathbill (*Chionis minor*), and is effectively displayed in certain kinds of short-range visual threat (Figs. 3, 4; Burger, 1979, 1980a,b,c). Other facial features also change with age: the head crest becomes more prominent, the black caruncles cover a larger part of the face anterior to the eyes, and the fleshy eye-rings thicken and change from very pale to bright pink (Fig. 3a; Burger, 1980a,c). The significance of morphological features that provide information about age may lie in the simultaneous transmission of information about two age-dependent qualities: experience and social status. There is no available evidence on this point, though plumage darkness, fighting success, and territory quality are positively correlated in Greater Golden Plovers (*Pluvialis apricaria*; Edwards, 1982), and birds appear to mate positive-assortatively according to extent of blackness in plumage (Parr, 1980). Plumage blackness does not appear to change with age in this species (Parr, 1980). However, age-related differences in breeding success arising from prior experience and foraging efficiency provide a possible mechanism for the evolution of enhanced discriminatory behavior, based on external features (see Cadman, 1980; Gratto *et al.*, 1981; Groves, 1978; Heppleston, 1971).

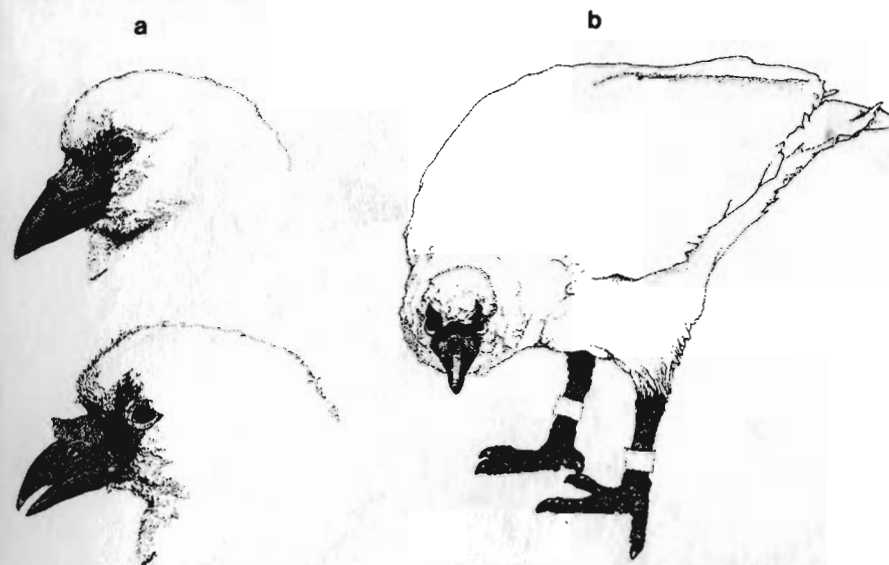


Fig. 3. (a) Changes with age in the facial features of the Lesser Sheathbill (*Chionis minor*). A 4-month-old juvenile is shown above, and a 4-year-old adult below [drawings by A. McClung, after photographs by A. E. Burger]. (b) Forward (threat) display by a Lesser Sheathbill [drawing by A. McClung, after photograph by A. E. Burger].

Short-term physiological changes can be reflected in the appearance of soft parts, thereby providing other kinds of information to receivers. Pupillary contraction and dilation are probably important sources of information in short-range interactions in species with brightly colored irides, including Burhinidae, Haematopodidae (Fig. 1b), Magellanic Plovers (*Pluvianellus socialis*), etc. In the latter species, "vivid iris coloration is featured prominently in courtship and territorial displays . . . or when a bird is excited . . . the eye is opened wide and the pupil contracts, giving added prominence and brightness to the expanded coral iris. At these times, the inner rim of the iris is yellow" (Jehl, 1975, p. 46). Alteration of blood flow can also alter the appearance of soft parts. In the Comb-crested Jacana (*Irediparra gallinacea*), the cephalic shield can change quickly between rich yellow and orange-red (Hindwood, 1934; Potter, 1934). Most soft parts apparently cannot undergo such short-term transformations, though seasonal changes in color, size, or distension to signal breeding condition may be widespread. Possible candidates include tarsi, wattles, and fleshy eye-rings (Fig. 1b). I know of no published observations on this matter.

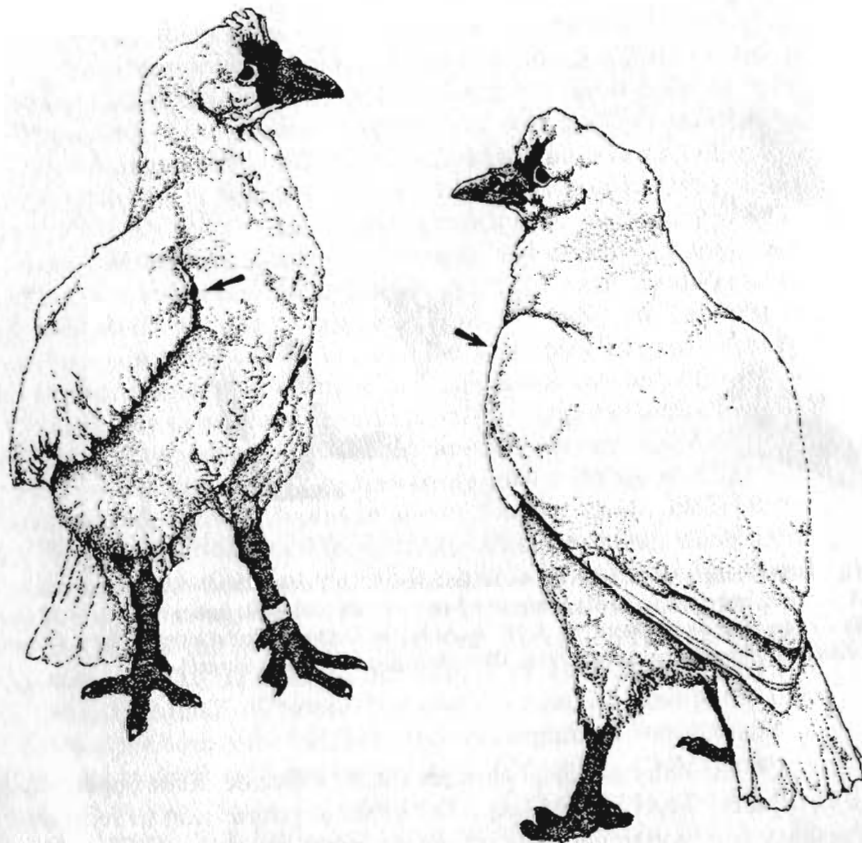


Fig. 4. Male Lesser Sheathbills (*Chionis minor*) in "aggressive upright" postures during a pause in fighting. The arrows point to the black carpal spurs. [Drawing by A. McClung, after photograph by A. E. Burger.]

To summarize, there are many kinds of nonbehavioral and some behavioral (physiological) information made available, in a static-optical way, by the external appearance of shorebirds. It is likely that many external features that passively encode and emit such information owe their characteristics to selective pressures favoring (or disfavoring) communication. It is most tempting to invoke adaptive interpretations for features that are displayed, exaggerated, or modified through stereotyped motor patterns, of course. Thus, the carpal spurs of the Northern Jacana (*Jacana spinosa*) are rich yellow in color, with a naked area of the same color around their base. In several types of agonistic display with the wings extended, the spurs and the striking yellow primaries are clearly

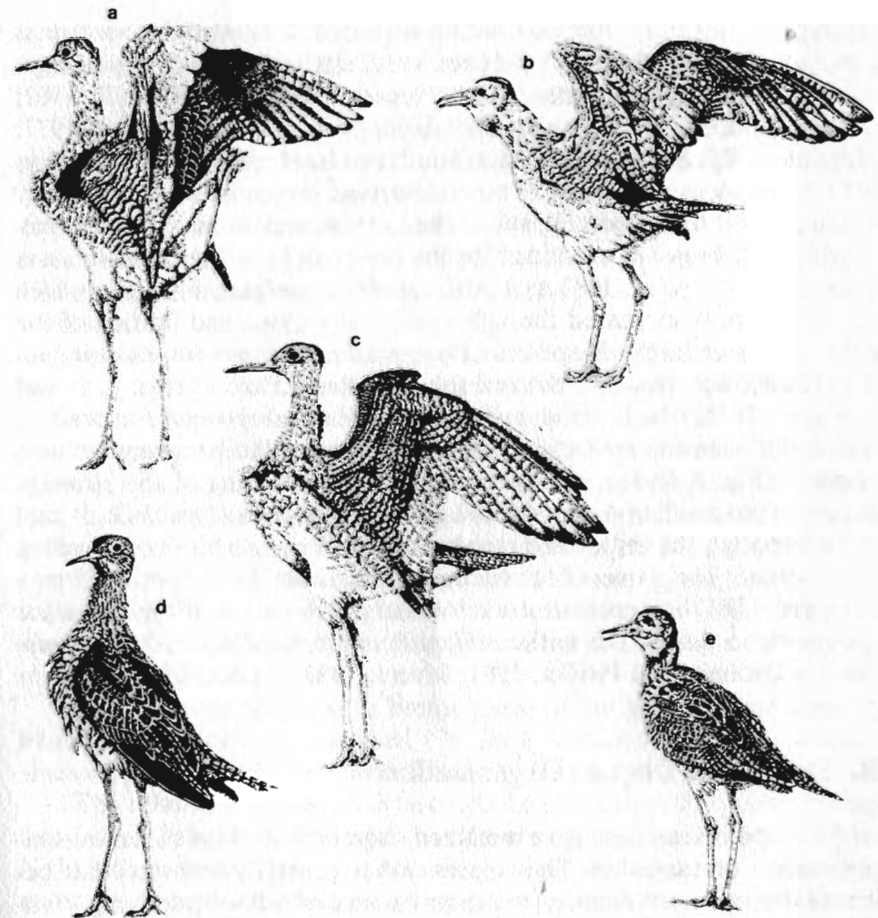


Fig. 5. Male Upland Sandpiper (*Bartramia longicauda*) in various stages of display upon landing [drawing by A. McClung, after photographs by E. H. Miller and D. R. M. Hatch].

visible (Fig. 1c). Similarly, the black carpal spurs of the Lesser Sheathbill contrast with the surrounding white plumage, and are displayed when the wings are lifted out from the sides (Fig. 4; Burger, 1980b,c). Numerous examples could be added, of features that are hidden except when in display. Particularly notable are the striking patterns on individual feathers, and on surfaces of wings and tails in many species, including *Vanellus*, *Burhinidae*, *Rostratulidae*, Egyptian Plover (*Pluvianus aegyptius*), *Gallinago*, some *Haematopodidae*, etc. (Fig. 5).

Many optical characteristics can be altered through modification of the plumage, or by adoption of suitable postures or orientation to re-

ceivers. In many species of *Charadrius* plovers, an upright posture is adopted in which the bird stretches vertically and fluffs the plumage, thereby increasing the extent of the breast bands (Cairns, 1977, 1982; Cunningham, 1973; Glutz von Blotzheim *et al.*, 1975; Maclean, 1977; Mundahl, 1977; Simmons, 1953a,b; Smith and Hosking, 1955). In the Wrybill (*Anarhynchus frontalis*), "a resident bird drives out an intruder by running at it in a horizontal posture. The run [can end] in an upright display in which the breast is expanded. In the horizontal run the chest stripe is expanded . . ." (Hay, 1983, p. 11). Comparable upright postures in which apparent size is increased through vertical stretching and fluffing of the plumage occur in the Magellanic Oystercatcher (*Haematopus leucopodus*) (Miller and Baker, 1980) and the Magellanic Plover (Figs. 5, 6, and 8 of Jehl, 1975); the latter also shares with Haematopodidae, Jacanidae, and Burhinidae the trait of increasing the size of the nape during such displays (Fig. 6 of Jehl, 1975; Maclean, 1972). Fluffing of the plumage occurs in postlanding displays of the Upland Sandpiper (Figs. 5a,c,d), and in this species the throat is distended and strikingly white while calling (Figs. 5b,e). The same effect occurs in the Least Sandpiper, and may have provided the impetus for evolutionary elaboration of the throat for distension in display, as in the related Pectoral Sandpiper [*Calidris melanotos* (Holmes and Pitelka, 1961; Myers, 1982; Pitelka, 1959)].

B. Studies on Display Organization

Several researchers have analyzed shorebird displays based on simple models of causation. This approach has generally assumed that behavioral structure reflects a particular balance of a few underlying "tendencies" or neurophysiological states. Behavioral characteristics that have been viewed in this light include the component structure of displays, quantitative changes in display components, and the structure of sequences, as related to different social circumstances. The premises upon which such research is based are not widely accepted, but the analytic procedures and results provide useful information about the composition of shorebird display behavior. In this section, I outline a few examples of detailed research along these lines.

1. Ground Display in the Black-tailed Godwit

Black-tailed Godwits (*Limosa limosa*) show a number of distinctive visual displays during short-range agonistic interactions on the ground. Lind (1961) has described and analyzed them in detail, and this section

discusses his findings. He recognized five major display types used in the context mentioned [see Figs. 3 and 9a of Lind (1961), Figs. A–E of Cramp (1983), and Fig. 40 of Glutz von Blotzheim *et al.* (1977)]:

Upright. Attitude upright; legs stretched; carpal joints slightly exposed; neck usually extended vertically; dorsal plumage sleeked to slightly ruffled; tail often lowered, never spread [note: in this and other displays, the tail is rotated "round the longitudinal axis and always in such a way that the upper part (= surface) faces the opponent" (Lind, 1961, p. 26); this degree of rotation varies with spreading]; bill 0–60° below horizontal.

Upright-II. Attitude upright; legs stretched; carpal joints not exposed, but wing tips slightly elevated; neck extended vertically; dorsal plumage ruffled; tail lowered and maximally spread; bill horizontal.

Forward. Attitude almost horizontal; legs not stretched; carpal joints not exposed; neck extended obliquely forward; dorsal plumage usually very ruffled; tail lowered and spread (seldom maximally); bill generally forms an angle with neck of 90°, but may be kept horizontal.

Crouch. Attitude horizontal; legs strongly bent; carpal joints slightly exposed only when dorsal plumage sleeked (it varies from ruffled to sleeked); neck withdrawn; tail may be lowered and spread (seldom maximally); bill position varies.

Tilt. Attitude tilted, with breast close to the ground; legs strongly bent; carpal joints not exposed (?); neck withdrawn; dorsal plumage sleeked; bill "most often points forward" (Lind, 1961, p. 26).

The relative frequencies of occurrence of the display types are summarized in Table I, across columns that are approximately ordered from high "attack drive" (left-most column) to high "escape drive" (right-most column). Overall, there is no striking correspondence of most display types with attack/retreat tendencies, though Forward occurred in 35% of Retreat contexts vs. only 16% of Attack contexts, and Upright-I occurred in 33% of Attack contexts vs. only 24% of Retreat contexts (based on data in Lind's Table 2). Yet Upright-II, which is similar in many components to Upright-I, is very dissimilar in distribution, occurring in 5% of Retreat contexts and 4% of Attack contexts. The heterogeneous distribution of Crouch across columns further emphasizes the complex relationship of display type to attack/retreat tendencies.

The distribution of display components shows comparably complex trends, for no component simply becomes more or less common as contexts move from Attack to Retreat (Table II). Ruffling of the dorsal plumage, for example, is about twice as common in Crouch postures during Retreat as during Attack (100 vs. 52%), but occurs in only 5% of Upright-I postures during Retreat—about a third the incidence of Upright-I during

Table I. Relative Frequency of Occurrence (in Percent) of Five Display Postures Used during Agonistic Ground Encounters by Black-tailed Godwits (*Limosa limosa*)^{a,b}

Posture	Context					
	I. Attack		II		III. Retreat	
	During	Preceding	Intermediate	Preceding	Direct orientation	Orientation away
Upright-I	25	44	34	33	18	18
Upright-II ^c	5	1	3	2	0	18
Forward	21	9	11	32	45	26
Crouch	44	41	29	26	28	38
Tilt ^d	5	6	23	6	10	0

^a Data from Table 2 of Lind (1961).

^b Social contexts are arranged from attack (left-most column) to retreat with orientation away (right-most column).

^c Termed "Hostile tail-display" by Lind (1961).

^d Termed "Tail-up" by Lind (1961).

Table II. Relative Frequency of Occurrence (in Percent) of Certain Components in Agonistic Ground Encounters by Black-tailed Godwits (*Limosa limosa*)^a

Posture	Context ^b	Display component		
		Dorsal plumage ruffled	Tail lowered and/or spread	Bill 0-30° below horizontal
Upright-I	Attack (I)	14	86	31
	Retreat (III)	5	72	76
Forward	Attack (I)	54	73	48
	Retreat (III)	86	95	0
Crouch	Attack (I)	52	67	63
	Retreat (III)	100	100	0
Tilt	Attack (I)	0	70	90
	Retreat (III)	0	38	46

^a Data from Table 3 of Lind (1961).

