PROBLEMS OF DISPLAY POSTURES IN THE CHARADRII (AVES: CHARADRIIFORMES)

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ABSTRACT

Studies of displays in the Charadrii (= waders or shorebirds) show that the same posture in different species, even quite closely related, may have a different function in a given context. As a corollary to this, two species even in the same genus may have quite different display postures to convey the same message. The problem is thus twofold: (a) to interpret the function of the display in the bird's world and (b) to trace the evolution of the display within a single well-defined suborder of birds such as the Charadrii. Threat displays are especially informative in such studies, but courtship, distraction and other displays are also useful. The value of display postures in the systematics of the waders is discussed.

INTRODUCTION

The Charadrii, or waders as they are commonly known, have been fairly well studied behaviourally. There are nevertheless many problems that arise from these studies, concerning the interpretation of display postures, both in their context as "language" and in their use as systematic tools. This is illustrated by the work of Simmons (1953) who showed that three species of plovers in the same genus have quite remarkably different threat postures, which can yet be derived from a common threat display basic to all three; there is no doubt in these cases about the meaning of the display, but their differences might initially throw into doubt the use of such behaviour as a systematic criterion.

Many of the observations reported on in this paper are my own, derived from several years' field experience of waders in ten of the 12 living families in North and South America and in southern Africa. Other information is taken from the literature. I shall deal separately with contextual problems and with phylogenetic or systematic problems as far as possible. I have chosen as examples those display postures that most clearly illustrate the nature of the problems.

PROBLEMS OF INTERPRETATION

The initial difficulty in any behaviour study is to determine the meaning, or signal function, of a particular display posture. This meaning can very often be deduced quite simply from the context in which the display is performed, such as a pre-copulatory soliciting posture by a female to her mate. But there are displays, many of them well known, whose meaning is obscure, although the context in which they occur is always the same and quite predictable. Such a display is the post-copulatory wing-raising run in plovers of the genus *Vanellus*. It occurs almost invariably after copulation and differs only in detail from one species to the next; it is usually accompanied by a

FIGURE 1
Mutual post-copulatory-run display in the black-winged plover *Vanellus melanopterus*. (From field sketches).

characteristic vocalization. In the blacksmith plover *Vanellus armatus* the wing-raising has been largely suppressed and the vocalization correspondingly elaborated to become an essential accompaniment to the post-copulatory run. The wing-raising posture is typically shown by the black-winged plover *V. melanopterus* (Fig. 1) in which the wing away from the partner is raised by each bird, but the hand is kept folded.

What does the post-copulatory run display of *Vanellus* mean? That it has signal function is indisputable, but the nature of the function is unclear, while its context could not be clearer. It is surely an extrapolation of the entire courtship ritual involving elements of the advertising-threat display which is dealt with later. Wing displays are frequent in *Vanellus*, as might be expected in a genus with such a conspicuous wing-pattern, but not all these wing-displays have a sexual context.

Raising of both wings fully opened over the back appears to have an advertising function when performed without vocalization or body movement. However, when such a wing-display is accompanied by alarm or threat notes and a rush at an intruder near the nest, it becomes a threat or distraction display as in *V. coronatus* (Fig. 2) and *V. senegallus* (Little 1967), usually directed towards animals of other species. Threat toward an intruder of another species is not necessarily the same as threat toward a conspecific bird. For example, one type of conspecific threat in *V. chilensis* consists merely in showing the bright red wing-spurs by removing the wrists from their pectoral "pockets" (Fig. 3A). Two opponents may square up facing each other in the

FIGURE 2
Advertising-threat display and vocalization of the crowned plover *Vanellus coronatus* toward a human intruder near the nest. (From a photograph).

posture called "upright threat" in *V. senegallus* whose "dark, inch-long, needlelike spurs on the wing were clearly seen" (Little 1967).

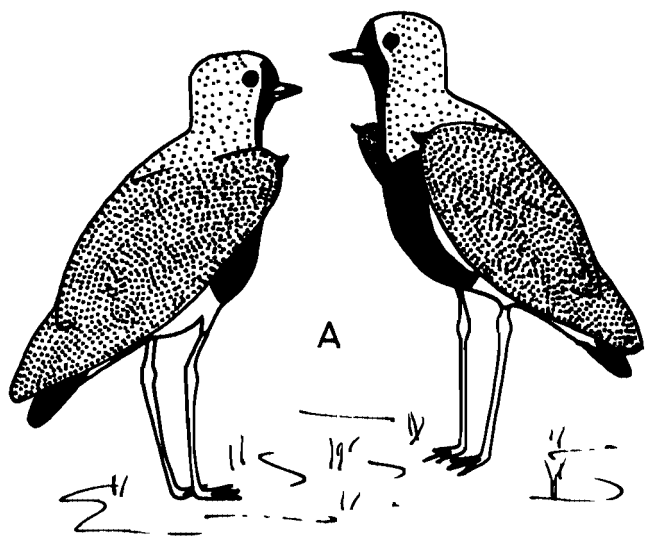
Another aggressive posture of *V. senegallus* is what Little (*loc. cit.*) terms "ground-pecking" threat; this is a head-down display which is also known in *V. malabaricus* (Jayakar & Spurway 1965). The difference in context and meaning between the head-up and head-down threat postures in *Vanellus* has been stated with certainty only for *V. vanellus* by von Frisch (1959), who claims that a head-up posture indicates defensive threat and a head-down posture aggressive threat. He appears to be correct, for the other species bear out this interpretation, although the observers have not specifically mentioned it.