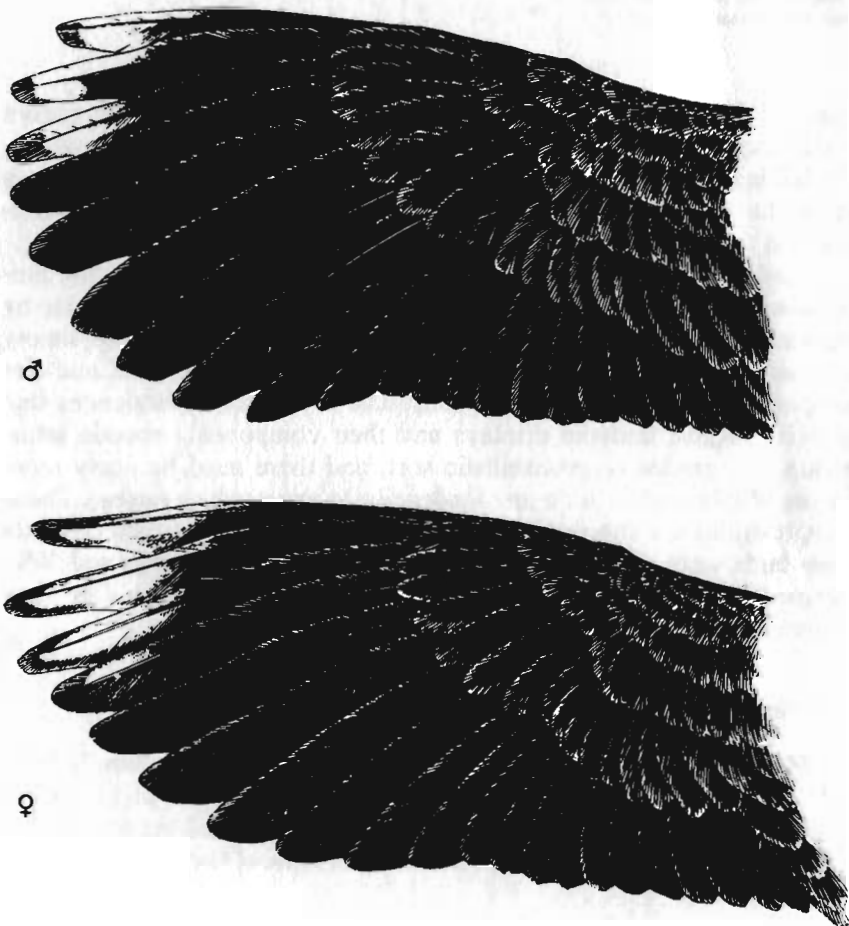
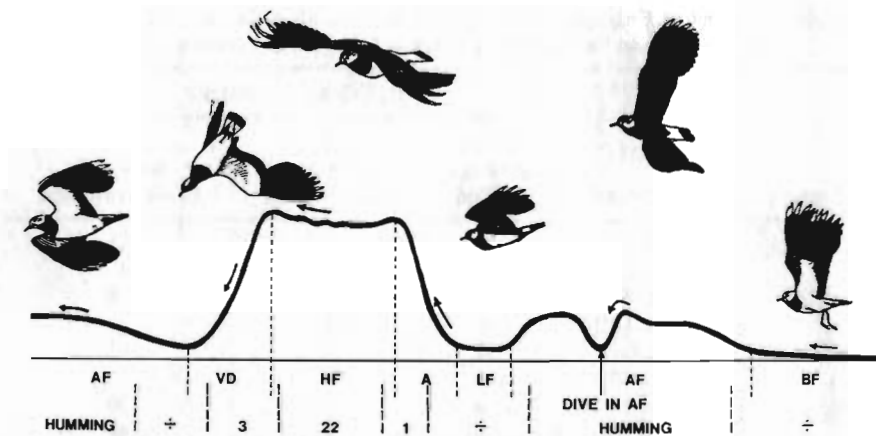
^b See column headings, Table I.

Attack. Tail lowering and/or spreading, and the position of the bill relative to the horizontal, likewise show no systematic relationship to context. The bill is held near the horizontal most often during Attack contexts in which the bird is in Forward, Crouch, or Tilt; but this strong trend is reversed for Upright-I.

Lind treats these and selected data in detail, in discussing the motivational basis for godwit displays. Here it is sufficient to summarize by emphasizing that the displays and their components do not map simply onto social contexts. Rather, each occurs in various contexts, and (for components) in various combinations. The rough correspondences that do exist suggest that the displays and their components encode information of a graded or probabilistic sort, and there must be many more classes of information than just tendencies to approach or retreat. These interpretations are supported by other of Lind's data: in Attack contexts when birds were separated by less than 2 m, Upright-I comprised 30%, Forward 20%, and Crouch 33% of the displays; at more than 4 m, they comprised 0, 6, and 65%, respectively.

2. Aerial Display of the Northern Lapwing

Many species of shorebirds have aerial displays (see Section II.E.2), and the first to be described in detail was the "ceremonial flight" of the Black-tailed Godwit (Lind, 1961). That study documented the remarkable stereotypy of the display sequence, as well as some of the external factors



that can modify its structure. More detailed research was carried out on the Northern Lapwing (*Vanellus vanellus*) by Dabelsteen (1978), along the same lines.

Aerial display in the Northern Lapwing occurs in the following main contexts: (1) apparently spontaneous; (2) in response to predators; (3) on returning to the territory (e.g., early in the season, males are absent from the territory all night, and return in the morning); (4) in response to other males; and (5) in response to females.

The basic unit of aerial display in the Northern Lapwing has several distinct phases (Fig. 6, upper part). (1) The male takes flight with slow, deep wing-beats ("butterfly flight," BF). (2) During the last few beats of BF, flight speed and wing-beat frequency increase, and the bird revolves about its long axis every four wing-beats or so. "The revolving . . . is made by one wing-beat, and takes place in the upstroke, whereas the downstroke is made with the opposite wing tip pointing downwards" (Dabelsteen, 1978, pp. 139–140). When the bird revolves, it changes course to the same side, resulting in a zigzag flight course. This display component ("alternating flight," AF) is always accompanied by "humming" sounds, made by the modified outer three (and to some extent the fourth) primaries, which vibrate during the downstroke (Fig. 6, lower part). (3) The bird stops the AF and proceeds with slow wing-beats of very small amplitude just above the ground ("low flight," LF). (4) Ascent, during the end of which motif 1 of song is uttered. (5) Following ascent, the bird flies straight in "high flight" (HF) and emits the end of motif 1 plus motif 2, and the start of motif 3 of song. Toward the end of HF, the bird revolves on its long axis so that the inclination of the wing plane exceeds 90°, and slows down during a slight rise. (6) "Vertical dive" (VD) follows HF. During one or two wing-beats following HF, the bird turns on its back with its back down more or less vertically toward the ground. During descent, the bird often makes a few wing-beats while revolving back on its long axis. VD is accompanied by motif 3 of song. Other units can follow VD.

The preceding description conceals the numerous variations that can occur. Nevertheless, there is strong sequential dependency of the components: Takeoff is followed by BF nearly 70% of the time, BF by AF

Fig. 6. (Upper) Diagram of a typical aerial display in the Northern Lapwing (*Vanellus vanellus*). BF, butterfly flight; AF, alternating flight; LF, low flight; HF, high flight; VD, vertical dive. Song consists of motifs 1, 2, and 3; "÷" = silence. See text for further details. [From Dabelsteen (1978, Fig. 1).] (Lower) Typical wing shapes of male and female Northern Lapwings, showing the sexual difference in length of the primaries, the outermost three or four of which produce the "humming" sound in the downstroke of AF. [From Glutz von Blotzheim *et al.* (1977, Fig. 54).]

Table III. Transition Matrix for Components of Aerial Display in the Northern Lapwing (*Vanellus vanellus*)^a

Preceding component	Following component							Row totals
	BF	AF	LF	A	HF	VD	Landing	
Takeoff	106	27	2	19	—	—	—	154
Butterfly flight (BF)	—	48	4	26	—	—	8	86
Alternating flight (AF)	—	—	111	157	—	—	120	388
Low flight (LF)	—	11	—	103	—	—	1	115
Ascent (A)	—	—	—	—	465	—	7	472
High flight (HF)	—	—	—	—	—	504	—	504
Vertical descent (VD)	—	299	14	38	—	—	82	433
Column totals (N)	106	385	131	343	465	504	218	2152

^a Data from Fig. 6 of Dabelsteen (1978). Certain impossible transitions are indicated by dashes.

nearly 60%, HF is always followed by VD, and so on (Table III). Much of the variation results from differences in display form according to context. For example, the number of components per flight display varies significantly according to context. Fewest components occur in displays elicited by females, and upon returning to the territory, and most occur in displays elicited by other males. The larger number of components in the latter context is accompanied by a great variety of deviations from "normal" display. For example, song motifs may be repeated or omitted, revolutions may be increased or absent, etc. In all, nearly half of the initial part of aerial display involving other males shows deviations of some sort, as compared with only 15% in displays elicited by females, and 19% in spontaneous displays. Thus, when aerial display occurs in response to other males, it is apparently less stereotyped and more frequently modified than when emitted in response to other females, or spontaneously. This tendency is clearly shown by dives, which may be oriented toward males some distance away. Then "they are performed like attack dives . . . with the ventral side turned toward the adversary, and are often repeated" (Dabelsteen, 1978, p. 164). Dives may also be oriented toward females, but "they are less violent and are rarely repeated" (Dabelsteen, 1978, p. 164). In Ascent, males often rise in one another's direction, then fly in HF parallel to or away from one another, orientations that are rarely shown to females.

The flight display of the Northern Lapwing is a complex but remarkably stereotyped sequence of optical and acoustic components. It is given only by males, so is influenced by endocrinological factors, and various of its characteristics (including overall incidence) vary according

to date, stage of the breeding cycle, weather, time of day, and other nonsocial factors (e.g., they are generally very brief in the morning). The display contains components of ritualized attack, approach, and other tendencies, and variation in underlying physiological states affects display form. Finally, variations in form result from proximate social factors. The large number of known or probable sources of variation make it likely that the communicative significance of the display and its components varies greatly for different classes of receivers and for different contexts of occurrence. In this way it resembles the agonistic ground displays of the Black-tailed Godwit.

3. Ground Display by Lekking Male Ruffs

The preceding accounts of godwits and lapwings focused on general aspects of display organization and variation, but did not consider contributions to variation by individual or class differences. One of the clearest cases where socially distinct classes of individuals exist is on leks of the Ruff. There, males fall into two classes based on their behavior and plumage: "independent" males include territorial and potentially territorial individuals, which tend to have dark or colored ruffs and ear tufts; "satellite" males are nonterritorial but often associate with residents, and tend to have white ruffs and tufts (see Fig. 2c; Hogan-Warburg, 1966; Shepard, 1975). The behavioral differences between members of these two social classes have been studied intensively by van Rhijn (1973), whose work is summarized here (see also van Rhijn, 1983).

Main behavioral units recognized by van Rhijn are shown in Fig. 7A. They are based mainly on posture, relative position of the head and bill to the body, and erection of the ruff and head tufts. These units occur with different frequencies for satellites and residents. Thus, Upright comprised about 9% of 395 postural displays by residents, but did not occur in 428 displays by satellites. Conversely, Tiptoe and Strut accounted for about 18% of satellite displays, but none of the residents' (see marginal totals, Table IV). The organization of behavioral sequences also differed strongly. Squat was followed by Forward far more often in residents than satellites, and was followed by Half-squat far less frequently (tabled figures of +75% and -71%, respectively). This difference is related to the higher frequency of occurrence of Forward in residents, particularly when satellites were present: residents spent 13% of their time in Forward when females were with them, and 34% when satellites were also present. On these sorts of evidence, van Rhijn proposed a simple model for causation of the displays (Fig. 7B). At least two variables (H, V) are needed to explain resident behavior, and at least one for satellites (and females).

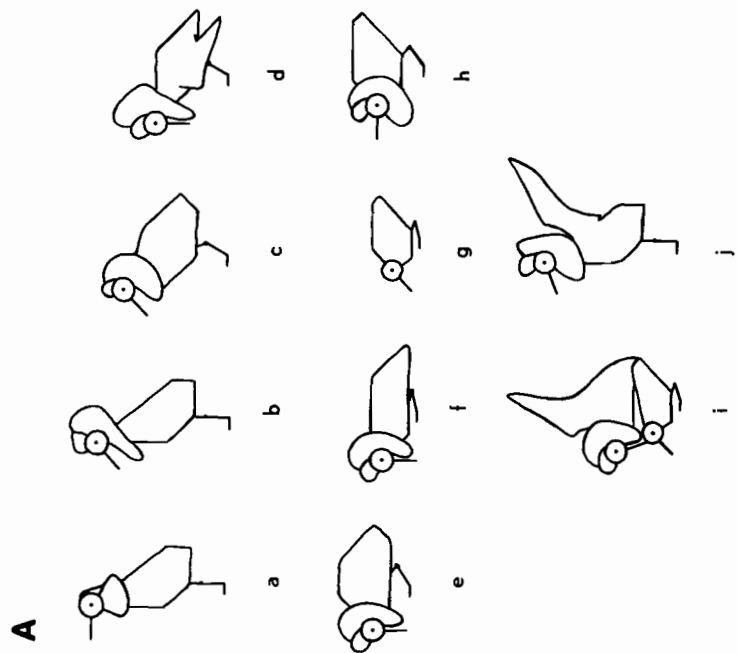


Fig. 7. (A) Major behavioral units recognized by van Rhijn in his study on Ruffs (*Philomachus pugnax*). a, Upright (upr); b, Tiptoe; c, Oblique (obl); d, Strutting; e, Half-squat (hsq); f, Squat (squ); g, Crouching; h, Forward (fow). [After van Rhijn (1973, Fig. 1).] (B) Causation and function related to major behavioral units recognized by van Rhijn. A, behavior in aggressive situations; S, behavior in sexual situations; P₁, protective behavior (flying away); P₂, protective behavior (lying flat); P₃, protective behavior (after fights). Variables H and V are postulated underlying variables. [From van Rhijn (1973, Fig. 8).]

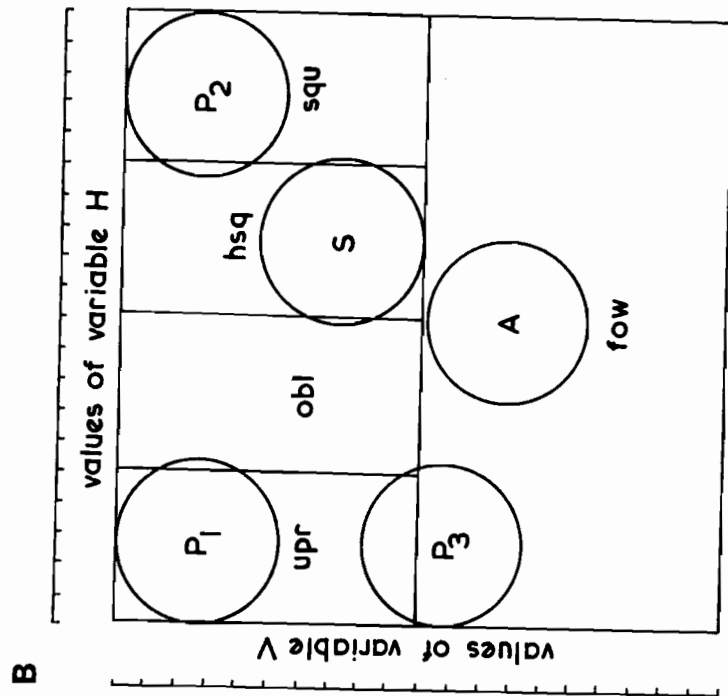


Table IV. Transition Matrix for Postural Displays of Resident and Satellite Male Ruffs (*Philomachus pugnax*) on Leks^a

Preceding component	Following component							Totals ^d
	Obl	Hsq	Squ	Fow	Upr ^b	Tip ^c	Str ^c	
Oblique (Obl)	—	-34	N	+56	(+24)	(-46)	(-1)	86, 140
Half-squat (Hsq)	-37	—	+9	+28	(+1)	(-1)	(-1)	67, 142
Squat (Squ)	-4	-71	—	+75	(N)	(N)	(N)	34, 52
Forward (Fow)	+6	-17	+5	—	(+5)	(N)	(N)	171, 4
Upright (Upr) ^b	(+81)	(N)	(N)	(+19)	—	—	—	37, 0
Tiptoe (Tip) ^c	(-94)	(-1)	(-1)	(N)	—	—	(-4)	0, 83
Strutting (Str) ^c	(N)	(-57)	(-29)	(N)	—	(-14)	—	0, 7
Totals ^d	88, 143	80, 129	94, 80	102, 3	31, 0	0, 67	0, 6	395, 428

^a Data after Table 1 of van Rhijn (1973). Each cell entry shows the percent occurrence of a particular transition, for residents relative to satellites, based on row totals. For example, the Obl-Hsq transition occurred 34% less in residents than in satellites, and the reverse (Hsq-Obl) occurred 37% less (N = no observations).

^b Upr was given only by resident males, in the sample.

^c Tip and Str were given only by satellite males, in the sample.

^d Totals are shown first for residents, then for satellites (total samples are thus 395 and 428, respectively).

Satellite behavior is intermediate between that of residents and females, and two unique components to it (Tiptoe, Strut) were judged to be similar to the more generalized displays, Upright and Oblique.

The general significance of van Rhijn's study lies in the documentation of substantial communicative differences among social classes, differences that can be explained by a model that assumes a common causal structure. In addition, it is unnecessary and misleading to simply label the differences as due to variation in "aggressiveness," "submissiveness," etc.

C. Acoustic Communication

1. Review

Vocal and nonvocal sounds of shorebirds range from soft, short-range calls like those between adults and young, to loud nuptial aerial song that may carry for miles. Such variation even occurs within species so it is perhaps not surprising that few comprehensive studies on acoustic communication in shorebirds have been made (Table V). In addition, most studies have focused on a particular aspect of communication. In the American Woodcock (*Scolopax minor*), for example, nearly all research

Table V. Summary of Available Information on Sound Analyses in Shorebirds^a

Family and species ^b	Comments ^c	Analysis ^d	References ^e
Burhinidae (9)			
<i>Burhinus oedicnemus</i>	B, DD	s	10
<i>B. senegalensis</i>	B, D	s	10
Charadriidae (63)			
<i>Anarhynchus frontalis</i>	B, DD	s	54
<i>Charadrius alexandrinus</i>	B, DD	s	10, 16
<i>Ch. bicinctus</i>	B, DDD	s	54
<i>Ch. dubius</i>	A, B, DDD	s	10; 16, 64
<i>Ch. hiaticula</i>	A, B, DD	s	10; 16, 63, 66, 67
<i>Ch. montanus</i>	B, C, DDD	s	18, 44
<i>Ch. morinellus</i>	B, D	s	10
<i>Ch. novaeseelandiae</i>	B, C, DDD	s	53
<i>Ch. obscurus</i>	B, DD	s	54
<i>Ch. semipalmatus</i>	D	s	44
<i>Ch. vociferus</i> ^f	B, C, DDD	s x	10, 19, 21, 50, 52
<i>Chettusia</i> (= <i>Vanellus</i>) <i>leucura</i>	B, D	s	10
<i>Ch.</i> (= <i>Vanellus</i>) <i>gregaria</i>	D	s	10
<i>Hoplopterus</i> (= <i>Vanellus</i>) <i>spinosus</i>	B, D	s	10
<i>Pluvialis apricaria</i>	B, D	s	10
<i>P. dominica</i>	D	s o x	19, 44, 66
<i>P. squatarola</i>	A, B, D	s	10, 44, 64
<i>Vanellus chilensis</i>	D	s	44
<i>V. vanellus</i>	A, B, DD	s	10, 11, 72
Chionididae (2)	No published analyses	—	—
Dromadidae (1)	No published analyses	—	—
Glareolidae (16)			
<i>Cursorius cursor</i>	D	s	10

^a Only species whose sounds have been analyzed graphically in some way are included. See the text for discussion.

^b Number of species in each family is listed in parentheses.

^c A = analytical; B = with behavioral observations; C = comprehensive survey; D = descriptive (D = few calls, . . . , DDD = many calls); E = experimental.

^d s = sound spectrograms; o = oscillograms; p = power spectra; a = amplitude profiles; x = other.

^e 1, Adret (1982); 2, Ailes (1976); 3, Baker (1974); 4, Baker (1982); 5, Beightol (1972); 6, Beightol and Samuel (1973); 7, Bourgeois (1977); 8, Bourgeois and Couture (1977); 9, Bursian (1971); 10, Cramp (1983); 11, Dabelsteen (1978); 12, Dowsett *et al.* (1977); 13, Ferdinand (1966); 14, Forsythe (1967); 15, Forsythe (1970); 16, Glutz von Blotzheim *et al.* (1975); 17, Glutz von Blotzheim *et al.* (1977); 18, Graul (1974); 19, Greenewalt (1968); 20, Grudzien (1976); 21, Heckenlively (1972); 22, Heidemann and Oring (1976); 23, Hirons (1977a); 24, Hirons (1977b); 25, Holmes (1973); 26, Howe (1972); 27, Howell (1979); 28, Jenni *et al.* (1974); 29, Knudson (1972); 30, Kroodsmas and Miller (1983b); 31, Labutin *et al.* (1982); 32, Lemnell (1978); 33, Mace (1981); 34, Mal'chevskii (1981); 35, Marström (1974); 36, Miller (1977); 37, Miller (1979a); 38, Miller (1979b); 39, Miller (1979c); 40, Miller (1982); 41, Miller (1983a); 42, Miller (1983b); 43, Miller (1983c); 44, Miller (this chapter); 45, Miller and Baker (1980); 46, Miller *et al.* (1983); 47, Myers (1982); 48, Nemetschek (1977); 49, Nethersole-Thompson and Nethersole-Thompson (1979); 50, Nol (1980); 51, Oring (1968); 52, Phillips (1972); 53, Phillips (1977); 54, Phillips (1980); 55, Reddig (1978); 56, Samuel and Beightol (1972); 57, Samuel and Beightol (1973); 58, Skeel (1976); 59, Skeel (1978); 60, Sordahl (1979); 61, Sordahl (1980); 62, Thönen (1968); 63, Tikhonov and Fokin (1979); 64, Tikhonov and Fokin (1980); 65, Tikhonov and Fokin (1981a); 66, Tikhonov and Fokin (1981b); 67, Tikhonov and Fokin (1982); 68, Veprintsev and Zablotskaya (1982); 69, Warham and Bell (1979); 70, Weir (1979); 71, Weir and Graves (1982); 72, Wollemann (1978); 73, Wollemann and Olasz (1977); 74, Zvonov and Tikhonov (1981).

^f Additional sound spectrograms are in Gaunt (1983b; *Ch. vociferus*) and Mal'chevskii (1982; *S. rusticola*).

Table V. (Continued)

Family and species ^b	Comments ^c	Analysis ^d	References ^e
<i>Glareola pratincola</i>	D	s	10
<i>G. nordmanni</i>	D	s	10
<i>Pluvianus aegyptius</i>	B, C, DD	s	10, 27
<i>Rhinoptilus cinctus</i>	D	s	12
Haematopodidae (9)			
<i>Haematopus ater</i>	A, B, D	s	37, 44, 45
<i>H. chathamensis</i> (= <i>H. unicolor</i>)	B, D	s	3
<i>H. leucopodus</i>	B, D	s	45
<i>H. ostralegus</i>	A, B, DD	s	3, 10, 63–65, 67
<i>H. palliatus</i>	B, D	s	44, 45
<i>H. unicolor</i>	B, D	s	3
Ibidorhynchidae (1)	No published analyses	—	—
Jacanae (8)			
<i>Jacana spinosa</i>	A, B, C, DDD	s	28, 33
Pedionomidae (1)	No published analyses	—	—
Pluvianellidae (1)	No published analyses	—	—
Recurvirostridae (13)			
<i>Himantopus himantopus</i>	B, DD	s	10, 72
<i>H. mexicanus</i>	B, D	s	61
<i>Recurvirostra americana</i>	B, D	s	61
<i>R. avosetta</i>	A, B, DD	s	1, 10, 63, 64, 67, 73
Rostratulidae (2)	No published analyses	—	—
Scolopacidae (90)			
<i>Actitis hypoleucos</i>	A, B, DD	s	10, 17, 65, 66
<i>A. macularia</i>	B, D, E	s	10, 22, 29, 44
<i>Arenaria interpres</i>	A, B, D	s	10, 63–65, 67
<i>Bartramia longicauda</i>	B, D	s	2, 10, 17, 44
<i>Calidris alba</i>	B, DD	s	10, 16
<i>C. alpina</i>	A, B, DD	s o p x	4, 10, 16, 19, 42, 44
<i>C. canutus</i>	B, DD	s	10, 16
<i>C. ferruginea</i>	B, D	s	10, 16
<i>C. fuscicollis</i>	B, D	s	16, 44
<i>C. himantopus</i>	B, D	s o p	29, 42
<i>C. maritima</i>	B, DD	s	10, 16, 44
<i>C. mauri</i>	B, D	s	25
<i>C. melanotos</i>	A, B, D	s	16, 47, 64
<i>C. minuta</i>	B, DD	s	10, 16, 65, 66
<i>C. minutilla</i>	A, B, D	s o p	10, 29, 36–39, 41, 43, 44
<i>C. pusilla</i>	B, D	s o p	42, 44
<i>C. temminckii</i>	A, B, DD	s	10, 16, 64, 66
<i>Catoptrophorus semipalmatus</i>	B, C, DDD	s	60
<i>Coenocorypha aucklandica</i>	B, D	s	69
<i>Gallinago gallinago</i>	A, B, DD, E	s	10, 17, 20, 55, 62
<i>G. media</i>	A, B, D	s	10, 13, 17, 32
<i>G. stenura</i>	B, D	s	10, 31
<i>Limicola falcinellus</i>	B, D	s	10, 16
<i>Limnodromus griseus</i>	B, D	s o	19, 43, 46

(Continued)

Table V. (Continued)

Family and species ^b	Comments ^c	Analysis ^d	References ^e
<i>Limosa lapponica</i>	B, DD	s	10, 17✓
<i>L. limosa</i>	B, DD	s	10, 17, 73
<i>Lymnocyptes minimus</i>	B, D	s	10
<i>Numenius americanus</i>	B, C, DDD	s o	14, 15, 19, 60
<i>N. arquata</i>	B, DDD	s	10, 17
<i>N. minutus</i>	B, C, DD	s	30, 68
<i>N. phaeopus</i>	B, C, DDD, E	s	10, 17, 58, 59
<i>Phalaropus fulicarius</i>	B, DD	s	10, 44
<i>Ph. lobatus</i>	B, D	s	10
<i>Ph. tricolor</i>	B, C, DDD	s	26
<i>Philomachus pugnax</i>	B, D	s	10, 66
<i>Scolopax minor</i>	A, B, DDD	s o p x	5-8, 19, 40, 56, 57, 70, 71
<i>S. rusticola</i> ^f	A, B, D	s o a	10, 17, 23, 24, 34, 35, 48
<i>Tringa erythropus</i>	B, DD	s	10, 17
<i>T. flavipes</i>	B, D	s o	10, 19, 44
<i>T. glareola</i>	A, B, DD	s	10, 17; 64, 66
<i>T. (= Heteroscelus) incanus</i>	D	s	44
<i>T. melanoleuca</i>	D	s o x	19
<i>T. nebularia</i>	A, B, DDD	s	10, 17, 44, 49, 65, 66, 74
<i>T. ochropus</i>	B, C, DDD	s	10, 17, 51, 65, 66
<i>T. solitaria</i>	B, C, DDD	s	10, 51
<i>T. stagnatilis</i>	B, DD	s	10, 17
<i>T. totanus</i>	B, DDD	s	10, 17, 72, 73
<i>Xenus cinereus</i>	B, D	s	10
Thinocoridae (4)	No published analyses	—	—

has concerned individuality in the "peent" call of males as a tool facilitating estimation of population size (Table V references; see also Thomas and Dilworth, 1980). Other common, widespread, and easily studied species remain unstudied or understudied. There has been no general study of acoustic signaling in the Common Snipe (*Gallinago gallinago*), an abundant breeding species in Europe, Asia, and North and South America; none of the nine species of oystercatchers has been adequately studied, despite their wide geographic distribution, conspicuousness, and approachability; and no repertoires of calidridine sandpipers (Holarctic, 24 species) have been well documented. Sound analyses are completely unavailable for certain key taxa, as well: Chionididae, Dromadidae, Ibi-dorhynchidae, Pedionomidae, Pluvianellidae, Rostratulidae, and Thino-coridae. Finally, relatively few studies have been quantitative, only one has involved experimentation (playback experiments; Refs. 22, 29), and none has used captive birds.

In light of the major gaps in our knowledge, it would be premature to review many facets of acoustic communication by shorebirds, but certain widespread trends in structural characteristics are suggested by available studies (see references in Table V). Many sounds are long and of narrow bandwidth, and are spectrally simple with weak or no overtones and little frequency modulation (Figs. 8, 9, 12, 14, 17). Many kinds of sounds, including those just mentioned, exhibit sudden frequency shifts, with the call continuing unbroken at much lower or higher frequency (Figs. 8E, F, 12A, 14). Simple harmonic overtones occur commonly (Figs. 8C, E, I-L and 17E; see Gaunt, 1983a). Single brief calls are widespread; these often have simple patterns of frequency and amplitude modulation (e.g., simple increase then decrease), and are highly variable even within species. Such brief sounds, plus various sorts of trills, are abundant in shorebirds (Figs. 8, 12, 17). Structurally complex sounds with strong sequential organization occur in many species, and are equivalent to primary song of many oscines in their beauty and presumed functions. No song repertoires have been reported for any species of shorebird.

It is not possible to judge how closely the structure or sequential organization of shorebird sounds matches Morton's (1977, 1982) generalizations about links between behavioral tendencies and acoustic morphology ("motivation-structural rules"). However, the varied structure of calls uttered by shorebirds even in a single context, such as when a potential predator is near their brood, suggests that any correspondence is likely to be complex (Fig. 8; see also Sections II.C.2 and II.E.1). For example, brief calls occur in most species, "noisy" (unpatterned broadband) calls occur in others, and strong rhythmic frequency modulation characterizes some call types; but there are no obvious common characteristics. Similarly, the structure of soft calls by adult birds brooding young or tending them at close quarters varies greatly among species (Fig. 17; see Section II.E.1). The relationship of sound features to the physical and social environment is considered in Section II.D.

2. Repertoire Characteristics and Functional Classes

Characterization and classification of signals are essential preliminary stages in the study of communication, regardless of how much subsequent refinement may be necessary. Signals are usually classified within a structural-functional framework simultaneously. No particular conceptual or theoretical significance can be attached to such a classification, however, unless there is prior reason to expect structural and functional classes to correspond. Correspondence is probably closest between physical characteristics of certain stereotyped, long-distance sounds, for which

adaptations to combat environmental degradation and frequency-dependent attenuation are likely. Such a generalization applies to many vocalizations used by males to attract females or to deter competitors of the same sex. Here, sound classes are often discrete and context-specific, but most sounds defy simple structural or functional classification, as can be illustrated by a few examples.

Oring (1968) studied two species of Tringini, the Green Sandpiper (*Tringa ocrophus*) of the Palearctic and the Solitary Sandpiper (*T. solitaria*) of the Nearctic (see also Oring, 1973). Based on call structure and use, Oring identified seven sound types common to adults of the two species, plus three more for juvenile *T. ocrophus* and six for juvenile *T. solitaria*. The juvenile sounds varied greatly, and their classification was more difficult than for adult sounds. The main functional classes for the latter were sexual-agonistic (two "song" types, plus "epigamic chatter" and "epigamic long whistle"), "alarm-attack," "alarm-flee," and "contact." The general contexts of occurrence for the latter three are suggested by Oring's names for them.

A significant point that emerges from Oring's study is that apparently simple sound types can serve more than one function, and several sound types can overlap in apparent functions. Thus, "alarm-flee" calls are given by either species when danger is imminent, but also "when a bird takes off spontaneously . . . as a bird flies by or from its nest prior to the start of incubation . . . and . . . when a strange pair attempts to establish itself in the territory of another pair" (Oring, 1968, p. 409). In the first context, there is overlap with the "alarm-attack" call, which, however, is used "when danger is apparent but not imminent" (Oring, 1968, p. 406) as well as in other, very different contexts.

Sordahl's (1979) fine study of Willet (*Catoptrophorus semipalmatus*) vocalizations revealed similar trends. "Thus *kyah-yah* serves as a greeting and contact call, an indication of flight intention, and a flight enticement call" (Sordahl, 1979, p. 563). At the other extreme, Sordahl heard two call types ("klik" and "dik" calls) only during copulation attempts. In the Whimbrel (*Numenius phaeopus*), "low trill calls" are used commonly by both sexes, as when gliding in to land, by incubating birds calling in response to their mates, and during changeovers at the nest (Skeel, 1976, 1978; see also Cramp, 1983). This species also has at least three calls used in response to potential predators: "short predator alarm trill," "long predator alarm trill," and "scolding trill call" (Skeel, 1976, 1978).

Examples of multiple functions of single sound classes and common functions by different sound classes could be multiplied (e.g., Adret, 1982; Graul, 1974). Some of the apparent problems can be resolved by studying the structure and function of calls very closely. Thus, the "alarm-flee"

call of the Green Sandpiper had a median number of three repetitions when an adult or its brood was directly threatened, but only one in response to a strange intruding pair (Oring, 1968), suggesting that finer classification using structural features might yield closer correspondence with function. Similarly, Sordahl (1979) noted that "kleep" calls of Willets in response to predators tended to occur at a more rapid rate during aerial than terrestrial harassment. In the Spotted Sandpiper (*Actitis macularia*), "song" used in aggressive contexts is of higher amplitude, higher frequency, and faster tempo than in reproductive contexts (Heidemann and Oring, 1976). Conversely, Skeel (1976, 1978) points out that the Whimbrel's "short predator alarm call" is used only in chasing aerial predators, indicating that greater attention to contextual features can improve understanding of structural and functional correspondence.

Elaboration of classification schemes using finer structural and functional criteria will inevitably lead to improved congruence between them. However, the generality of such schemes decreases correspondingly, and the crucial questions about why general structural classes span diverse functions, and why general functions involve more than one sound type, become more remote. A solution to this problem can come from determining which factors are held in common by different contexts, along lines suggested by Smith (1977). Why should incubating Eurasian Avocets utter rhythmic call series when another bird, be it a conspecific or non-predatory heterospecific, passes or flies over the nest (Adret, 1982)? The appropriate focus in assessing the message in the call is at a level that merges all contexts, so that common features can be extracted. Communication is egocentric, according to Smith's paradigm, so that a caller signals something about its behavioral state, or its readiness or likelihood to engage in various behaviors. Often this information indicates a bird's inclination to locomote, interact, etc.—information that can be appraised and placed in appropriate contexts by receivers in imbuing the messages of signals with more specific and specialized meanings. An example using calls of adult Calidridini attending their young can illustrate this approach.

Various species of calidridines use two distinct classes of sounds when they are attending their broods, and are approached by humans (and presumably by other kinds of predators). These are: (1) a relatively brief, frequency-modulated call; and (2) a trill. The two call types are emitted in similar circumstances in all the species shown in Fig. 8 (I–L): trills are most common on the ground, or at a great distance from the nest or brood; brief frequency-modulated calls are most commonly uttered as a parent flies toward or near an intruder, or when close to the nest or brood. The latter call type is also the one normally given when a parent jumps into flight. In general, then, the call types reflect a parent's "excitement."

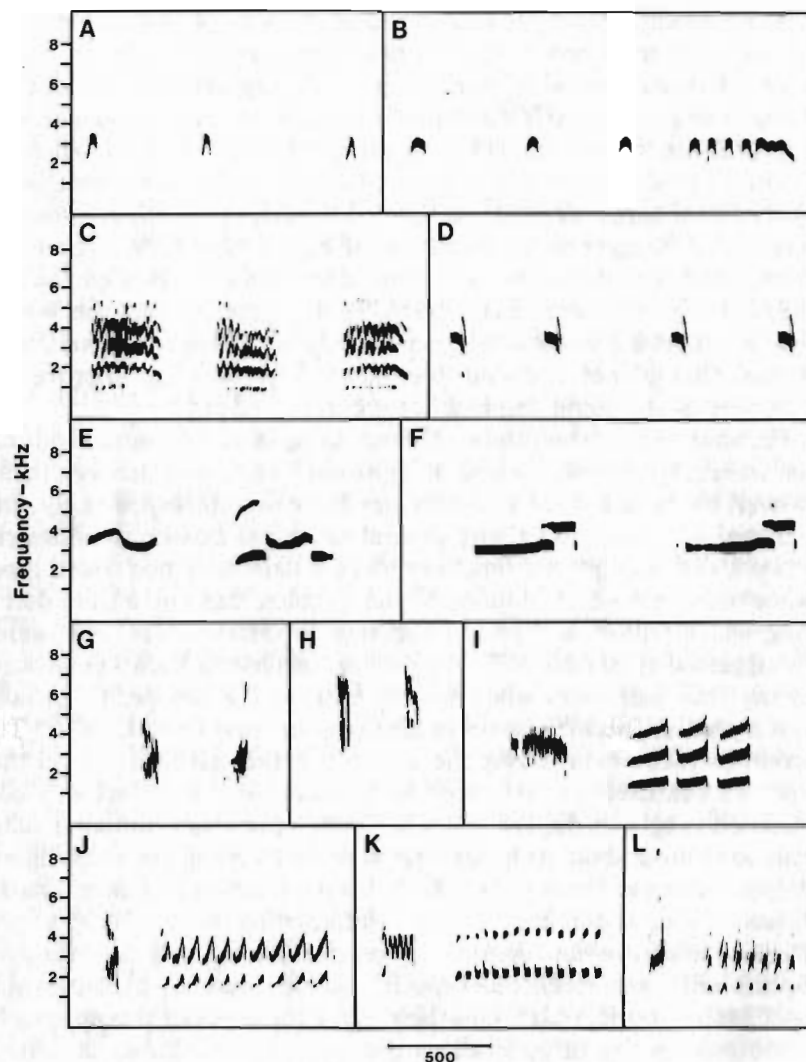


Fig. 8. Sound spectrograms of calls by adults near their nests or young, in response to human intrusion [to *Larus* gull in (E)]. (A) Sequence of ground calls by American Oystercatcher (*Haematopus palliatus*; Punta Tombo, Argentina). (B) Sequence of ground calls by Blackish Oystercatcher (*Haematopus ater*; Punta Tombo, Argentina). (C) Sequence of flight calls by Southern Lapwing (*Vanellus chilensis*; near Rio Gallegos, Argentina). (D) Sequence of ground calls by Semipalmated Plover (*Charadrius semipalmatus*; near Churchill, Manitoba). (E) Two flight calls by Black-bellied Plover (*Pluvialis squatarola*; Coats Island, Northwest Territories). (F) Two ground calls by American Golden Plover (*Pluvialis dominica*; near Churchill, Manitoba). (G) Two flight calls by male Red Phalarope (*Phalaropus fulicarius*; Coats Island, Northwest Territories). (H) Ground and flight calls by female White-rumped

The two call types are thus associated predictably with locomotory mode, and provide reliable information about a signaler's ongoing and (short-term) future behavior. This is a fairly simple outline of what actually goes on, which I have studied intensively only in the Least Sandpiper. In that species, the relative frequency of occurrence of trills and short calls changes even as a bird alters direction in flying toward or away from an intruder, and structurally intermediate sounds to trills and short calls occasionally occur. The calls are given in response to human intruders, to dogs, horses, and gulls—in brief, to almost any large animal whether or not it is a potential predator. It seems most straightforward to attempt to characterize these sound types functionally by the contexts in which they occur, in respect to the caller's behavior, and to determine the main classes of receivers (chicks?, mate?, predator?, etc.). A striking feature of this communication system is how individually distinctive different birds are, both in the physical characteristics of their calls and in how often the two types are used. One male I studied rarely uttered trills, and another almost never gave short sounds; individuality would thus seem to be a crucial part of context when receivers evaluate meaning in such a system of sounds.