Interspecific threat displays are usually more elaborate and conspicuous than intraspecific threat postures. The reasons for this are not hard to find. The signal function of threat must be quite clear to the threatened animal; a conspecific understands the language of the aggressor easily, so that the display can be minimal and still have its effect without drawing the attention of

possible predators to the displaying bird. The meaning of threat must be equally clear to an intruder of another species, especially if it is potentially dangerous, but the display must necessarily be more elaborate to get the meaning across; since the danger is so close anyway, the threatening bird need not take into account the possibility of attracting further danger by making itself conspicuous. In fact conspicuousness is all-important in this context. It is therefore interesting to encounter a raised-wing threat display in *Tringa totanus*, which it uses toward conspecific birds (Rüppell 1962). As in *Vanellus* the wing of *T. totanus* has a conspicuous white lining which is visible from a long way off, like the *Vanellus* advertising display. Probably both threat and advertisement are conveyed by these wing-postures, since aggression is closely tied to territorial behaviour.

Among other wing displays that I have seen in *Vanellus chilensis* is one in which two birds run together with wings opened vertically, unlike the post-copulatory display in which only one partly folded wing is raised, and resembling a moving advertising display (Fig. 3B). Another consists in holding one wing open, the other closed but with the spur exposed, and the body tilted forward as if the bird were feeding (Fig. 3C). This is no doubt a combination of ground-pecking (head-down aggressive) threat, advertising (wing-raising) display and the exposed-wrist element of the upright (defensive) threat posture. Only further study of this and other species will elucidate the function of these postures, which are almost certainly sometimes a mixture of several elementary ones combined to convey a particular meaning in a given context. The displays illustrated in Fig. 3 were in fact being performed simultaneously by birds in a single flock of *Vanellus chilensis* in an open field, and might have reflected some sort of socially facilitated ritual.

The question of what constitutes threat and what distraction is an interesting one because the difference is not always apparent. It does not lie entirely in whether the bird is moving toward or away from an intruder. There is the further complication of two types of threat behaviour: aggressive and defensive. In aggressive threat the drive to attack is uppermost; in defensive threat the drive to escape is dominant. There may also be a difference between threat directed toward a conspecific animal and threat toward one of a different species. I know of no species of wader in



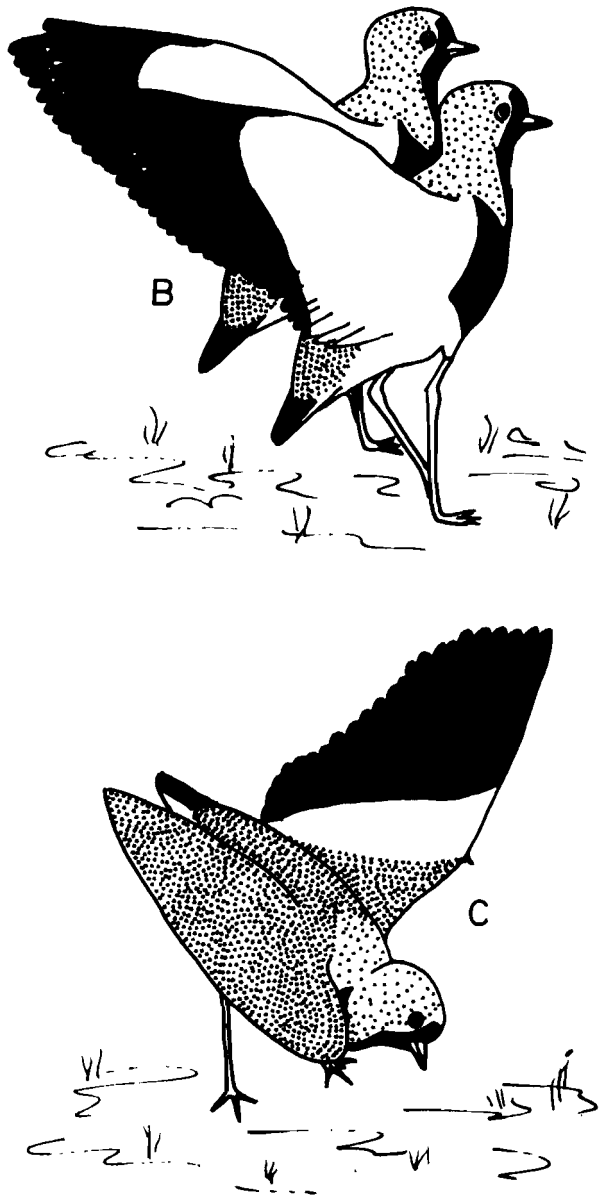


FIGURE 3
Displays of the southern lapwing *Vanellus chilensis*: A. Upright defensive threat in which the bright red wing-spurs are displayed; B. Mutual advertising-threat; C. Composite threat display involving head-down aggression, advertising-threat with left wing, and defensive threat with right wing. (From field sketches).

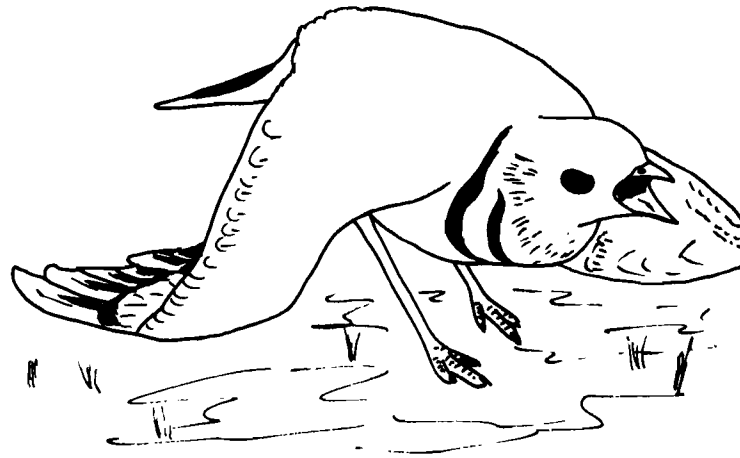


FIGURE 4
Aggressive threat display of the double-banded courser *Rhinoptilus africanus* attacking human intruder at the nest. (From a photograph).