Smith's approach is useful in specifying a repeatable, objective method for determining many kinds of information that are available to receivers, and it avoids interpretive terms like "mobbing sounds," "alarm calls," "warning calls," etc. In our present state of knowledge, the approach does not fully explain the existence of two sound types in the contexts outlined, which also occur in the distantly related Red Phalarope (*Phalaropus fulicarius*; Fig. 8G), several oystercatcher species (Fig. 8B; Miller and Baker, 1980), Black-winged Stilt (Wollemann, 1978), and Eurasian Avocet (Adret, 1982), but apparently not in the closely related White-rumped Sandpiper (Fig. 8H), or in Charadriidae (Fig. 8C–F) (also see Oring, 1968; Skeel, 1976, 1978, Sordahl, 1979). *A priori*, it would seem as reasonable for "design" of such a communication system to encode information in graded features (as in Charadriidae?), rather than in different call types, especially as grading is apparently built into many of

Sandpiper (*Calidris fuscicollis*; Coats Island, Northwest Territories). (I) Two calls (not in sequence) illustrating two call types in Dunlin (*Calidris alpina*; near Churchill, Manitoba). (J) Two calls (not in sequence) illustrating two call types in Semipalmated Sandpiper (*Calidris pusilla*; Coats Island, Northwest Territories). (K) Two calls (not in sequence) illustrating two call types in Least Sandpiper (*Calidris minutilla*; Sable Island, Nova Scotia). (L) Two calls (not in sequence) illustrating two call types in Purple Sandpiper (*Calidris maritima*; Coats Island, Northwest Territories).

Analyzing filter bandwidth throughout, 300 Hz. Time marker is in msec.

these sound types anyway (see remarks above about the Willet's "kleep" call).

Because of the complexities surrounding congruence between structure and function, and because our current knowledge is so meager, it seems pointless to attempt any interpretive synthesis of repertoire size in shorebirds at present. In addition, studies to date suggest that complete repertoires have not been documented for many species, if any: why should juvenile Solitary Sandpipers have twice as many call types as juvenile Green Sandpipers (Oring, 1968), or young Long-billed Curlews (*Numenius americanus*) have twice as many as young Whimbrels (Forsythe, 1967, 1970; Skeel, 1976, 1978)? Why should adults of a highly visual, colonial species like the Eurasian Avocet have 10 distinct sound classes in the perinatal phase alone, while cryptic, dispersed breeders like Whimbrels have the same number for the entire breeding period (Adret, 1982; Skeel, 1976, 1978)? And why should Common Greenshank (*Tringa nebularia*) chicks have at least 10 structurally different sound types, when Willet chicks have only one (Nethersole-Thompson and Nethersole-Thompson, 1979; Sordahl, 1979)? These comments are not meant as criticism, but only to stress the inadequacy of current documentation; it is not surprising that the most diverse repertoire known (several times the size of any other) belongs to the most intensively studied species (Nethersole-Thompson and Nethersole-Thompson, 1979).

3. Graded Communication

An area crucial to further understanding of vocal communication in shorebirds concerns structural variation within sound classes (Klingholz and Meynhardt, 1979; Maier, 1982; Marler, 1976). Is such variation disorderly and meaningless, or does it encode slight shifts in probabilities of subsequent behavior, or reveal minor behavioral changes in signalers? An example of variation of this nature is in the long rhythmic series of simple calls that characterize aerial displays of unpaired Least Sandpipers (Miller, 1979a, 1983a). Major breaks in the rhythm of calling usually co-occur with obvious structural deviations of calls (Fig. 9). More subtle, systematic variations occur during unbroken rhythms, including a correlation between call duration and the presence of frequency modulation of the carrier frequency (Fig. 9A). The regularity of such trends may impart communicative significance to them, but whether they are significant or simply adventitious remains speculative. The bounds of such structural variation, their relationship to signaler behavior, and their meaning to receivers are badly in need of research (see Section II.B.2).

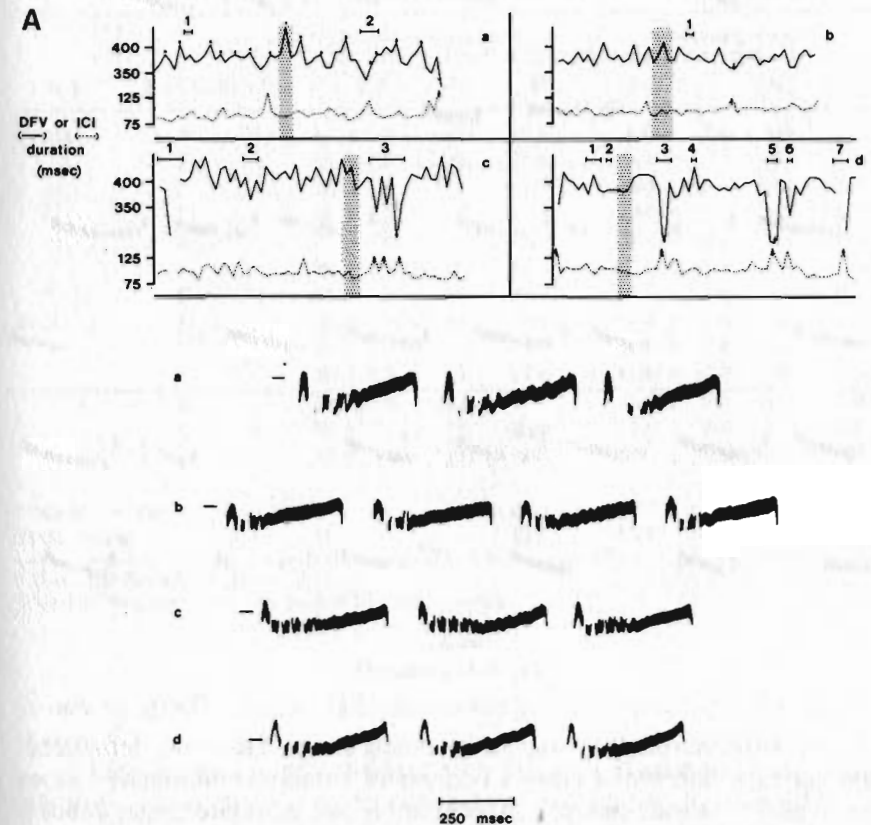


Fig. 9. Sequence plots of portions of call sequences in aerial displays of male Least Sandpipers (*Calidris minutilla*), illustrating variations in form and duration of components. DFV, display flight vocalization; ICI, intercall interval.

(A) Sequence plots and typical elements. The stippled portion in each of the four upper diagrams covers the call sequences illustrated in the lower figures. The numbers in each plot refer to the segments shown in (B). Downward- and upward-pointing arrows indicate that calls were too brief, or intervals between calls too long, respectively, to plot. In the record for male *a*, each call with conspicuous frequency modulation (FM) of the long terminal portion is signified by a small "x" above the line for DFV durations. Examples of FM are shown in the short sequences below: see *a*—second, *b*—third (weakly, second), and *c*—second.

(B) Segments of calling sequences for the males referred to in (A). The letters refer to those males' records, and the numbers correspond to those in the plots in the upper part of (A).

This figure is of tracings of the first harmonic overtones of the calls. Analyzing filter bandwidth, 300 Hz. Frequency markers, 3 kHz.

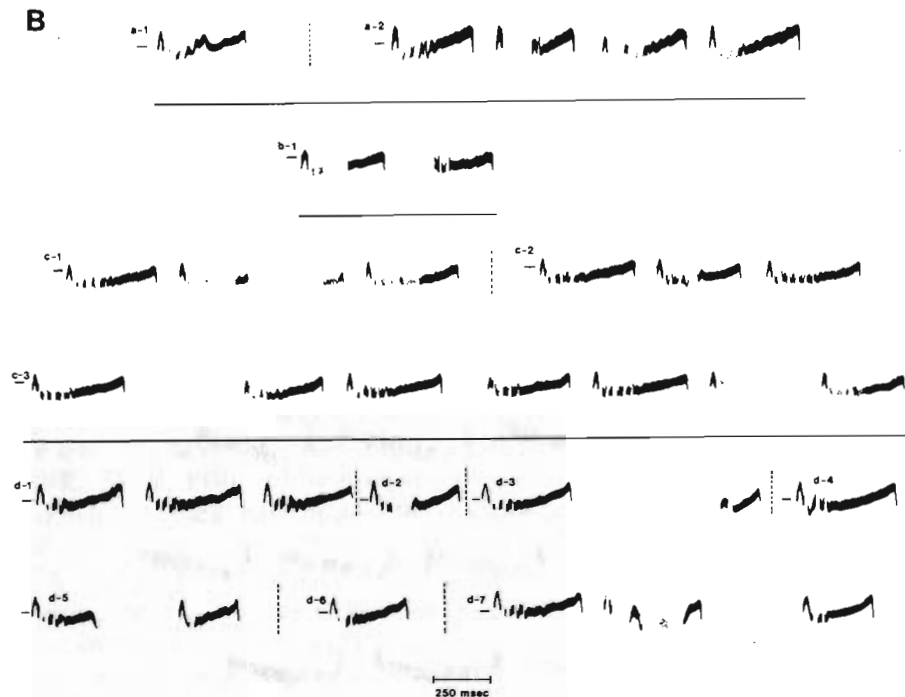


Fig. 9. (Continued)

Acoustic morphology also varies among sound classes (by definition), and varies within sound classes because of numerous proximate causes (anatomical, neural, endocrinological, etc.) and correlates (age, gender, individuality, etc.). Extensive structural intergradation of sounds is often referred to as "grading," a term lacking adequate definition or use. Consider the assignment of a sample of sounds, from a population or species, into different sound classes. If classes emerge from the study only with difficulty, often because of the presence of numerous sounds of intermediate form, the system is often considered to be graded. If classes are readily established, the repertoire can be considered as relatively "discrete" (the term generally used as an antonym to "graded"), but variation within classes becomes of interest, and those classes with high levels of variation are relatively graded. Yet within sound classes we must recognize many important sources of variation that vary systematically, including age, gender, individuality, breeding status, etc. We could therefore focus on, say, a particular sound type emitted by breeding males, and assess the extent to which it is graded. Finally, characteristics of sound types will exhibit different levels of variation, so it becomes nec-

Table VI. Variation in "Contact Ernts" of Wilson's Phalarope (*Phalaropus tricolor*) by Gender, Individual Identity, and Acoustic Dimension^a

Sex	Individual	Duration (msec)			Frequency ^b (Hz)		
		$\bar{Y} \pm S.E.$	(N)	C.V.	$\bar{Y} \pm S.E.$	(N)	C.V.
Female	A	44 ± 3.2	(8)	20.9	930 ± 17.0	(8)	5.2
	B	36 ± 4.0	(5)	24.8	910 ± 12.5	(5)	3.0
	C	38 ± 2.6	(12)	23.1	1000 ± 6.4	(12)	2.2
	D	46 ± 2.2	(5)	11.9	1040 ± 22.4	(5)	4.8
	E	65 ± 5.0	(4)	15.4	930 ± 12.0	(4)	2.5
	F	36 ± 8.5	(5)	31.2	960 ± 12.5	(5)	2.9
	G	60 ± 2.3	(9)	20.4	1000 ± 1.0	(9)	0.3
Male	H	54 ± 1.8	(8)	9.6	1080 ± 32.0	(4)	5.9
	I	48 ± 2.5	(4)	10.5	1070 ± 22.0	(4)	4.2
	J	38 ± 2.3	(9)	17.6	1110 ± 11.7	(9)	3.2
	K	39 ± 2.0	(12)	17.1	1110 ± 9.5	(12)	3.0
	L	50 ± 3.8	(7)	20.0	1240 ± 9.8	(7)	2.1
	M	30 ± 0.0	(5)	0.0	1230 ± 18.3	(5)	3.3
Female average		46		21.1	967		3.0
Male average		43		12.5	1140		3.6

^a Data after Table 12 of Howe (1972).

^b Maximal frequency estimated on first harmonic overtone.

essary to specify the acoustic dimension in which grading is being estimated.

These points can be illustrated with Wilson's Phalarope (*Phalaropus tricolor*), acoustic signaling in which has been studied by Howe (1972). One call type used over short distances, the "Contact Ernt," varies substantially among individuals and between sexes, and varies much more in duration than in frequency (Table VI). Duration of this call type shows greater variation within individual females (average C.V. = 21) than males (average C.V. = 13), and maximal call frequency is substantially higher in males than females (in keeping with the smaller size of males in this species). Clearly it is necessary to ask quite specific questions about components of variation in such data; there is no single "natural" level at which grading can be assessed.

The concept of structural grading is most usefully applied to two distinct levels of syntactic analysis: (1) the entire sound communication system of a species and (2) in reference to emissions of individual animals. The former is of particular interest in ultimate levels of explanation and the latter at proximate levels, especially with regard to the nature of the communication process and perception by receivers (e.g., do receivers

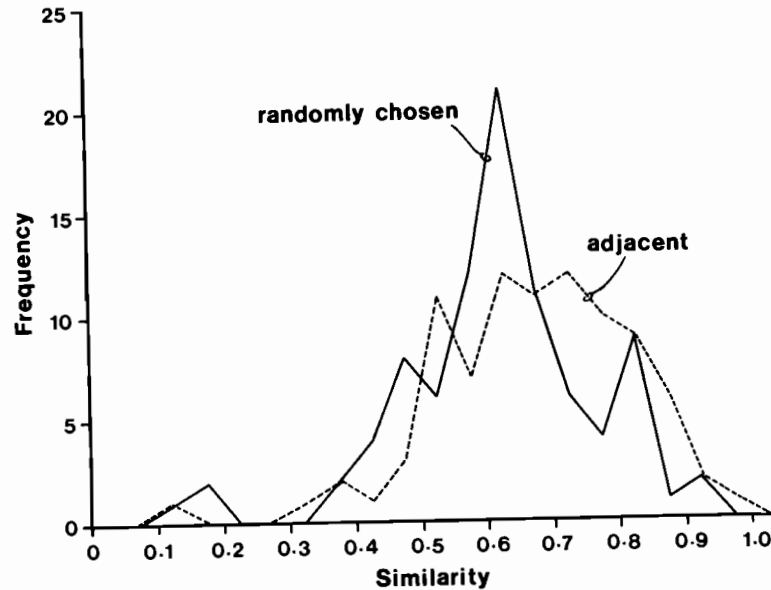


Fig. 10. Frequency polygons for similarity values between adjacent and randomly chosen calls of Blackish Oystercatcher (*Haematopus ater*) disturbed by me near its nest [After Fig. 5 of Miller (1979c)].

perceive and respond to slight variants in a continuously varying fashion?). In terms of individual emissions, there are two logical extremes to structural grading: (1) consecutive sounds are very similar to one another, and less similar to sounds separated by greater intervals; and (2) morphological similarity of sounds occurs at random, in the sense that there is no tendency for consecutive sounds to be more similar to one another than to sounds uttered at other times. These two extremes can be referred to as systems of "adjacent" and "nonadjacent" or "separate" grading, respectively (Marler, 1976; Marler and Tenaza, 1977). Most or all systems fall between the logical extremes. For example, nesting Blackish Oystercatchers (*Haematopus ater*) utter simple "alarm" calls at irregular intervals at the approach of a human (Fig. 8B; Miller, 1979c; Miller and Baker, 1980). Consecutive calls are significantly more similar to one another than are calls sampled at random from the same sequence (Fig. 10; Miller, 1979c). Such a trend is probably widespread, and results from common causation shared by consecutive calls, as well as the likelihood of the stimulus situation being similar for them. Nonadjacent grading is probably uncommon for converse reasons, and also because accurate

Table VII. Summary of Chosen Variables That Differ Significantly between "Repeated-Note Calls" (RNCs) and "Note-Group Calls" (NGCs) of the Northern Jacana (*Jacana spinosa*)^a

	RNCs	NGCs
Minimal frequency of the dominant frequency band (kHz)	3.92	4.17
Highest detectable frequency (kHz)	7.38	7.18
Bandwidth of the dominant frequency band (kHz)	2.14	1.73
Duration of individual element (msec)	81.9	32.7
Total number of elements	12.3	72.2
Relative loudness (arbitrary scale)	3.1	1.6

^a Data from Table 22 of Mace (1981).

rapid responses by receivers must be quite difficult in the absence of immediate standards for comparison.

Acoustic signals of the Northern Jacana provide an example of the application of the concept of grading at the levels of syntactics, semantics, and pragmatics. Mace (1981) has described and exhaustively quantified acoustic signals of the species, a polyandrous resident of the neotropics that calls frequently (4–7 calls/hr by breeding birds). Most calls consist of brief broadband elements, and have effective ranges varying from only a few meters to several hundred meters. Classification of calls is difficult, because they consist of from one to many elements each, and each group of elements can be repeated in a regular cadence. Thus, structural grading must be considered at several hierarchical levels. Mace distinguished "repeated-note calls" (RNCs), consisting of from 1 to about 60 (average 12) regularly repeated elements, from "note-group calls" (NGCs), characterized by repetition of *groups* of rapidly repeated elements (average 2.3 elements/group). Elements within RNCs were separated from one another by about 162 msec, on average, as compared with only 46 msec between successive elements *within* groups, and 211 msec *between* groups, for NGCs. Some other important differences between RNCs and NGCs are summarized in Table VII.

Fourteen behavioral contexts were identified by Mace, and RNCs occurred in all but one of them (copulation). In sharp contrast, NGCs occurred in only four: "attentive to mate," "escorting chicks," "copulation," and "nervous/alert." Structural characteristics of both RNCs and NGCs varied significantly across contexts; RNCs can serve as an example. In these calls, numerous variables concerned with frequency and temporal characteristics varied significantly across contexts. For example, the variable "element duration" by itself defined four statistically separable groups of contexts (Fig. 11). Discriminant analysis on these

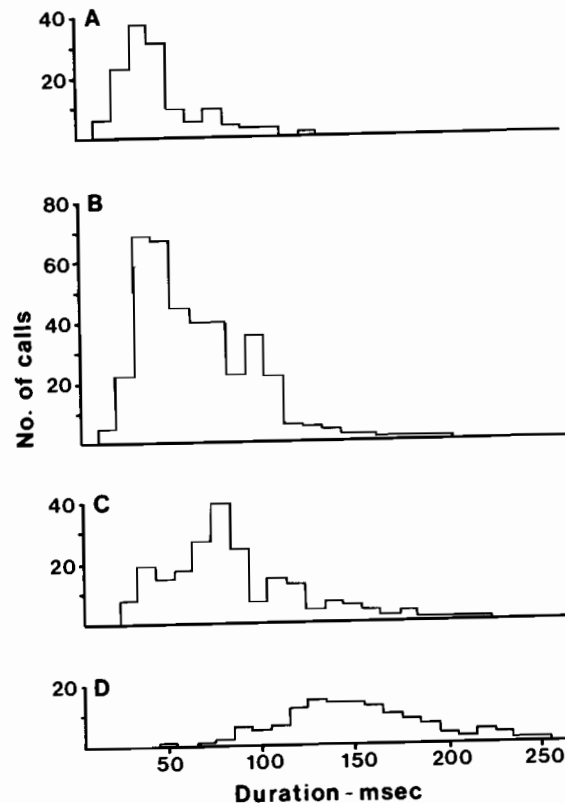


Fig. 11. Frequency histograms for the duration of elements within "repeated note calls" of the Northern Jacana (*Jacana spinosa*), for four groups of contexts: (A) nervous/alert; attentive toward a mate; response to flying conspecific intruder; (B) flight across, to, or from territory; flutter-hop; (C) encounter with predator on the substrate; response to something in the water; male's chase of intruding juvenile; male's encounter with conspecific intruder on substrate; (D) aerial attack on predator; male landing over his mate; female's encounter with conspecific intruder on substrate. [After Fig. 15 of Mace (1981).]

four groups, using an additional four variables, revealed considerable overlap between adjacent groups (Table VIII). These and other analyses affirmed that there was some correspondence between behavioral context and call structure, but it was very general and showed extensive overlap. Thus, structure by itself was not capable of transmitting specific kinds of information.

The final part of Mace's analysis addressed the effects of sound signals upon receivers. He noted substantial variation in the responses of receivers depending upon the context in which particular calls were given.

Table VIII. Classification Results from Discriminant Analysis on Four Groups of Behavioral Contexts in Which Northern Jacanas (*Jacana spinosa*) Call (Five Variables)^{a,b,c}

Actual group membership ^b	Predicted group membership (%) ^b			
	1	2	3	4
1	70	17	8	4
2	24	42	28	5
3	12	19	49	21
4	2	1	13	84

^a Data from Table 41 of Mace (1981).

^b Contexts in each group are: 1, attentive to mate; response to flying conspecific intruder; nervous/alert; 2, flight across, to, or from territory; flutter-hop; 3, encounter with predator on the substrate; startled; response to something in water; male's encounter with conspecific intruder or substrate; male's chase of intruding juvenile; and 4, aerial attack on predator; female's encounter with conspecific intruder on substrate; male landing over his mate.

^c Variables are: bandwidth of dominant frequency; element duration; interval between successive elements; relative loudness; and total number of elements.

However, in converse analyses, by examining receivers' responses to signal variants within contexts, much less variation was detected. One situation with clear results was in the context of aerial attack upon a predator by female jacanas; here, calls resulting in the departure of the predator had significantly greater intervals between elements, and significantly more elements.

In summary, Northern Jacanas use an acoustic signaling system built around two structurally defined types of calls. Structural and contextual variation considered together provide a greater understanding of communication and its effects than either does when considered in isolation. Even this detailed study did not reveal whether structurally similar call types evoke a continuous range of responses, and it is possible that uncontrolled field studies cannot answer that question. However, the study documents a clear example of structural grading at the level of the repertoire. It also demonstrates the necessity of including contextual information, and semantic and pragmatic analysis, in such research.

D. Ecological and Social Effects

Communicative behavior must meet both ecological and social demands, so many characteristics of signaling reflect the resolution of complementary or opposing selection pressures from the two spheres. Nevertheless, some ecological and social factors act independently of one

another, so certain features of communication can be best examined if their selective bases are discussed separately.

1. Transmission Distance

The distance over which signals are regularly transmitted, plus sources of degradation along the route of transmission, are two crucial forces in the evolution of signaling behavior and of the physical characteristics of signals (Konishi, 1970; Wiley and Richards, 1982). If the average transmission distance is great, there is selection against high-frequency acoustic signals because they attenuate rapidly with distance. Similarly, spectrally complex sounds undergo differential frequency attenuation with distance, and are likely to be selected against as long-distance signals. A long transmission path also exposes sounds to various kinds of degradation from background noise, wind, etc., which should place a premium on signals with simple patterns of amplitude modulation, and that contrast with the background. In general, then, long-distance sound signals are predicted to be high in energy, low in frequency, spectrally pure, and with simple or no amplitude modulation. To compete with background noise they should also be stereotyped and repetitive; the latter feature also improves locatability [see Green and Marler (1979) for other comments on characteristics that enhance locatability]. Do long-distance sound signals of shorebirds have characteristics that agree with these predictions?

Many species of shorebirds in open-country environments emit loud, repeated sounds to attract mates and repel other conspecifics, in displays given in flight, which further increases transmission distance (Fig. 12; see Miller, 1983a,b). All meet with general predictions about optimal physical characteristics for faithful transmission and accurate locatability over long distances, though there are many differences among species (see Section II.E.2). The calls used by parental shorebirds in the presence of potential predators may be designed for long-distance transmission, to recruit other birds (even heterospecifics) in "mobbing"; these calls' features are also in generally good agreement with those predicted.

Wiley and Richards (1982) discuss many factors additional to those summarized above that must be considered for shorebird species that live in physically complex environments like forests (e.g., Subantarctic Snipe, *Coenocorypha aucklandica*; Solitary Sandpiper; etc.), or reside near sources of loud frequent noise, such as seacoasts or rivers. Certainly, the latter must have helped effect the remarkably loud piercing quality of many call types of oystercatchers, Wandering Tattler [*Heteroscelus incanus* (E.H. Miller, unpublished observations)] and Diademed Sandpiper-

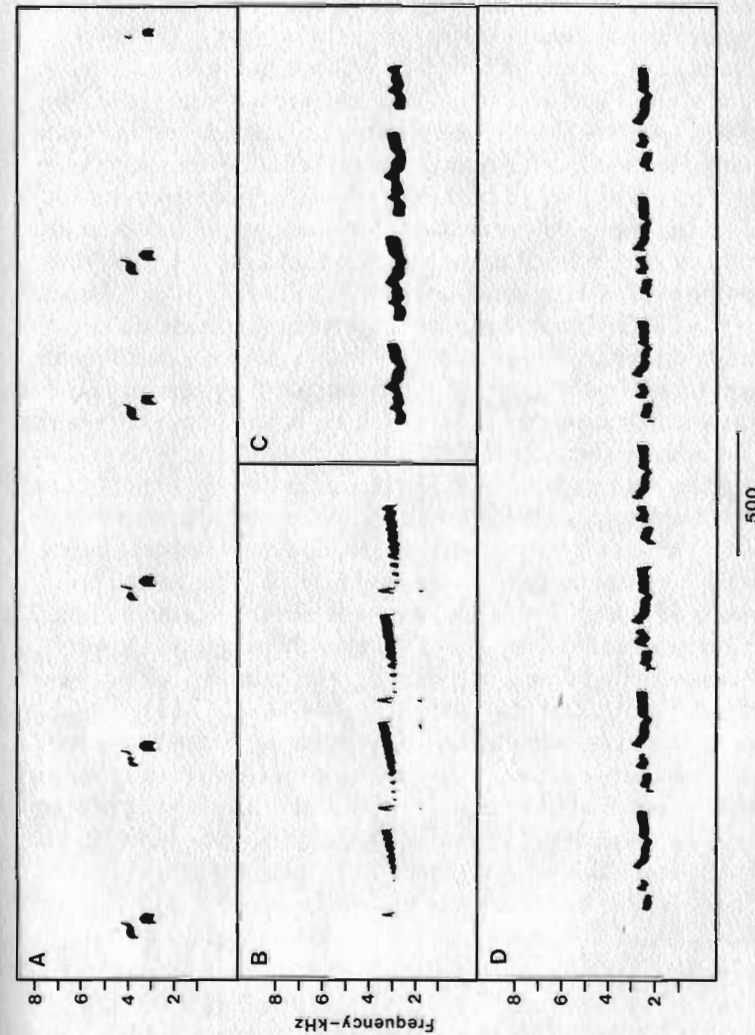


Fig. 12. Sound spectrograms of call sequences during aerial displays. (A) American Golden Plover (*Pluvialis dominica*; near Churchill, Manitoba). (B) Least Sandpiper (*Calidris minutilla*; near Churchill, Manitoba). (C) Wandering Tattler (*Heteroscelus incanus*; Blackstone River Valley, Yukon Territory). (D) Lesser Yellowlegs (*Tringa flavipes*; near Fort St. John, British Columbia). Analyzing filter bandwidth throughout, 300 Hz. Time marker is in msec.

plover [*Phegornis mitchellii* (Johnson and Goodall, 1965)]. Short-distance sounds in general are not subject to any of the same considerations as long-distance ones, for there is so little degradation or frequency-dependent attenuation of their features. Finally, many features are not predictable based just on considerations like those above, and certainly the differences among species are not. Phylogeny does explain many such differences, however (see Section II.E).

Visual signals are far less effective than acoustic ones for long-distance communication. The aerial maneuvers and strong markings of large birds like lapwings are visible from great distances though, and acoustic and visual components of such displays are mutually complementary in drawing attention to a displaying bird. Most visually inconspicuous species that use aerial displays have ritualized motor components that are visible from afar, including wing action, dives, undulations, ascents, rolls, etc. (see Cramp, 1983; Glutz von Blotzheim *et al.*, 1975, 1977; Miller, 1983a,b; Nowicki, 1973). Such components certainly increase a displayer's transmission distance, but the relative value of different components can only be speculated on at present. As for acoustic signals, some features of motor components can be explained most parsimoniously with reference to phylogeny (Section II.E.2).

Because many shorebird species do not signal very frequently from elevations, they are limited in long-distance visual communication except when in flight. Numerous species accentuate landing or takeoff by exposure of wings or tail, or both, however (Hale, 1980). The Upland Sandpiper exemplifies this trend, with both sexes (but particularly males) going through elaborate extension then slow folding of the wings and lowering of the tail after landing on fenceposts (Fig. 5). Males of two lekking species, the Ruff and the Buff-breasted Sandpiper (*Tryngites subruficollis*), greatly increase their conspicuousness by leaping up from the ground surface in a ritualized form of flutter-fighting, so common in their relatives (Fig. 16a; see also Fig. 3 of Holmes, 1973). The Buff-breasted Sandpiper has strikingly white underwing surfaces, which allow even birds on the ground that raise and "flash" their wings to be seen for long distances (Myers, 1979; Oring, 1964; Parmelee *et al.*, 1967).

2. Activity Budgets

The preceding discussion addressed the adaptiveness of sound structure, but omitted consideration of the facultative responses of shorebirds to ecological factors. For example, do individuals call more frequently, or engage in higher wider-ranging aerial displays, in years or habitats of low density? Here, some studies on activity budgets are discussed. These

should be extremely labile according to local ecological conditions, and need detailed work to evaluate the ecological significance of how time spent communicating is apportioned. It is difficult and somewhat artificial to estimate the amount of time spent by shorebirds in display, because communication can coincide with other activities and because static-optical signaling may be essentially continuous, especially in well-marked open-country species.

Gibson (1978) used general functional categories in his study of the American Avocet, and quantified the fraction of time spent in "aggressive behavior," "mating behavior," and "diversionary behavior." Certain other of his categories probably include much communication, as he points out, including nest building, parental care, and vigilance behavior. For comparative purposes, it is best to specify functional categories like his, or to focus on discrete and conspicuous display types. An alternative approach could be built around different classes of signaling modes, distinguishing different forms of active and passive communication, but this has not been attempted, to my knowledge. In Gibson's study, prenesting avocets spent 4.6% (males) and 3.5% (females) of their time in predator distraction, mating, and aggression. The latter two classes accounted for 4.4 and 3.4% of male and female time then, respectively, and declined sharply in incubation (to 0.8 and 1.0%). Mating did not appear in samples later in the nesting cycle, but aggression returned to a high level: about 3.2% in males and 1.6% in females, during the period of brood attendance. Aggression subsequently decreased again. This study was the first to provide rough estimates of the time budget of a breeding shorebird, and established a lower bound to time spent in active display. Inclusion of appropriate contexts of nest building, nest relief, and parental care could easily double the estimate of 4.6% for males in the prenesting period, when most time is spent in obvious display. Estimates of time spent in passive forms of display would further increase this figure, but would be of greatest significance to understanding social dynamics, for the energetic cost is low (though an elevated risk of predation may figure into this component).

A detailed study of time and activity budgets of the Semipalmated Sandpiper (*Calidris pusilla*) was carried out by Ashkenazie and Safriel (1979). This species is much more difficult to observe than the colonial avocet, so behavioral categories necessarily omitted or lumped some important displays including ground courtship and scraping. Unpaired Semipalmated Sandpiper males engage in a conspicuous aerial display, and time spent in this is easily quantified, however. Ashkenazie and Safriel estimated that unpaired males spent 18% of their time in flight, most of which was in aerial display. Flight required around 56 kJ/day, nearly 7%

Table IX. Daily Time and Energy Allocations to Behavior That Included Much Communication, for Lesser Sheathbills (*Chionis minor*) Rearing Chicks^a

		Pair displays	Brooding	Territorial defense	Antipredator aggression
Males	% ^b	0.1	18	1.3	1.4
	kJ/day	0.4	33	20	7
Females	%	0.1	22	1.8	0.8
	kJ/day	0.4	37	25	4

^a Data from Tables 2 and 3 of Part Six of Burger (1980c).

^b Percent of diurnal time budget.

of total requirements for this phase of the breeding cycle. Clearly, this one display form by itself figures significantly in both time and energy budgets (see Erckmann, 1981).

The time and energy budgets of Lesser Sheathbills were estimated by Burger (1980c), at Marion Island in the subantarctic. His study began at hatching, and continued until the chicks left the nest to follow their parents (at around 7 weeks). Of the eight behavioral categories recognized by Burger, three were dominated by communicative acts ("territorial defense," "antipredator aggression," "pair displays"), and one presumably included much communication ("brooding"). Displays between paired birds occupied only a few minutes each day, and were energetically cheap (Table IX). Aggressive acts toward potential predators and territorial defense occupied more time and were more energy-demanding, together accounting for 5% of the daily energy budget. Brooding was the most significant behavior in terms of both time and energy (Table IX). It was particularly important when chicks were young, occupying over 40% of the parents' time then. Territorial adults advertised conspicuously but cheaply at other times, simply by resting or preening on prominences, which could be done with only normal maintenance costs. The pairs studied by Burger had noncontiguous territories centered on Rockhopper Penguins (*Eudyptes chrysocome*), which they kleptoparasitized; those pairs must have had much lower costs in active territorial defense than pairs occupying smaller, contiguous territories in colonies of King Penguins (*Aptenodytes patagonicus*).

The most detailed study on activity budgets of breeding shorebirds is by Maxson and Oring (1980), who made extensive observations on Spotted Sandpipers over several years. This species is polyandrous throughout much of its range, with males taking major or sole responsibility for incubation and brood rearing. The main investments made by females are in egg production, and in agonistic activity related to defense

Table X. Relationship of the Percent of Time Spent in Agonistic Behavior, to Gender and to Stage of Breeding Cycle in the Spotted Sandpiper (*Actitis macularia*)^a

Stage of breeding	Percent of time in agonistic behavior ^{b,c}					Overall percent in agonistic behavior
	BAE	CH	U	A	FT	
Prelying	52/53	29/31	7.4/2.6	9.1/10.6	3.1/2.5	8.4/5.7
Laying	51/68	13/18	8.6/2.9	23/10.1	3.9/0.7	4.1/3.0
Incubation	58/59	28/28	4.7/3.3	8.0/6.9	1.3/2.1	4.7/1.7
Brood-rearing	—/61	—/29	—/1.9	—/5.2	—/2.4	—/5.5
Averages	53/60	23/27	6.9/2.7	13.5/8.2	2.8/1.9	

^a Data after Table 4 of Maxson and Oring (1980).

^b BAE, balanced aggressive encounters; CH, chasing; U, upright displays; A, appeasement; FT, fighting.