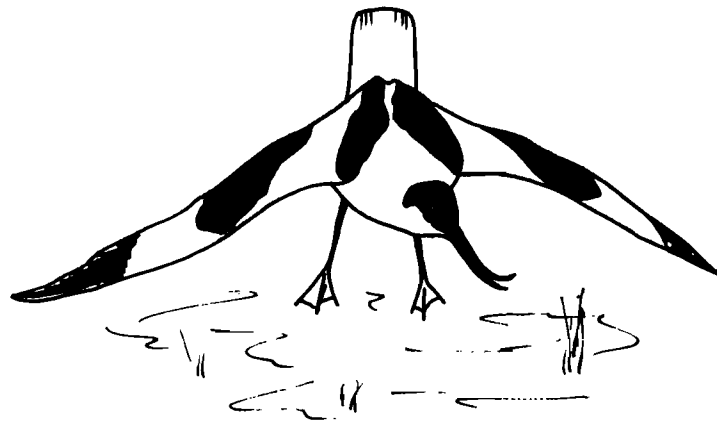


FIGURE 5
Aggressive threat display of avocet *Recurvirostra avosetta* at the nest. (From a photograph by Eric Hosking).

which all these nuances of threat and/or distraction display have been worked out. The whole series of displays includes the following intergrading elements:

1. Aggressive threat toward conspecific animal;
2. Defensive threat toward conspecific animal;
3. Aggressive threat toward animals of other species;

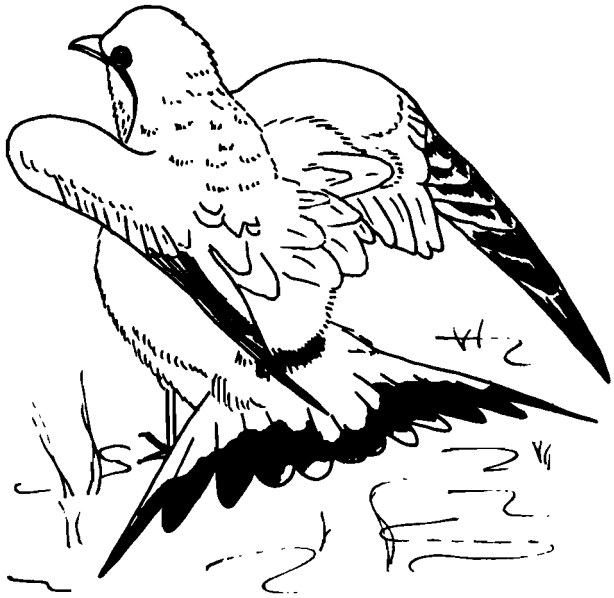


FIGURE 6
Aggressive threat display of the red-winged pratincole *Glareola pratincola* toward a conspecific bird near the nest. (From a photograph by Eric Hosking).

4. Defensive threat toward animals of other species;
5. Distraction with escape drive dominant;
6. Distraction with attack drive dominant.

The bird's behaviour will vary further according to whether the animal of another species is harmless or a predator. Each display may also be modified by alarm reactions involving fear, which will manifest itself as a strong escape tendency. A given display-complex can vary still further according to its intensity.

Threat displays usually concern conspecifics, or animals of other species that are not predators. Distraction displays involve dangerous animals of other species, whether predatory or not. Because of its relative inconspicuousness, conspecific threat is less well documented than interspecific threat in the Charadrii. Aggressive threat postures in one family may resemble defensive threat postures in another; for example the head-down element indicates aggression in the double-banded courser *Rhinoptilus africanus* (Maclean 1967) and in the avocet *Recurvirostra avosetta* (Figs. 4 and 5), but defence in the Cape dikkop *Burhinus capensis* (Maclean 1966), at least towards man. Indeed the highest intensity of interspecific aggressive threat display in the courser resembles the contextually quite different greeting display of the dikkop in all respects except that the courser's tail is depressed, the dikkop's raised. An example of aggressive threat differing within a single family is shown by the double-banded courser's head-down attack and the head-up attack of the red-winged pratincole *Glareola pratincola* (Fig. 6).

This introduces two further problems – one of definition and one of interpretation. Authors

differ in their definitions of aggressive and defensive threat. I have distinguished between them in *Burhinus capensis* which accompanies aggressive threat with advance toward the intruder and may end the display with attack, while its defensive threat is accompanied by retreat and finally departure (Maclean 1966). Von Frisch (1959) describes three types of threat display in *B. oedicnemus*, which I have translated freely as attack-threat, flight-threat and neutral (or defensive) threat. Thus the term "defensive" means flight-threat in my sense and "neutral" threat in von Frisch's sense. The concept of neutral threat seems to me to be somewhat nebulous; if further disturbed, the bird's threat display will become better defined in terms of flight or attack, depending on the type of disturbance. Thus it seems as if neutral threat is an ambivalent state between flight and attack. In the following account I shall use my own original meanings for these two displays, namely aggressive (= attack-threat) and defensive (= flight-threat).

It is perhaps significant that Rüppell (1962) did not see either "neutral threat" or *Rangordnungsdrohen* (= peck-order threat) (von Frisch 1959) in *Tringa totanus* in the field. Rüppell (*loc. cit.*) distinguishes only between flight-threat and attack-threat, as I do, although he describes also a "forward-threat". This last-named type seems to be simply a rather low intensity aggressive threat posture accompanied by movement towards the opponent.

There is disagreement also in the matter of interpretation of these threat postures in the genus *Burhinus*. Von Frisch (1959) assumes that all Charadrii are showing aggressive threat when the head is down, and defensive threat when the head is up. This is not so. He complicates the issue by saying respectively "Kopf und Schnabel tief" and "Kopf und Schnabel hoch", implying that the posture of the bill is also important, since the bird could hardly lower its head without also lowering the bill with it. Bill posture is important in some Charadrii, but von Frisch does not show that it is significant in *Burhinus oedicnemus*.