^c Each cell entry is shown as: male/female.

of mate or territory. Overall, time spent in agonistic behavior differed insignificantly between the sexes, but forms of behavior varied according to sex and stage of breeding cycle (Table X). Females spent about twice as much time in agonistic behavior in the prelying stage as subsequently, and components varied substantially. In particular, appeasement was very high during the laying stage, perhaps to minimize energy expenditure and potential damage to developing eggs. Males showed different trends, with less time in agonistic behavior at all stages (partly because of incubation duties), and much less use of upright displays. The resurgence in agonistic behavior by males after hatching was due to the need for defense of chicks, who sometimes suffered severe injury or death from attacks by foreign adults. Activity budgets were strongly influenced by food availability. For example, females spent 70% of their time foraging and 5% in agonistic activity in one season with little food (terrestrial arthropods), compared with 48% and 9%, respectively, for two seasons with more abundant food. Comparable trends also occurred within years, corresponding to seasonal trends in food availability.

Other species for which time budgets are available are described in Erckmann (1981) and Walters (1980; this volume). For the polyandrous Red Phalarope, D. Schamel estimated that females spend about 8% of their time in ground display (cited by Ashkenazie and Safriel, 1979). As for the other species, this figure must be considered an underestimate of time spent in active display. Though there are large differences among species, it is clear that active forms of signaling constitute a significant fraction of the time budget, especially in the prenesting phase, and for that sex subject to strongest sexual selection. Mundahl (1977) summarizes some interesting trends for communicative behavior throughout the

breeding cycle of the Killdeer (*Charadrius vociferus*), which support this generalization. Detailed comparative work on this topic would surely repay the investment.

3. Diel Rhythms and Reactions to Predators

Display behavior in shorebirds is subject to numerous influences from weather, temperature, topography, time of day, etc., as in most bird species. One of the most clearly documented cases concerns evening and early morning "peent" display by male American Woodcock. The onset of display is closely tied to light level, and begins about 20 min before civil twilight from late March (when civil twilight occurs around 0640) through early June [when civil twilight is around 2010 (Leopold and Eynon, 1961)]. A similar relationship prevails for early morning display (Leopold and Eynon, 1961; Fig. 13). When there is reduced light because of clouds, fog, etc., evening display begins earlier and ends later throughout the breeding season (Fig. 13; Weeks, 1969). Such pronounced but modifiable display rhythms are a mixture of flexible and inflexible responses and patterns, the inflexible ones in this case relating to responsiveness to light intensity.

Favorable physical conditions for transmission presumably explain why strong display rhythms occur in at least some shorebird species. Many others must be compromises, set particularly by the nature and intensity of predation. Crepuscular or nocturnal display by taxa like woodcock (*Scolopax*), Great Snipe (*Gallinago media*), Burhinidae, and Rostratulidae seems likely to have evolved in response to predation pressures of some sort. However, the only form of display behavior in which species differences can be confidently linked to predation is in diversion or distraction. Sordahl (1981) reviewed the behavior of 51 species of breeding North American shorebirds in response to potential predators, and noted a strong tendency to mob by large species. None of the *Charadrius* plovers exhibits mobbing (by Sordahl's definition), but both large *Pluvialis* species do, as well as the Jacanidae, Haematopodidae, and Recurvirostridae. The most telling evidence is from Tringini, for all mob except the two smallest species (Solitary and Spotted Sandpipers) plus the Wandering Tattler. Sordahl suggests that small species expose themselves to danger when they mob. This factor may help explain the trends, though other ones must be involved. For example, why do turnstones mob, but not dowitchers? The Killdeer does not mob according to Sordahl, yet Nol (1980) documented outright attacks by this species on model gulls and raccoons, and aerial chases of live gulls. It seems likely that increased attention to details of reactions by nesting or parental birds will improve our under-

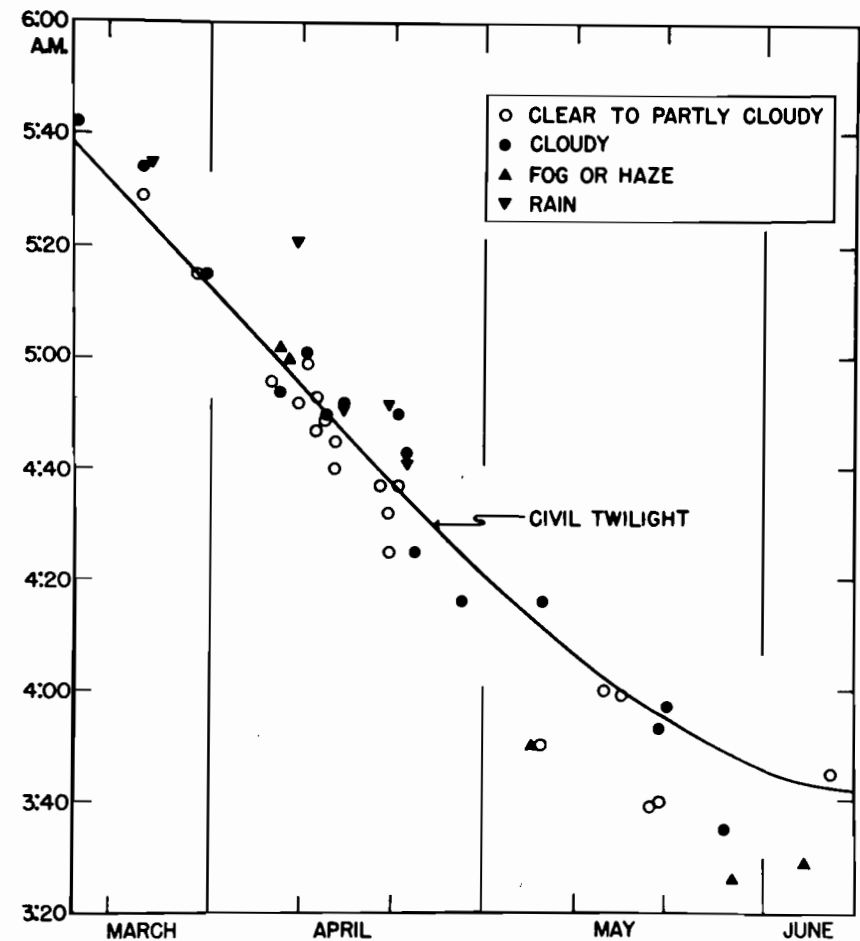


Fig. 13. Relationship of the cessation of "peent" calls by male American Woodcock (*Scolopax minor*) to civil twilight. Each circle or triangle represents a single observation for the last call heard in a morning. [From Leopold and Eynon (1961, Fig. 8).] A similar relationship holds for the onset of calling (Leopold and Eynon, 1961, Fig. 7).

standing of their adaptive responses to predators (see Chapter 8, this volume)

Responses to predators by nesting shorebirds vary geographically, but are not easily explained just by reference to predation pressures. The best documented cases of such variation in various forms of display behavior evoked by predators are by Williamson (1943, 1946, 1948, 1950, 1952). He described mobbing and diversionary behavior by several spe-

cies of shorebirds on the Faeroes, and noted that the expression of such behavior there was quite different from that recorded elsewhere. For example, for the Eurasian Oystercatcher (*Haematopus ostralegus*) "in Holland and Cumberland displacement butterfly-flight with its accompanying 'kleu, kleu' call-note, is the normal reaction to human intrusion at the critical hatching time and when the young are small. At Fair Isle butterfly-flight, modified by the absence of the call-note and the low altitude of the display, is the usual reaction, sometimes culminating in an incipient lure display. At Unst, nearly 100 miles to the north, the butterfly-flight has become modified to the extent that a terrestrial pattern embracing its main elements is developing; whilst in the Faeroes, 200 miles farther N. W., the evolution of the new and striking lure pattern and its ritualization into mobile and stationary figures is virtually complete" (Williamson, 1952, p. 93). The geographic variants he noted for this and other species do not appear to be related to predation pressure in any simple way.

4. Social System and Sexual Selection

Social characteristics evolve within broad sets of ecological constraints, and many characteristics of signaling can be related most easily just to social pressures. For example, in colonial species like stilts and avocets, much communication reflects adaptation to coloniality, and not to the important factors related to (say) food and predation which have led to coloniality. In this section, I discuss a few features of social systems that have had important influences on some characteristics of signals: parental feeding; monogamy; and intrasexual selection.

Parents feed their young in Dromadidae, Glareolidae, Burhinidae, Chionididae, Pluvianellidae, Haematopodidae, and Scolopacidae (*Philomachus*, *Scolopax*, and *Gallinago* only). Communication between parents and young in the first two of these is facilitated by the young remaining in one place, for crab plovers are burrow-dwellers, while glareolids return to their young to feed them. In the Australian Dotterel (*Peltohyas australis*) and Australian Pratincole (*Stiltia isabella*), such sedentariness is related to the need for chicks to locate and remain in relatively cool microhabitats, to avoid hyperthermia and dehydration (Maclean, 1976a,b). Species in which parents feed their chicks must have particular signals used in soliciting feeding, or attracting young, a matter that has been studied only in the Eurasian Oystercatcher, by Lind (1965) and Norton-Griffiths (1969). These two workers have provided the most detailed studies on shorebird parent-young behavioral relationships to date.

Adult oystercatchers initially bring food to the newly hatched young just around the time of nest relief, but the precision of this timing weakens quickly. Within a day or so of hatching, adults lure the young from the nest by calling and probing near the nest. Parents also lure the chicks "by presenting food 'just out of reach' . . . so that the young has to move away from the nest in order to be fed" (Norton-Griffiths, 1969, p. 79). During this phase, adults may briefly hold the bill in a posture resembling the feeding posture (see further), and the chicks closely follow the adult's bill. During the chicks' early life away from the nest, parents use several distinctive calls and visual signals in attracting them to feed and in feeding them. Upon obtaining food, a parent runs toward the chick quickly with neck withdrawn and bill pointing slightly down (at greater distances the adult flies). During the adult's approach, it uses one of two different call types, which depend on the mode of locomotion: loud Weep calls are used in 87% of flights, just before landing, and quite Chuck calls in the remainder; and Chuck calls occur in 99% of runs (generally when within about 10 m of the chicks) (Norton-Griffiths, 1969). Most commonly, parents stop some distance from the chicks, and stand while pointing the bill roughly vertically to within 2–3 cm of the ground [see Fig. 2 of Lind (1965) and Fig. 10 of Glutz von Blotzheim *et al.*, (1975)]. The food may be mandibulated or moved up and down the bill, dropped on the ground and then picked up again, or left on the ground while the parent "points" to it. In addition, parents sometimes hold the food while moving the bill around near the chick's face, or may just deposit the food on the ground and then leave. Static holding plus mandibulating occur in nearly all (90% or more) food presentations; other components are less common (Norton-Griffiths, 1969). The orientation and color of the adult's bill are important in eliciting feeding responses from chicks (Hørlyk and Lind, 1978; Lind, 1965), though initial responsiveness to it is in the context of brooding (Norton-Griffiths, 1969).

Developmental changes in how parents attract and feed their young, and in how chicks solicit food; interrelations between chick and adult behavior; and variations in all facets of the parent-young feeding relationship all speak for a complex, labile communication system. This is well illustrated by the tendency of adults to be less attentive to older chicks and less solicitous of them, which in turn affects the behavioral responses of older chicks: "When begging, the [old] chick assumes a posture similar to the submissive posture of the adult; the neck is withdrawn, the head is held at or below the level of the back, and the body is puffed out. . . . The chick approaches . . . usually rubs its head and neck against the flanks and, especially, the breast of the adult. It moves from one side of the parent to the other . . ." sometimes jerking its head

upwards, or pecking at the parent's head, bill, legs, and toes, and calling (Lind, 1965, pp. 15–16). In contrast, young chicks simply respond to the sight or calls of an approaching parent by direct approach with calls, and directly taking food from the adult (sometimes preceded by pecking at the food at the tip of the adult's bill).

Monogamous species that feed their young would be good subjects for research on intersexual selection, though none has yet been carried out on this topic, to my knowledge (see further). Monogamous mating systems have other signaling characteristics about which scattered information is available, though. Many authors have noted that display activity in experienced males is reduced or absent compared with inexperienced males, and this is particularly true of males that re-pair with the previous year's mate (Hale and Ashcroft, 1982; Jehl, 1970). Paired birds communicate with one another in numerous contexts, as in changing over at the nest, or in maintaining contact with one another while foraging. Response-calling or antiphonal calling is common in paired shorebirds, such as the Upland Sandpiper (Fig. 14). Antiphonal calling occurs in Jacanidae and Glareolidae, and is particularly common in all three species of phalaropes, though the calls are soft and short-range, often while the birds are close to one another while swimming/feeding (Howe, 1972; Maclean, 1967; Mathew, 1964; E. H. Miller, unpublished observations). Perhaps the loudest and most conspicuous form of simultaneous display by paired birds is piping in oystercatchers (Cramp, 1983; Glutz von Blotzheim *et al.*, 1975; Heppleston, 1970; Huxley and Montague, 1925; and references in Table V). This short-range display occurs in all Haematopodidae, and is characterized by striking postures and movements, and loud lengthy calling. It is not just restricted to communication within a pair though, but occurs commonly as a communal display.

Some of the most elaborate and intricate displays by paired birds are shown by *Charadrius* and *Recurvirostridae*. In many species of the former, there is a close relationship between nest-scrape displays and copulation, as nicely described by Clark (1982, pp. 120–121) for Kittlitz's Plover (*Charadrius pecuarius*): "the male sat in the hollow, scraping, [etc.] . . . he was approached by the female . . . and she replaced him; almost immediately the female got out and did a slow walk, with head level with body . . . This was the invitation walk . . . As he approached the female the male started 'high-stepping.' His head was lifted and his whole body raised on almost straight legs. The female stopped a few centimetres to 1 m away from the nest site, and lowered her body slightly. The male continued 'high-stepping' . . . lifting his tarsi and toes above the horizontal . . . and finally made a sudden jump. With tarsi resting on the female's back the male . . . adjusted his position [for 80–150 sec then]

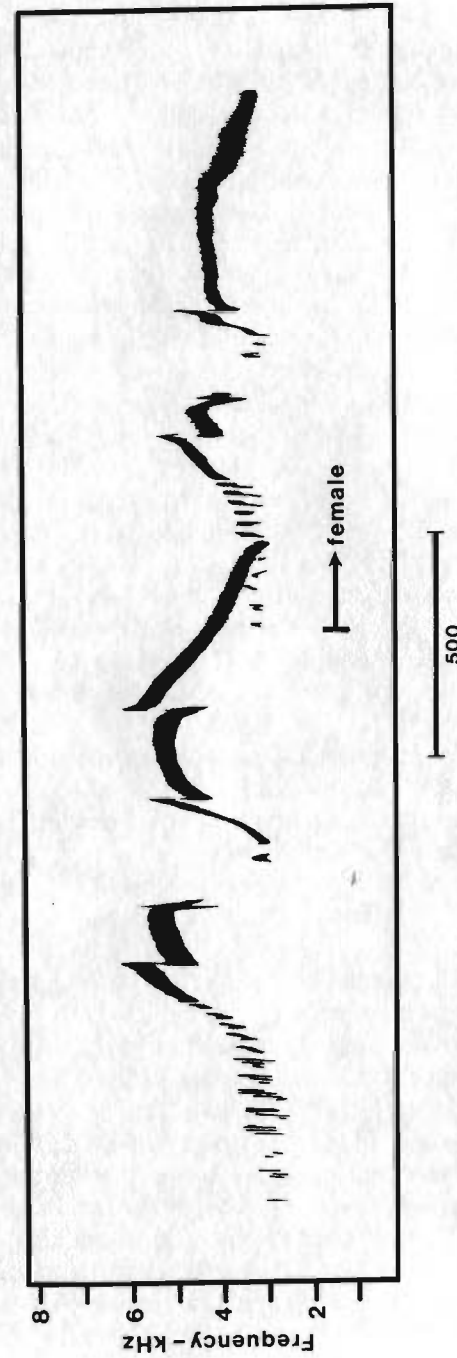


Fig. 14. Response-singing of female to male Upland Sandpiper (*Barrtramia longicauda*; near Oak Lake, Manitoba). The male was standing on a knoll, and the female was feeding nearby. [From E. H. Miller and D. R. M. Hatch (unpublished observations).] Analyzing filter bandwidth, 300 Hz. Time marker is in msec.

. . . took the female's nape feathers in his bill and, falling backwards, made cloacal contact. The male finished up on his back with wings spread and the female on top of him with legs in the air" [parts of a homologous sequence for the Snowy Plover, *Charadrius alexandrinus*, are shown as Fig. 39 of Glutz von Blotzheim *et al.* (1975)]. Similar remarkable performances occur in other *Charadrius* species (Clark, 1982; review by Cairns, 1977, 1982). The elaborate display sequences may be given throughout the egg-laying period, as in the Piping Plover, *Charadrius melodus* (Cairns, 1977, 1982), and may also begin well before it starts. In Kittlitz's Plover, Clark (1982) noted copulations up to 11 days before egg laying, and these were repeated frequently (at intervals of 10–45 min). Thus, it seems likely that display behavior involved with scraping and copulation in *Charadrius* species is widespread and is at least partly ritualized, serving functions associated with pairbond maintenance in these generally monogamous species.

In Recurvirostridae and Vanellinae, complex ritualized mutual displays occur between mated birds, and in contexts suggestive of a function in pairbond maintenance. In *Vanellus*, a postcopulatory wing-raised run (and calls) is widespread, for example (Maclean, 1972). Pre- and postcopulatory displays in the colonial, monogamous Black-winged Stilt have been described in detail by Hamilton (1975) and Goriup (1982, pp. 20–21); the latter's description is excerpted here: "As soon as the female assumed the copulation posture [Fig. 15a] . . . the male became very excited, puffing out his feathers to appear much larger than his mate, and striding in semicircles from one side of her to the other, always passing behind . . . Each time that he came up to her shoulder, he paused to bill-dip and preen his breast or underwing [Figs. 15b–d]. This cycle was repeated two to five times, ending when the male adopted an erect posture prior to mounting [Fig. 15e]. To achieve cloacal contact, the male flexed his legs so that . . . the tarsi rested on the female's back . . . [Fig. 15f]. After dismounting, both male and female adopted upright postures and performed the bills-crossed ceremony: standing close to the female, the male crossed his bill over hers and extended his wing over her back; in this pose, both walked about a metre . . . [Figs. 15g,h]" [see also Fig. 17 of Hamilton (1975) and Fig. 129 of Glutz von Blotzheim *et al.* (1977)].