Broekhuysen (1964) and Maclean (1966) have described the head-up threat posture of *B. capensis* as aggressive. Broekhuysen's photographs clearly show the bird attacking with head raised high and tail fanned and cocked up. I have also shown (Maclean *loc. cit.*) that the defensive threat of *B. capensis* is a head-down posture, rather similar to the submissive posture, but accompanied by the distinctive threat note.

Clearly one cannot generalize about threat postures within the Charadrii as a suborder, nor even within the same genus as Simmons (1953) has shown.

The position of the tail is as meaningful as that of the head and often indicates the intensity of the display. This has been well shown in *B. capensis* (Broekhuysen 1964). Not only the position of the tail, but also the extent to which it is fanned, depend upon the intensity of the display (Fig. 7A, B, C). Neck-humping is a further postural element in the threat display of *B. capensis*, as well as of oystercatchers (Fig. 8) and jacanas (Fig. 9); the bill in these last two families is pointed downwards during the display. The question here is whether the meaning of neck-humping in these three families is the same. At higher intensities of threat the Magellanic oystercatcher *Haematopus leucopodus* raises the tail (Fig. 8A) but, like the dikkops, not at lower intensities. I have not seen tail postures in threat displays of the African jacana *Actophilornis africana;* moreover the body position differs quite markedly. The dikkops and oystercatchers hold their bodies upright, the jacana more horizontally with legs flexed (Fig. 9).

The African jacana's threat posture actually looks more like a submissive or appeasement posture, but its context as threat is quite clear. Less clear in meaning is the horizontal

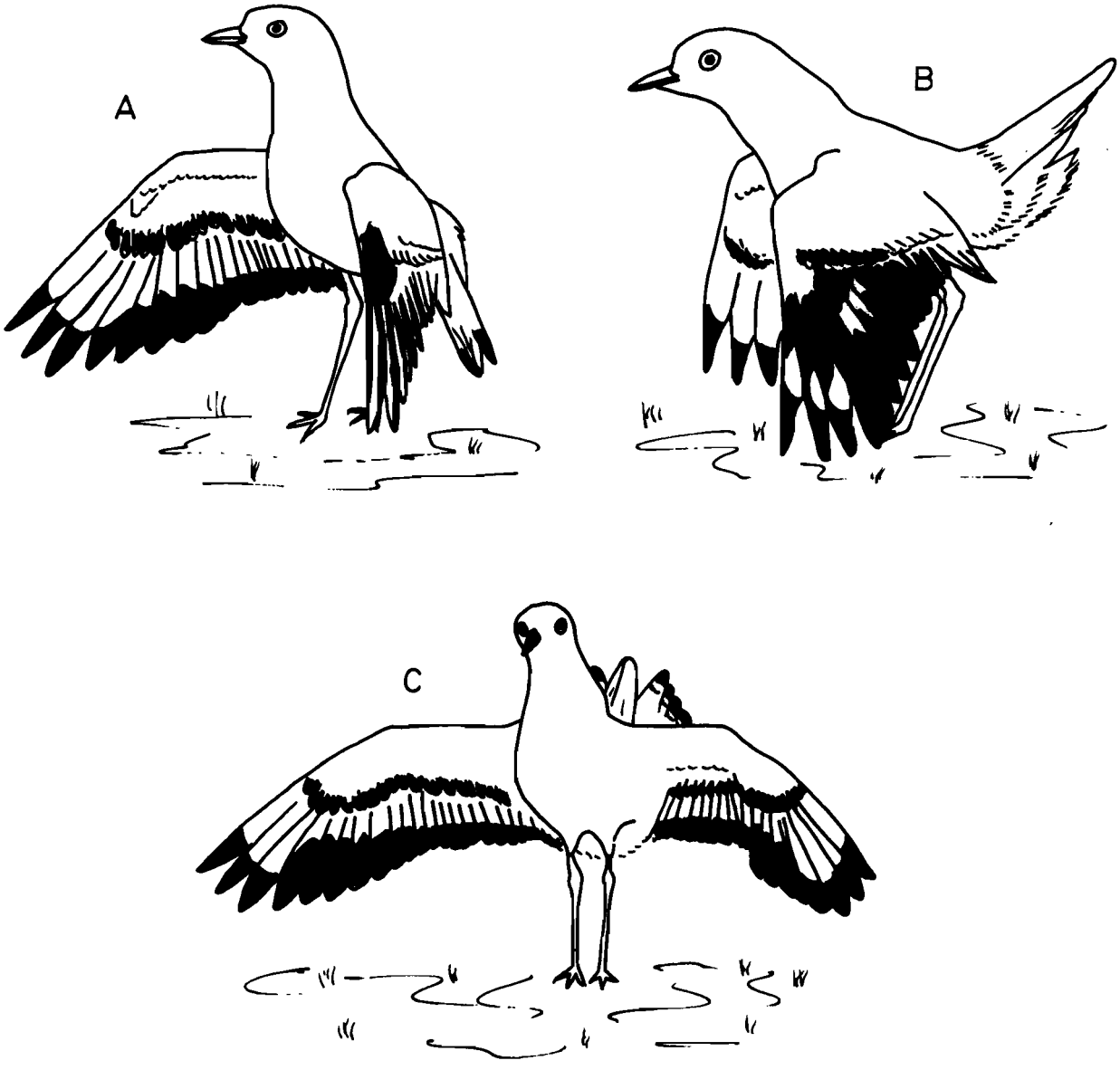


FIGURE 7
Aggressive threat display of the Cape dikkop *Burhinus capensis*: A. Low-intensity; B. Medium-intensity; C. High-intensity. (From photographs by G.J. Broekhuysen).