The elaborate ritualized nature of displays such as those outlined above suggests that intersexual selection is an important factor in monogamous mating systems of shorebirds. Very little on this topic has been published, though Jehl (1975) notes that courtship feeding occurs in the Magellanic Plover, a species that feeds its chicks; such behavior could be very important in assessing potential mates. McGilp and Morgan (1931) observed Banded Stilts (*Cladorhynchus leucocephalus*), a poorly known

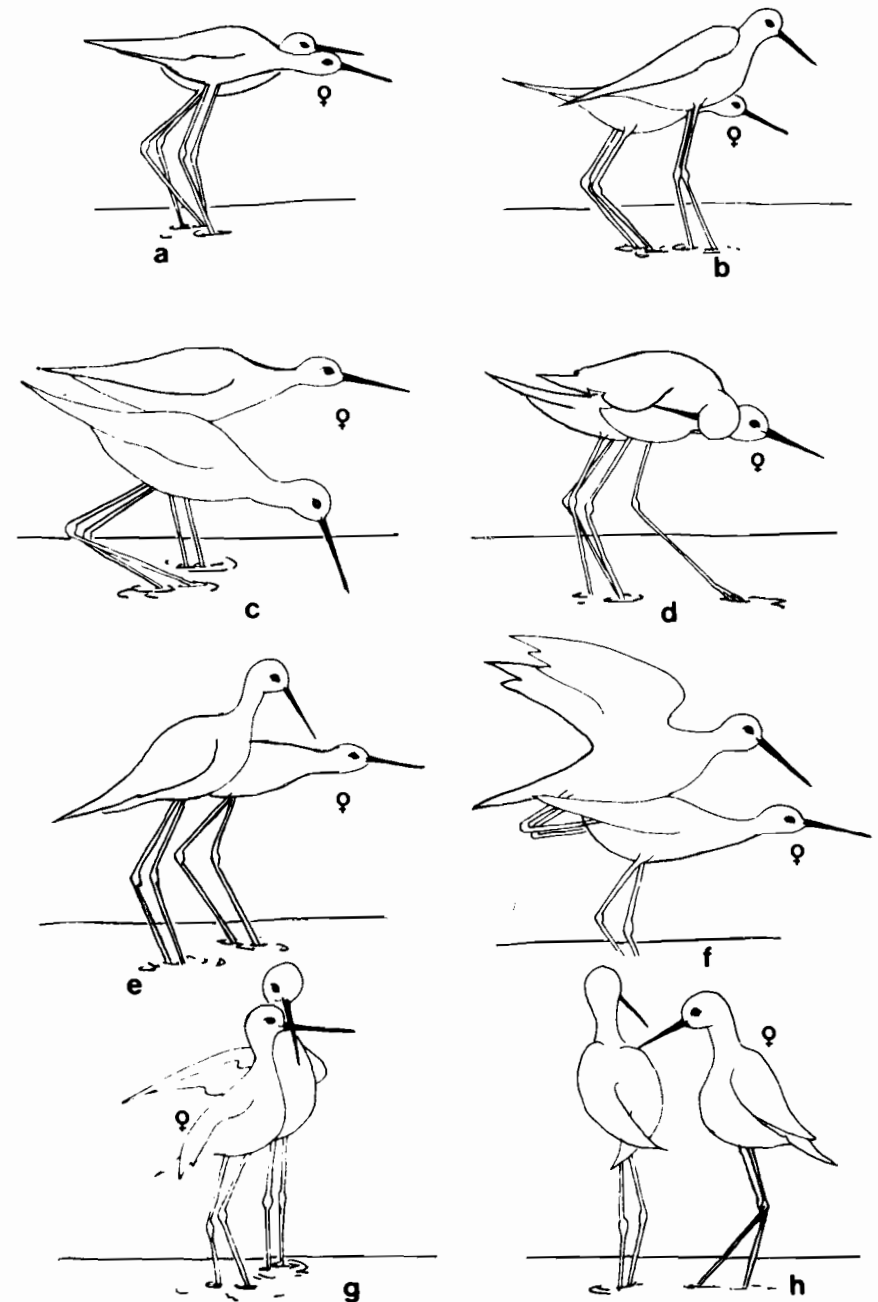


Fig. 15. Sequence of pre- and postcopulatory displays by Black-winged Stilts (*Himantopus himantopus*). See text for discussion. [From Goriup (1982, Fig. 6).]

Australian species that nests in large colonies depending upon the unpredictable occurrence of rainfall: "every now and then a bird would run up from the water and feed its sitting mate" (p. 41). I know of no comparable observations on other species.

A few lekking species of shorebirds have been well studied, and contributions of male behavior to mate choice by females have been examined. The Ruff is best known of such species, but despite intensive research by various workers, very little evidence has been found for display characteristics that seem to influence female choice. Some compelling data are discussed by Hogan-Warburg (1966) and van Rhijn (1973), who determined that female responsiveness was related to quantitative variations in certain forms of male behavior. However, no major conclusions could be formed. Display behavior of lekking Great Snipe has also been described in detail, but no simple relationships between signaling and mate choice have been detected (Avery and Sherwood, 1982; Ferdinand, 1966; Ferdinand and Gensbøl, 1966; Swanberg, 1965). The lack of simple correlations in social species is perhaps unsurprising, for competition among males for positions on leks has already winnowed the number of males from which females must choose: much of the choice has already been made for them (Miller, 1975).

Contest behavior among males has been studied little. In the Least Sandpiper, males early in the breeding cycle (especially unpaired males) engage in several kinds of vigorous hostile display (Fig. 16). One of these involves lengthy sprinting without reference to any territorial boundaries (which do not exist as such in this species). If one male assumes too great a lead, the other bird often makes a short low flight to catch up, or just to move ahead; several quick exchanges like this give the appearance of leapfrogging. Such running may continue between two males, with pauses of various durations, for hours. It seems plausible that this demanding form of contest exerts strong intrasexual selection upon males. In general, in this and in other shorebird species, it is difficult to attribute variations in displays to the action of sexual selection, though it is often straightforward to assign epigamic or hostile functions to displays.

E. Evolutionary and Phylogenetic Considerations

Several lines of evidence suggest that shorebird displays may provide good material for inferring evolutionary trends, and may be sensitive indicators of phylogenetic affinities. In this section, several examples that support this impression are outlined. For example, numerous visual displays and display sequences in Recurvirostridae are nearly invariant even

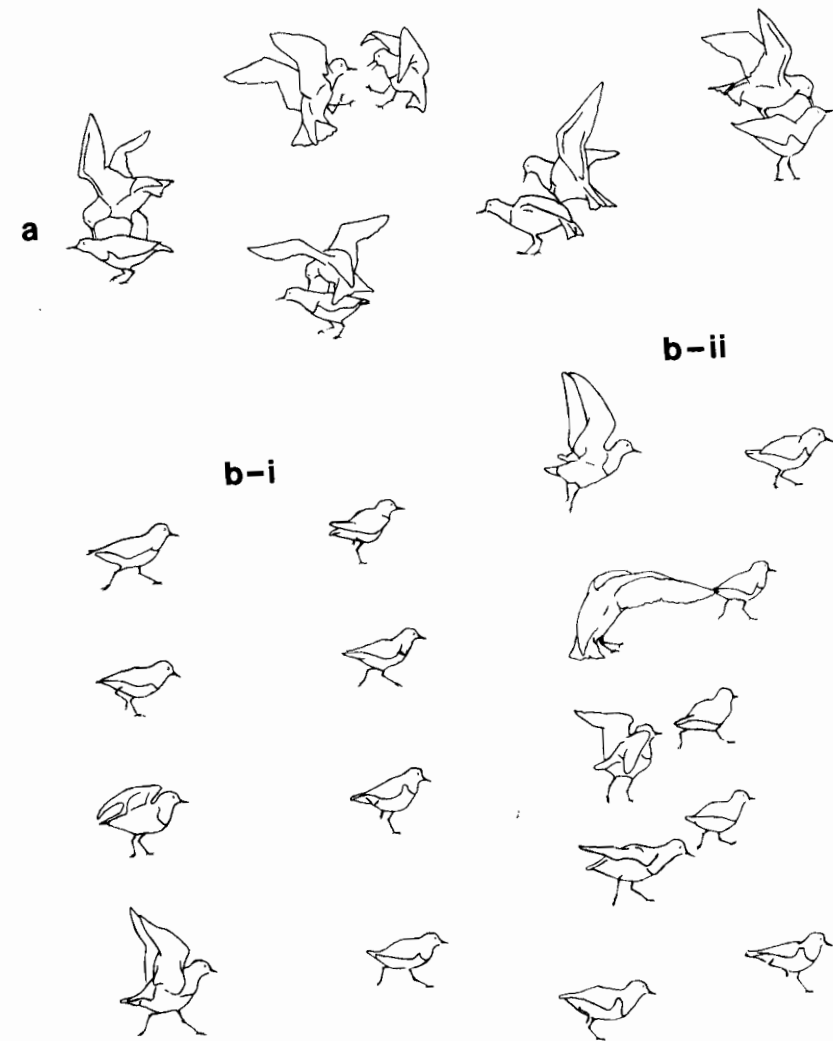


Fig. 16. Agonistic displays between male Least Sandpipers (*Calidris minutilla*). (a) Five sketches based on three different fights. (b) Sequence of contest-running, showing a "catch-up" flight by the trailing bird. Columns b-i and b-ii are viewed from the top down; the top sketch in b-ii follows the bottom sketch in b-i. [Sketches are based on super-8-mm movie films; drawings by A. McClung.]

between continents, and are easily homologized across genera (Cramp, 1983; Goriup, 1982; Glutz von Blotzheim *et al.*, 1977; Hamilton, 1975); certain expressions of threat are strikingly similar in groups as distant as Burhinidae, Haematopodidae, and Jacanidae (Maclean, 1972); etc.

1. Calls by Adult Birds Tending Their Young

Species distinctiveness is not generally selected for in short-distance "alarm" signals, and these can be examined to determine how conservative their structure is across species. Most, perhaps all, shorebirds call softly to their young during and after hatching, but these calls show an unexpectedly high amount of species distinctiveness (Fig. 17). For example, the Common Greenshank commonly emits a broadband "gruff" sound, while Mountain Plovers (*Charadrius montanus*) and Least Sandpipers use many soft low-frequency trills (Graul, 1974; Nethersole-Thompson and Nethersole-Thompson, 1979; Wallis and Wershler, 1981). The latter species also "clucks" frequently, while the Spotted Sandpiper gives one to several repetitions of a much higher-frequency call (Fig. 17). Close study of related species may reveal more obvious similarities, a prediction upheld by examination of parental calls given in response to human intrusion (Fig. 8). Oystercatchers have two quite different call types, with intermediates: single, brief calls; and fairly long, pure-frequency calls introduced by several brief calls (Figs. 8A,B; Miller and Baker, 1980). Two *Pluvialis* species emit long, pure-frequency calls with sudden frequency shifts (Figs. 8E,F), and all *Calidris* species I am familiar with (except the White-rumped Sandpiper) have two apparently homologous calls: a single type characterized by conspicuous frequency modulation; and a trill (Figs. 8I-L). No analyses exist to permit discussion of other species illustrated in Fig. 8 (*Vanellus*, *Charadrius*, *Phalaropus*), but the utility of "alarm" calls in systematic research certainly seems to be limited to lower categories, to judge from these examples.

2. Aerial Display

Most species of shorebirds inhabit fairly open environments during the breeding period and, like many open-country bird species, have well-developed aerial displays (Armstrong, 1963). The ultimate explanation of this broad correlation presumably lies in the increased transmission distance that results from displaying at some height above the ground surface (Wiley and Richards, 1982; see Section II.D.1). The accomplished flying skills of shorebirds have resulted in great elaboration and complexity in their aerial displays, which have been accompanied in some cases by the

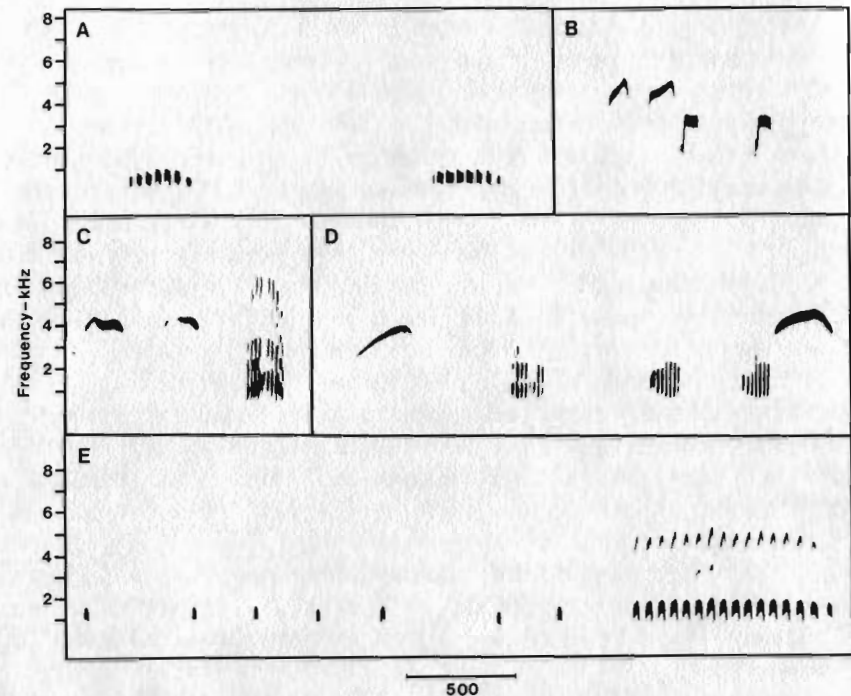


Fig. 17. Sound spectrograms of calls by undisturbed adults attending chicks at the nest, around the time of hatching (all are shown as natural sequences). (A) Mountain Plover (*Charadrius montanus*; made from recording by W. D. Graul). (B) Spotted Sandpiper (*Actitis macularia*; Sable Island, Nova Scotia). Two chick calls precede the parent's two calls. (C, D) Common Greenshank (*Tringa nebularia*). Two chick calls precede the parent's call in (C), and one precedes and follows the parent's calls in (D). [From Nethersole-Thompson and Nethersole-Thompson (1979, Figs. 42 and 45, respectively).] (E) Sequence of clucks followed by trill of Least Sandpiper (*Calidris minutilla*; Sable Island, Nova Scotia).

Analyzing filter bandwidth throughout, 300 Hz. Time marker is in msec.

evolution of morphological features increasing display conspicuousness. The evolutionary impetus behind such elaborations comes from sexual and other forms of social selection, plus adaptations of display features to the physical environment (see Section II.D.1). Considering the diversity of these selective pressures, it is clearly not realistic to consider aerial display as a simple, unitary phenomenon even just within shorebirds. Nevertheless, the structure of this display form reveals evolutionary trends and patterns of adaptive radiation, and may also shed much light on issues surrounding variation, information content, and social significance of a stereotyped, complex display.

Aerial display includes elaborate forms of descent, which may be terminal and return the bird to the ground, or may occur throughout display. A simple form occurs in the Least Seedsnipe, in which males fly silently to a height of about 10 m, begin to sing as they flutter, then continue to sing while they glide slowly to the ground with tail spread; similar display occurs in the gray-breasted Seedsnipe, *Thinocorus orbignyianus* (Johnson and Goodall, 1965; Maclean, 1969; E. H. Miller, unpublished observations). Most or all species of Tringini engage in some form of undulating aerial flight, in which they beat the wings as they rise, then glide down with spread tail, flutter and rise again, and so on in alternating rhythm (Cramp, 1983; Glutz von Blotzheim *et al.*, 1977; Grosskopf, 1958; Hale and Ashcroft, 1982; Rowan, 1929; von Frisch, 1956). Much more complex flight patterns occur, as in Red Knot (Nettleship, 1974), Jacksnipe [*Lymnocyptes minimus* (Kliebe, 1974)], and Northern Lapwing (Dabelsteen, 1978; see Section II.B.2). Most of the striking display attributes are related to some kind of descent, often coupled with distinctive vocalizations. In *Gallinago*, embedded dives during protracted high display flights are typical, and have been studied in detail in the Common Snipe (reviews by Reddig, 1978; Tuck, 1972). A somewhat stylized description of aerial display in this species follows (after Reddig, 1978; see Fig. 18).

During ascent, the bird keeps the tail closed. After reaching maximal altitude, he leans to one side (reaching a sideways angle of 70° or more), spreads the tail, then dives at an angle of about 41° relative to the horizontal. The two outermost rectrices are widely spread, to about $70\text{--}80^\circ$ relative to the long body axis, and the extended wings are held so that the tenth primary is about 55° relative to the long body axis. The wings make fluttering motions during the dive, and this is the only time that sounds are emitted, due to vibration of the outer rectrices in the air current modified by the wing action. The sound's frequency increases slightly during each dive, whereas amplitude increases markedly, being loudest at the dive's end, when velocity is greatest. A glide follows, then the bird rises again; the bird drops about 15 m in a typical dive (Fig. 18A). Display flights of snipe may cover an area of 250-m diameter or even more, and often show a roughly circular flight path. Birds almost always orient their dive to the outside, then recover subsequently (Fig. 18B).

Aerial display in Common Snipe differs from many species in that nonvocal sounds predominate. These are coincident with the repeated phases of ritualized descent. The tail of snipe has been modified as a display structure and the mechanics of sound production by the specialized outer rectrices have been studied by numerous workers (reviews by Reddig, 1978; Rutschke, 1976; Tuck, 1972). There is only a rough cor-

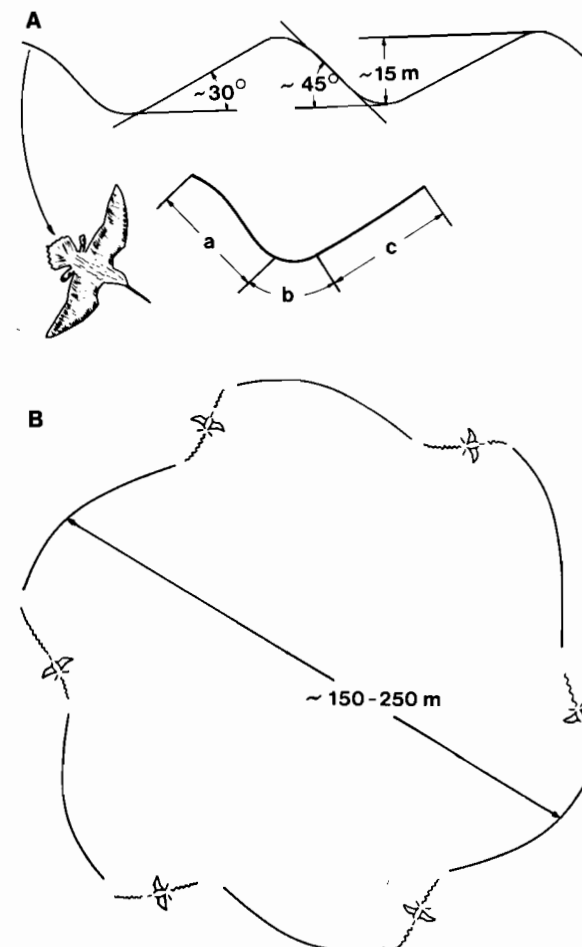


Fig. 18. Schematic diagrams of aerial display in the Common Snipe (*Gallinago gallinago*). (A) Phases of aerial display: a, dive with wing flutter; b, glide; c, steered flight during ascent. (B) Flight path during aerial display, showing the direction during drumming descent (wavy lines) and compensation during ascent and between dives (curved lines). [After Reddig (1978, Figs. 4 and 5, respectively).]

respondence between specialization of the tail and elaboration of the flight display, however (Sutton, 1981; see also Stettenheim, 1976). The Pintailed Snipe (*Gallinago stenura*) possesses up to 42 rectrices compared with about a dozen in Common Snipe, and the outermost of these are extremely stiff and narrow, "being about 1 mm wide from base to tip" (Sutton, 1981, p. 461). Males of this species apparently display communally in toks (a rough equivalent of an aerial lek) (Sutton, 1981; Tuck, 1972).

It is easy to envision the ritualization of descents from flight displays, because they are conspicuous and encode much information about the signaler's change in behavior. Further, because some nonvocal sound is invariably produced during rapid descent, the raw material for evolutionary elaboration of displays like those of snipe is present. A clear example of convergence on snipe aerial display is described by Labutin *et al.* (1982) and Veprintsev and Zablotskaya (1982) for the Little Curlew (*Numenius minutus*). This species shows embedded dives during its aerial displays, with remarkably snipe-like nonvocal sounds during the dives.

The taxonomic value of aerial displays has been discussed for vocal characteristics in Calidridini, most monogamous species of which use stereotyped, simple call sequences (Fig. 123; Miller, 1983a,b). The adaptiveness of such structure has presumably promoted convergence by other species, including American Golden Plover, *Pluvialis dominica* (Fig. 12A), and many or most *Charadrius* species (Cairns, 1977, 1982; Cramp, 1983; Glutz von Blotzheim *et al.*, 1975). Such convergence will make some taxonomic judgements difficult, but even in closely related groups like Tringini there are distinctive characteristics that set aerial displays apart. In many Tringini, calls uttered in aerial displays are roughly pure-tonal with stereotyped patterns of frequency modulation or occasional very short breaks, and in many contexts calls are given in bouts separated by longer pauses (Figs. 12C,D; Weeden, 1965). In general, the long-distance aerial displays of shorebirds do seem markedly conservative—at least as conservative as certain calls discussed in the previous section.

3. Agonistic and Sexual Ground Display

Visual components of agonistic and sexual ground display in shorebirds are very conservative across species. Three *Charadrius* species studied by Simmons (1953a,b) differ in their ground threat displays in ways that correspond to display intensity within species. Thus, the Ringed Plover (*Charadrius hiaticula*) normally leans slightly forward with the tail fanned and depressed (or elevated, at highest intensity), with the dorsal plumage fluffed, and with the black collar conspicuously displayed (Fig. 3 of Simmons, 1953a; Fig. A of Cramp, 1983). One male briefly assumed an upright hunched posture like that typical of the Kentish Plover. In addition, Ringed Plovers in low-intensity threat do not fluff the dorsal plumage, and initial phases of threat in the three species are highly similar. At very high intensity, threatening Snowy and Little Ringed Plovers (*Charadrius dubius*) may fluff the dorsal plumage, and the former may also fan the tail, thus resembling the Ringed Plover (see also Cairns, 1977, 1982; Edwards *et al.*, 1947; Glutz von Blotzheim *et al.*, 1975; Graul, 1973b;

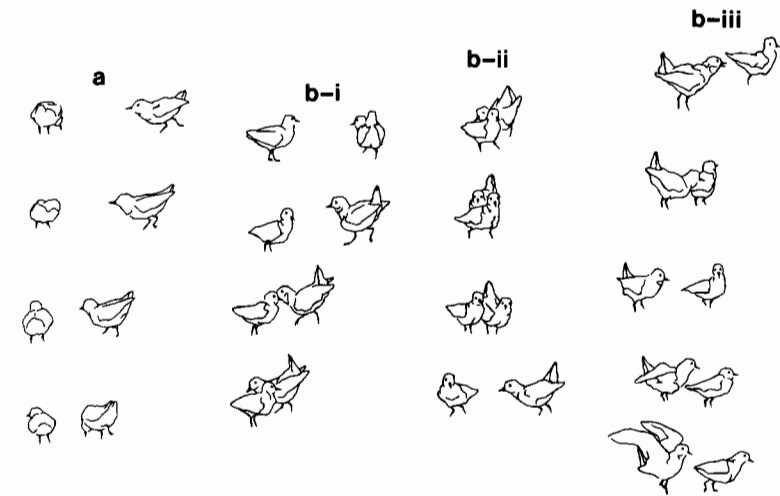


Fig. 19. "Courtship" approaches of female by male Least Sandpipers (*Calidris minutilla*) (two sequences). (a) The male approaches from the right with tail slightly erected, but begins feeding in the last sketch. (b) The male obliquely approaches the female from the right, with tail strongly erected and with body tipped up. The male sings in the top sketch of b-iii, and begins precopulatory flutter in the bottom sketch.

Columns are viewed from the top down; the top sketch in b-ii follows the bottom sketch in b-i, and similarly for b-iii. [Sketches are based on super-8-mm movie films; drawings by A. McClung.]

Phillips, 1972; Smith and Hosking, 1955). In the Little Ringed Plover, the typical threat posture is with a horizontal carriage, the flank feathers spreading over the closed wings, and the head retracted, resulting in a strikingly dorsoventrally flattened appearance in frontal view (Fig. 1 of Simmons, 1953a; Fig. B of Cramp, 1983). An almost identical posture is assumed in the Mountain Plover (Fig. 2 of Graul, 1973a) and the Semipalmated Plover [*Charadrius semipalmatus* (E. H. Miller, unpublished observations)]. Other widespread displays are precopulatory, including stereotyped high-stepping by the male preparatory to mounting (Boyd, 1972; Cairns, 1977, 1982; Clark, 1982; Cramp, 1983; Glutz von Blotzheim *et al.*, 1975).

In Scolopacidae, wing exposure and tail elevation are common in ground displays. Male Least Sandpipers approaching females or other males often just tilt forward and elevate the tail, both components becoming more extreme at close quarters (Fig. 19). Sexual approaches can often only be distinguished from aggressive ones by their slower tempo and more stereotyped actions. At higher intensity, one or both wings are lifted partially or fully, and (in the one-wing attitude) the wing may be

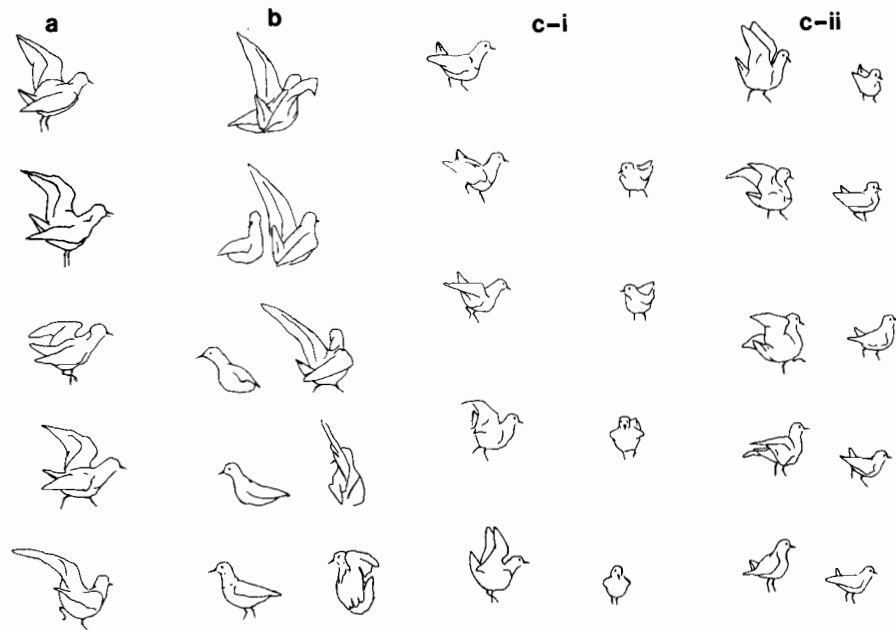


Fig. 20. "Courtship" approaches of female by male Least Sandpipers (*Calidris minutilla*) (three sequences). (a) The male stands (upper sketch), sings (second sketch), then rapidly approaches female, who is not illustrated. (b) The male fully erects his inside wing toward the female, adjusting his orientation to the female as she moves. (c) The male approaches the female from the left, with tail slightly erected, assumes a two-wing-up/tail-up display, then resumes a weak tail-up display (last sketch).

Columns are viewed from the top down; the top sketch in c-ii follows the bottom sketch in c-i. [Sketches are based on super-8-mm movie films; drawings by A. McClung.]

slowly and rhythmically pumped up and down (this is usually the wing closest to the other bird; Figs. 20, 21). Wing-up displays are so common in shorebirds that inferring their homology is difficult, though in the Calidridini alone strikingly similar displays to those mentioned have been described in many species (Bengtson, 1970; Cramp, 1983; Drury, 1961; Glutz von Blotzheim *et al.*, 1975). By using both structural and functional features (e.g., using contextual information), such inference can be strengthened, and it is thereby reasonable to point to tail-up postures of courting Upland Sandpipers and other curlew species as being homologous to those of calidridines (Fig. 22; Allen, 1980; Trimble, 1940).

4. Geographic Variation

No comprehensive studies of geographic variation in display behavior have been carried out, though Williamson made many significant obser-

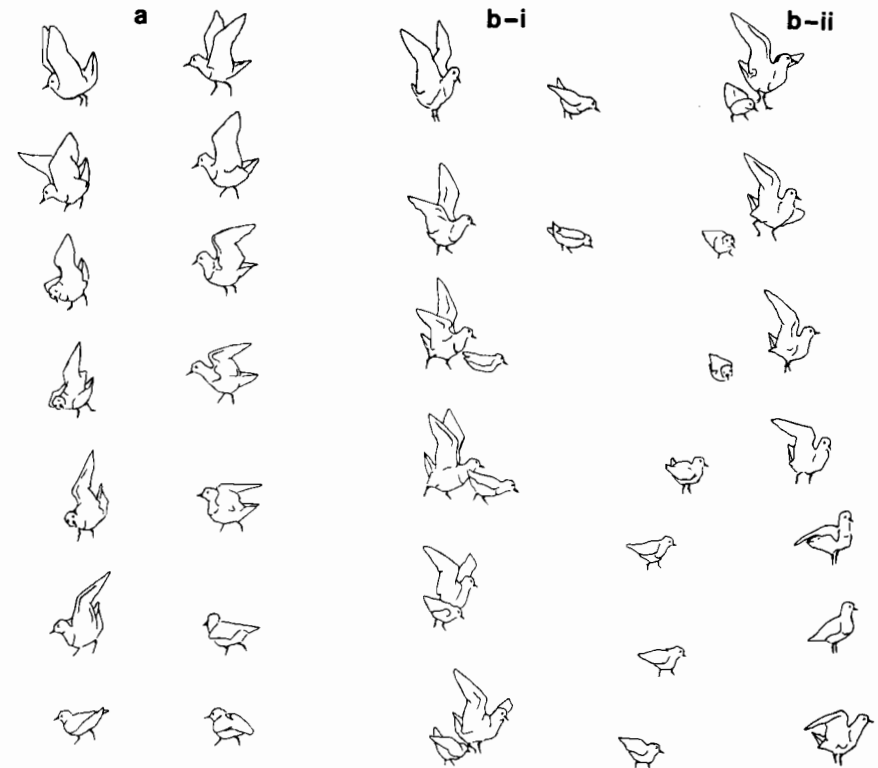


Fig. 21. Agonistic displays between male Least Sandpipers (*Calidris minutilla*) (three sequences). (a) Sequence during contest-running, beginning after the birds landed following a brief low flight together. The left-most bird has just landed in the top sketch, and twists to display broadside to the other (following four sketches). Meanwhile, the right-most bird assumes one-wing-up display and begins to run again; the left-most bird joins him (bottom sketch). (b) Approach by one male to another one feeding. The feeding male pays very little attention to the instigator, except to elevate the tail slightly and (bottom sketch in b-i) to tip.

Columns are viewed from the top down; the top sketch in b-ii follows the bottom sketch in b-i. [Sketches are based on super-8-mm movie films; drawings by A. McClung.]

variations in this regard for behavior in response to potential predators (see Section II.D.1). Thönen (1968) noted that drumming of Common Snipe in northern Alaska is different from that of European birds, and I have made a few comments on aerial displays of Least Sandpipers, Semipalmated Sandpipers, and Dunlins from different parts of North America (Miller, 1983a,b). Aerial song of Short-billed Dowitchers (*Limnodromus griseus*) is very similar in structure and organization throughout the breed-

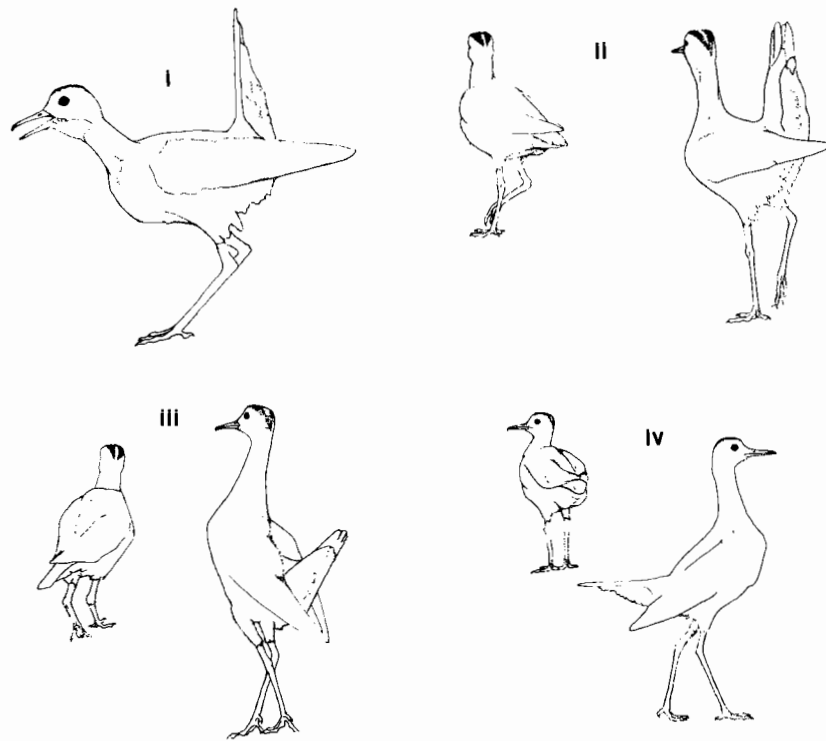


Fig. 22. "Courtship" approach of female by male Upland Sandpipers (*Bartramia longicauda*). The male quickly approaches the female (not shown) while calling softly (i), then chases her (ii); when the female slows down, the male stops and stretches vertically (iii), then both birds relax (iv). [Sketches are based on photographs by E. H. Miller and D. R. M. Hatch; drawings by A. McClung.]

ing range, based on recordings from northwestern British Columbia, northern Manitoba, and Labrador (Miller *et al.*, 1983). Though significant quantitative differences among these localities were detected, the same song components were present and they occurred in the same sequence in nearly all samples.

Fuller understanding of the significance of geographic variation can come through study of species with narrow or wide ranges, of closely related species, and of species on migration routes or wintering grounds. Ontogeny of display behavior is another crucial arena of investigation in this regard; preliminary work has been reported by Tikhonov and Fokin (1979, 1980).

III. CONCLUDING REMARKS

Our knowledge of communication in breeding shorebirds is based upon detailed studies of a few species, plus great numbers of general descriptions and anecdotes. In view of the large geographic ranges, ecological diversity, and variety of social systems exhibited even within many species of shorebirds, this is an unfortunate situation for it is not likely to be representative or fully revealing. Consider species like Common Snipe, which breed from Patagonia to Alaska, and in much of Europe and Asia; Killdeers, which breed in North and South America; Snowy Plovers of North America and Europe; and Eurasian Oystercatchers, which breed in Europe, Asia, and Australasia. Such widespread species are particularly attractive for research on geographic variation and species-specificity. Another important area for research is ontogeny, which could be studied for certain taxa able to be reared in captivity (e.g., see Schwinn, 1964; von Frisch, 1956). Species that are poorly known because of their inaccessibility, like Dromadidae, or their crypticity, like Rostratulidae and *Scolopax*, also await study. There is essentially no knowledge of tactual communication in shorebirds, though intriguing descriptions are available for a number of species: in Willets and many *Charadrius* species, males grasp the female during copulation (Cairns, 1982; Hansen, 1979); in the Piping Plover and Long-billed Plover (*Charadrius placidus*), females place their heads underneath the tail of the male in precopulatory display, and in the former species at least the female actually seems to place the tip of her bill against the male's cloaca (Cairns, 1977, 1982; Panov, 1963); and male Long-billed Curlews ruffle the shoulder feathers of the female in the stereotyped precopulatory "shaking" display (Allen, 1980). The nature, extent, and significance of tactual displays and display components merit detailed study. Finally, mechanisms of vocalization, and the relationship of sound characteristics to anatomy of syringeal and extra-syringeal sound sources are unexplored (see Gaunt, 1983b; Niethammer, 1966; Warner, 1969).

The burgeoning interest in shorebird biology has resulted in increased attention to all details of shorebird natural history, including social behavior. Detailed descriptions and basic documentation of behavioral biology in most shorebird species and populations are needed, but there are many ways to describe and quantify behavior, and these reveal different sorts of information and permit us to ask different kinds of questions. Further, our view of animal communication has been altered radically over the past few years, and any research into social behavior must

take this into account. For purely documentary purposes, one might hope that behavioral descriptions are of the most general but explicit form so as to make possible the posing of many different questions, and this is especially true for rare species and for those difficult to study. In general studies, or in studies with other purposes, workers should be particularly cautious about using interpretive or anthropomorphic terms as shorthand, and should try to base their descriptions upon observable motor patterns as much as possible.

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