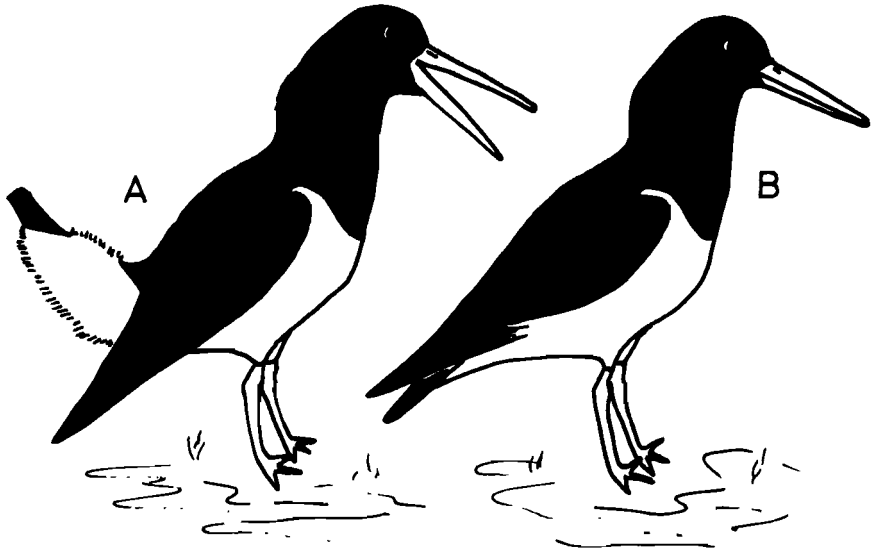


FIGURE 8
Aggressive threat displays of the Magellanic oystercatcher *Haematopus leucopodus* toward conspecific birds: A. High-intensity with piping call note; B. Low-intensity with neck-humping only. (From field sketches).

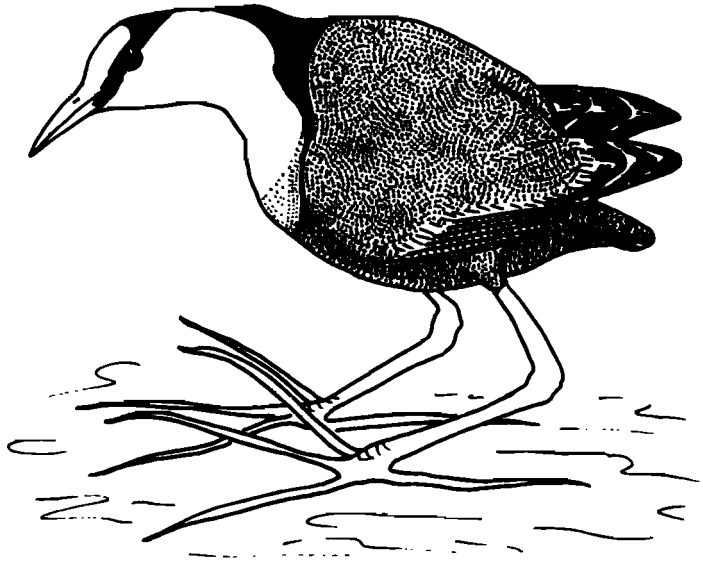


FIGURE 9
Aggressive threat display of the African jacana *Actophilornis africana* toward conspecifics and birds of other species. (From a field sketch).

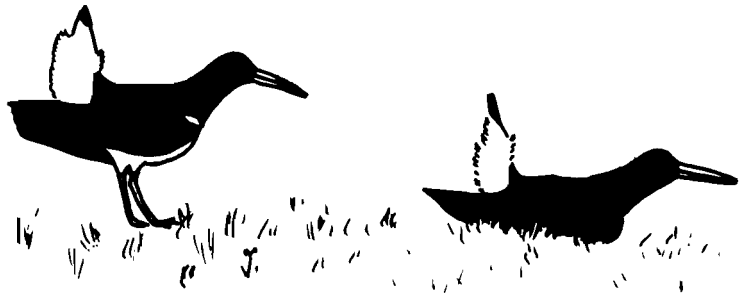


FIGURE 10
Mutual display of *Haematopus leucopodus* elicited by a human intruder near the nest. The right hand bird is also false-brooding. (From a photograph).

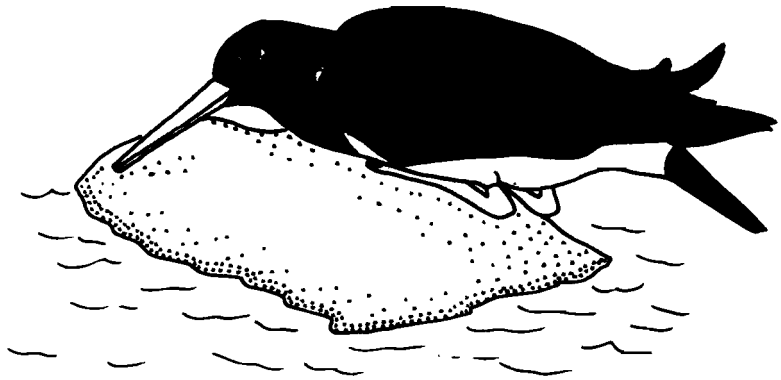


FIGURE 11
Haematopus leucopodus false-brooding on an offshore boulder in response to a human intruder near its chicks. (From a photograph).

body-posture of the Magellanic oystercatcher (Fig. 10) when disturbed near the nest. The raised tail probably shows aggression, while the horizontal body may indicate defence. The front bird in Fig. 10 is also false-brooding (or displacement-brooding); this is a common reaction to intruders at the nest or near the young (Fig. 11) but seldom incorporates other postural elements. The birds in Fig. 10 are reacting both to each other and the human intruder near their nest. The display seems to involve an element of "greeting" of the kind described for the Cape dikkop (Maclean 1966), as well as alarm with strong escape tendencies, and false-brooding which is in the nature of a distraction display. It is impossible to decide whether the function of distraction is incidental to this particular set of behaviour patterns, or if it is one of the ritualized distraction displays typical of this species. The elements of threat may throw some light on true distraction displays.

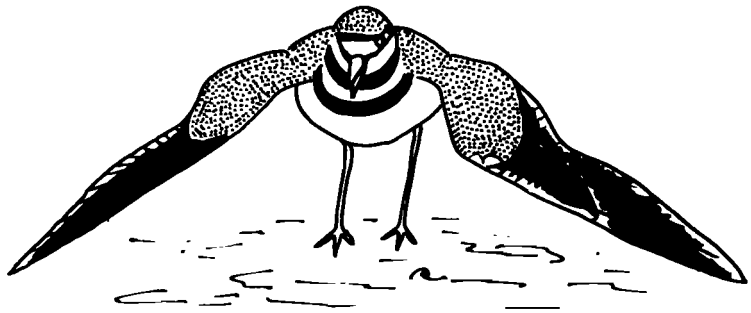


FIGURE 12
Attack phase of injury-feigning distraction display of the killdeer *Charadrius vociferus* toward a human intruder at the nest. (From a photograph).

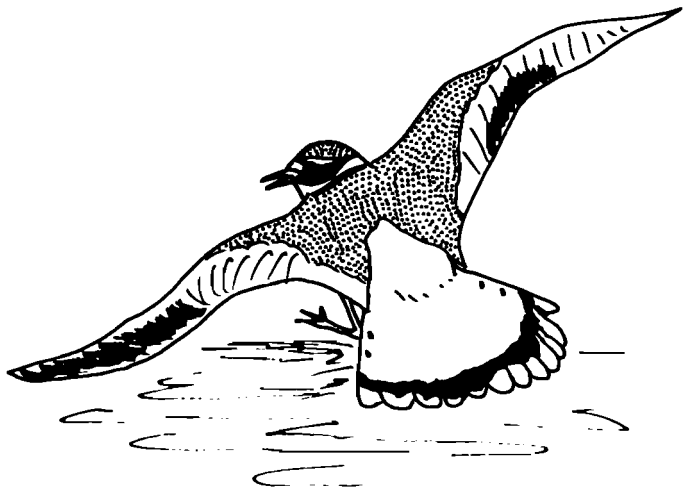


FIGURE 13
Escape phase of injury-feigning distraction display of *Charadrius vociferus* toward a human intruder at the nest. (From a photograph).

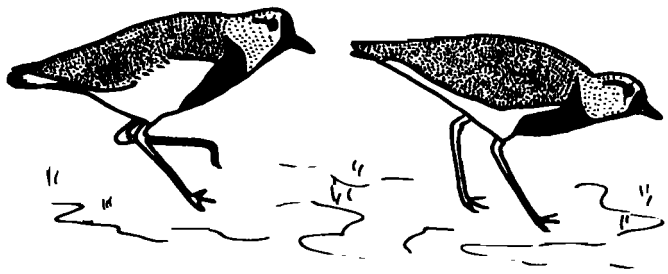


FIGURE 14
Low-intensity crouched run of *Vanellus chilensis* with chicks, reacting to human intrusion. (From a photograph).

Distraction displays reach a high degree of development in the plovers. The killdeer *Charadrius vociferus* of the New World is one of the best known examples. This species has an attack phase (Fig. 12) in which the intruder is approached to within a metre or less as the bird beats or drags its wings on the ground and stands high on its legs. This is followed immediately and repeatedly by an escape phase (Fig. 13) in which the bird totters away from the intruder, its body low on flexed legs, wings beating or vibrating and tail fanned to show a bright pattern of black, white and orange-chestnut; this is the classical "injury-feigning" display. Threat elements in the attack phase are easily distinguishable, but the apparent distress exhibited by the wing movements in both attack and escape phases may be a *de novo* development. The possible course of evolution in these displays can only be guessed at until more is known about their details.

Deane (1944) gives detailed descriptions of distraction displays in the killdeer, and ascribes "training and intelligence" to the execution of a perfect injury-feigning display. This is a doubtful notion in so stereotyped a behaviour pattern. The main value of his paper lies in its good descriptions and illustrations.

Injury-feigning displays are by no means confined to the Charadrii. They occur in such diverse groups of birds as sandgrouse, doves, larks and pipits: except for the doves, these birds invariably nest on the ground and it is surely significant that those doves in which the display is best developed also nest on the ground or near it in low vegetation (e.g. the Namaqua dove *Oena capensis*). The selection pressure for such distraction displays in ground nesters must therefore be intense.

Usually classed as distraction behaviour is the rodent-run type of posture found in nearly all Charadrii. It is an intruder reaction with intraspecific signal function, whose distraction effect on the intruder is probably a later incidental development. Attempts have been made to distinguish between different kinds of distraction display. For example Brown (1962) records six types of distraction behaviour in the Western sandpiper *Calidris mauri*: injury-flight (flight, in the sense of fleeing), rodent-run, crouched run, alert, squat and "approach and attack". Injury-flight seems to be the equivalent of injury-feigning as described for other waders; little is gained by the invention of new terms like this for well known displays. The impression I get from my own studies and those of others is that the rodent-run (tail depressed and spread, wings drooped and trailed and possibly flapped, head hunched, and feathers ruffled) is simply a low-intensity injury-feigning, while the crouched run (Fig. 14), which is similar to the rodent-run but with wings and tail held normally, is merely a low-intensity rodent-run. Brown says that it is often difficult to distinguish between one display and another, which seems to bear out my conclusion that these different distraction displays represent variations in the intensity of the same display.

The "alert" posture is common in waders and other ground-nesting birds. I do not consider it to be a distraction display, but rather one of alarm, especially since it is accompanied by alarm notes in most species in stress circumstances. It probably has intraspecific signal function, however, and may be regarded therefore as a display posture.

The squat is undoubtedly false-brooding, a common displacement activity in the Charadrii, Pterocli (sandgrouse) and other related birds (Maclean 1968). To call this display a "squat" may lead to confusion in this context, since Broekhuysen (1964) described a "squat" of a rather different kind in *Burhinus capensis;* in this species the squat may represent simple false-brooding, or it may be accompanied by spread wings and tail, indicating, as Broekhuysen says, a conflict of

threat and incubatory urges, much the same as the oystercatcher displays in Fig. 10. The combination of postures will certainly serve as a more effective distraction display than simple false-brooding and may illustrate the way in which true injury-feigning may have evolved. If wing and body movements are added to the highest intensity squat display of the Cape dikkop, a distraction display of the injury-feigning type may be derived.

Further clues to the relationships of distraction displays may be found in the European oystercatcher *Haematopus ostralegus*. Williamson (1952) describes a "furtive-run" (probably the equivalent of rodent-run) which he says is essentially a preliminary to false-brooding and also a component of "lure display" (by which he means injury-feigning). Indeed all these displays seem to be closely related. It is nevertheless useful to distinguish between false-brooding, rodent-runs of varying intensity, injury-feigning, and possibly the "squat" described by Broekhuysen (1964).

The literature on distraction displays brings out the confusion resulting from the welter of names used by different workers for the same display. This problem is not unique to the behaviour of the Charadrii, nor even to the science of ethology; it is a problem that should nonetheless be resolved by a standardization of terminology, using those terms that best illustrate the nature of the display and its possible derivation. Armstrong (1949) attempted to standardize the terminology of distraction displays, but his terms have not yet won general acceptance, possibly because they partly involve the substitution of a synonym for an established word (e.g. "diversion" for "distraction"), which is unhelpful. He also advocates such terms as "eccentric deportment", which is not sufficiently clear in itself to be of any use to ethologists. Armstrong's paper is, however, valuable in bringing together many of the different terms used by various authors for the same behaviour pattern.

Another problem of distraction displays is the question of how far they are intraspecifically meaningful. These displays are released by intruders, usually of a dangerous nature, and their function toward such animals is clear, but there is little information on the effect of the displays on other birds of the same species. It is my experience that a high-intensity distraction display of the injury-feigning type, especially when it is accompanied by alarm notes, quickly attracts the attention of the displaying bird's mate, and even of neighbouring conspecific individuals. This is probably more than a simple incidental effect of the display which may even be interspecifically effective. For example I have seen an injury-feigning yellowbill duck *Anas undulata* elicit alarm reactions from a large flock of little grebes *Podiceps ruficollis* on the same pond.

PHYLOGENETIC PROBLEMS

One might reasonably expect displays of a particular kind to be similar in related groups or species of waders. The differences in the threat displays of certain plovers of the genus *Charadrius* can be explained by the fact that they have been "developed and stereotyped" at different points of the same basic range of behaviour patterns (Simmons 1953). There are, however, many instances of very clear similarities between the displays of other waders that are obviously closely related. A universal alarm reaction of waders is the "bob", usually involving the head and body. In the coursers only the tail may be dipped or the body bobbed without involving the head (Maclean 1967). The seedsnipe (Thinocoridae) of South America bob only the head in low-intensity alarm situations; at higher intensities the tail is also rocked up and down asynchronously with the head

(Maclean 1969). Bobbing is also a common alarm display in the bustards (Otididae: Gruiformes) and may be an indication of phylogenetic relationship (a relationship that can be demonstrated on other grounds); but it occurs also in birds as diverse as ducks, parrots and kingfishers. The details of bobbing behaviour are important in a phylogenetic study, because it is hardly surprising to find a flight-intention movement ritualized into a bob in a wide variety of flying animals. Bobbing in the Charadrii has a characteristic quality, the details of which need to be worked out by a study of motion-picture sequences; only in this way can a wader-bob be defined accurately and distinguished from the bob of another taxon of birds.

Another display posture of possible phylogenetic significance is neck-humping. It is indicative of high-intensity threat displays in the dikkops (Burhinidae) and in Hartlaub's gull *Larus novaehollandiae* (Tinbergen & Broekhuysen 1954). It occurs also in the Magellanic oystercatcher (and possibly in other species too) in what also appears to be a threat display, as well as in the African jacana. Although the dikkops and oystercatchers are closely related (Jehl 1968), their relationship with the jacanas is not very close, and with the gulls (Laridae) not close at all, so that neck-humping may be an ordinal behaviour pattern throughout the Charadriiformes, if only intermittently. The problem here is to determine whether neck-humping has a common origin in those taxa where it occurs. It would also be valuable to know if it occurs in the threat displays of closely related orders like the Gruiformes.

I have observed another display posture performed by members of two widely separated wader families – the spotted sandpiper *Actitis macularia* (Scolopacidae) of North America (Fig. 15) and the three-banded plover *Charadrius tricollaris* (Charadriidae) of South Africa (Fig. 16) – in which the incubating bird raises the posterior part of the body, sometimes cocking the tail up and displaying the white undertail coverts. I have not seen this behaviour described in the literature, nor have I determined its meaning, but it seems to have an advertising function in signalling the presence of the incubating bird to its mate. However, it is not always possible to see the second member of the pair, especially when observation is being done from a hide at the nest.

The genus *Charadrius*, although structurally homogeneous and exhibiting clear similarities in other ways, shows quite remarkable variability in the occurrence and type of distraction displays from one species to another. The killdeer *Charadrius vociferus* has a highly developed form of the display as already described; other species have distinct, if less elaborate, injury-feigning displays, but the three-banded plover *C. tricollaris* has hardly any vestige of injury-feigning left in its brief and rarely performed distraction behaviour.

What determines the degree of development of distraction displays? Some of the factors involved must surely include the nature of the predators, habitat and social organization of the species concerned. The details of these factors must be worked out for a full understanding of distraction behaviour. Until this has been done, it will remain hard to know why two species of one genus of plovers, similar to one another in size and apparently similar in habitat and subject to similar predation, should have evolved widely different distraction displays. Another question to be answered is whether the simpler forms of the display are vestigial or primitive.

Wing postures in the Charadrii are as problematical as any. Patterned wings have arisen several times independently within the suborder (e.g. Vanellinae, Burhinidae, *Catoptrophorus*, Haematopodidae, to name a few), so it is more than likely that wing displays have similarly polyphyletic history. Within the Burhinidae wings spread in a vertical plane are indicative of threat, but in a

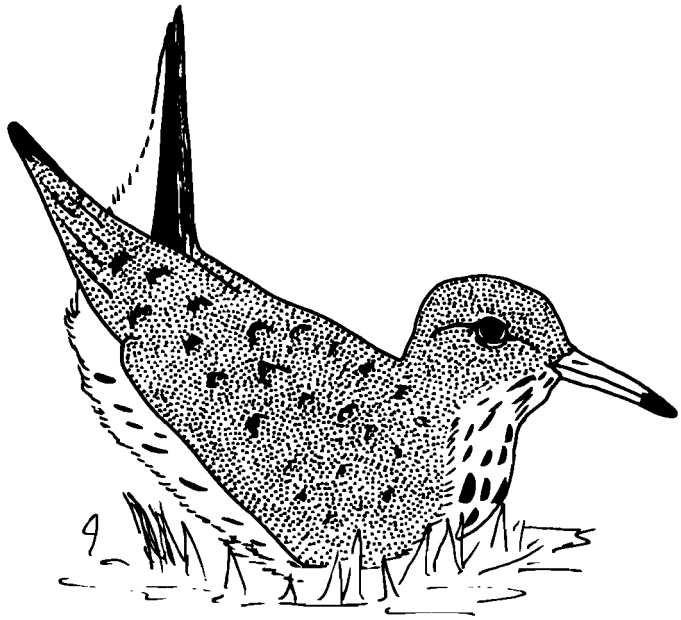


FIGURE 15
Incubating spotted sandpiper *Actitis macularia* displaying undertail coverts, probably to its mate. (From a photograph).

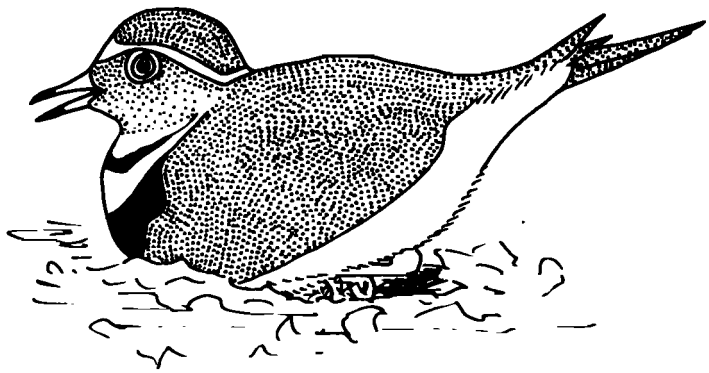


FIGURE 16
Incubating three-banded plover *Charadrius tricollaris* in a low-intensity display of the kind illustrated in Fig. 15. (From a photograph).

horizontal plane are a sign of greeting (Maclean 1966), whereas a very similar display to the latter in the avocet *Recurvirostra avosetta* (Fig. 5) indicates threat. These two families (Burhinidae and Recurvirostridae) are without doubt closely related (Jehl 1968), but their wing postures might well have independent origins. If they have a common origin, their meanings have changed with time – a frequent enough occurrence in animal behaviour. Only further analyses of the contexts, movements and postures involved may shed light on the phylogenetic relationships of these displays, if indeed they exist at all.

This discussion has only touched on some of the more obvious problems involved in a study of wader behaviour patterns. Others exist in great profusion, but this account should be enough to indicate the nature of the problems. The importance of further studies on wader behaviour has been stressed by Bock (1958) who said that "the comparative ethology of the plovers is still in its beginnings and of no help to our understanding of the specific relationships of the plovers at this time." The situation has changed little since then and, as he stated further, "the need and desirability of behavioural studies comparable to those done on the ducks, gulls and terns cannot be urged too strongly." Quantitative analyses of behaviour patterns with the aid of motion pictures are perhaps the most valuable.

SUMMARY

Interpretation of the meanings of display postures in the Charadrii (waders or shorebirds) may be inferred from the contexts in which they are performed. Similar meanings may be conveyed by radically different displays in different groups of waders, whether closely related or not, in similar contexts. The same posture in two different groups may convey different meanings in the same or in different contexts. These situations lead to difficulties of interpretation of the phylogenetic significance of display postures in these birds. Matters are further complicated by lack of standardization in the terminology of wader behaviour patterns. Only further study and standardization will result in better understanding of the meanings and phylogenetic relationships of display postures and other behaviour patterns in the Charadrii.

ZUSAMMENFASSUNG

Die Bedeutung des Imponiergehabens bei Charadrii (Watvögeln) kann gewöhnlich aus dem Zusammenhang abgeleitet werden, in dem es auftritt. Dabei können ähnliche Funktionen selbst in nahe verwandten Gruppen durch grundsätzlich verschiedene Verhaltensweisen erfüllt werden. Andererseits kann dieselbe Gebärde in zwei verschiedenen Artengruppen, entweder in demselben oder in einem anderen Zusammenhang, verschiedene Bedeutung besitzen. Diese Sachlage macht es schwierig den phylogenetischen Wert der Imponierverhaltensweisen dieser Vögel zu deuten. Das wird ferner kompliziert durch das Fehlen einer standardisierten Terminologie für manche Verhaltensweisen. Für das endgültige Verständnis der Bedeutung und des phylogenetischen Wertes des Imponierverhaltens sind daher weitere Beobachtungen und Standardisierungen dringend erforderlich.

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