

# Plumage colour and pattern in waders

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At least 16 of the hypotheses that have been proposed to explain the evolution of plumage colour and pattern in birds may be applicable to waders – five straightforward physical explanations, and the rest involving some form of communication between animals. Eight of the latter involve communication between different species (such as predator and prey) and the rest involve communication between individuals of the same species (such as potential mates). These hypotheses are reviewed and an additional one based on social selection proposed.

## INTRODUCTION

At least 30 hypotheses have been proposed to explain adaptive coloration in birds (Savalli 1995). The evidence usually consists of little more than a few examples, and it is often possible to cite just as many contradictory ones (Baker & Parker 1979). We tend to rely on our own judgement about what constitutes, for example, good camouflage, overlooking how easy it is to make the facts fit our preconceptions (see Fig. 1). Most mammalian and avian predators have vision that is very different from our own, probably better in the case of birds and worse in the case of mammals (Endler 1978, Jacobs 1993, Finger & Burkhardt 1994). This makes it difficult to design good experiments to test many of the ideas about animal coloration, but this should not discourage wader workers from trying to do so.

## TYPES OF PLUMAGE COLOUR

Plumage coloration can be produced by physical effects as well as by pigments, and there are examples of both of these in waders. Melanin is perhaps the most familiar and widespread pigment occurring in feathers. It is derived from the amino acid tyrosine and occurs in at least two quite different forms – eumelanin and pheomelanin. Eumelanin is responsible for the browns, greys and blacks that are present in at least some of the feathers in nearly every species of bird. The pigment occurs in granules that are restricted to the outermost layers of the feather keratin.

Pheomelanin produces various shades of brown, chestnut and red, including the bright red breeding plumage of many wader species, such as Red Knot *Calidris canutus*, Dunlin *C. alpina*, Curlew Sandpiper *C. ferruginea* and Bar-tailed Godwit *Limosa lapponica* (Harrison 1965, Lucas & Stettenheim 1972). Several other species have orange-brown or chestnut areas of feathering that are probably due to pheomelanin but in which the precise nature of the pigment remains to be established, e.g. Northern Lapwing *Vanellus vanellus* (vent), American Avocet *Recurvirostra americana* (head and breast), Red-necked Avocet *A. novaehollandiae* (head and neck), Banded Stilt *Cladorhynchus leucocephalus* (breast) and many plovers (breast and/or belly). Another form of melanin is responsible for the yellowish plumage of many young birds (Lucas & Stettenheim 1972) including the chicks of *Pluvialis* plovers.

Tyndall blue is one of the colours produced by physical effects. It is also referred to as incoherent Rayleigh or Nie scattering, though it is actually produced by coherent interference (Prum *et al.* 1998). This involves the reflection of shorter wavelengths of light by minute air bubbles in the feathers and the absorption of longer wavelengths by underlying melanin deposits. No waders show pure blue but the Ibisbill *Ibidorhyncha struthersii* has bluish-grey on the head and neck, and the Egyptian Plover *Pluvianus aegyptius* has blue-grey wing coverts and tail feathers. These probably owe their coloration to Tyndall effects since bluish pigments are extremely rare in bird feathers. Iridescence occurs more commonly in waders. For example, it is responsible for the glossy sheen on the back of many oystercatchers, the Red-kneed Dotterel *Charadrius cinctus* and Black Stilt *Himantopus novaehollandiae*, as well as the iridescent blue, green and brown of the mantle and wings in Northern Lapwings and Southern Lapwings *V. chilensis*. Typically, iridescence is produced by several evenly spaced and parallel layers of melanin granules, separated by keratin. Light is reflected by the top of each layer and the interaction between the refractive index of keratin and the spacing of the layers determines the colour produced (Lucas & Stettenheim 1972).

Carotenoids are the other main group of pigments found widely in bird feathers. They are responsible for a range of bright red, orange and yellow colours. Most of the yellows and reds in wader plumage are produced by pheomelanin (Harrison 1965, Lucas & Stettenheim 1972). Indeed, the only published evidence of carotenoid pigment in the feathers of a wader, refers to an unidentified one responsible for the greenish-yellow wing feathers of the Northern Jacana *Jacana spinosa* (Auber 1957). In waders, therefore, carotenoids are largely restricted to the iris, orbital ring, legs and beak. The red colour of all of these areas in oystercatchers *Haematopus* spp. is probably due to carotenoids.

## TYPES OF PLUMAGE PATTERN

The transition between differently coloured areas of plumage can be divided into three different types – (i) gradual, (ii) abrupt and irregular, and (iii) abrupt and regular. In the case of a gradual transition, the colours merge into one another, and it is impossible to define a precise border. For example, the orange-brown neck of the American Avocet fades gradually into the white of the rest of the body. Irregular, abrupt



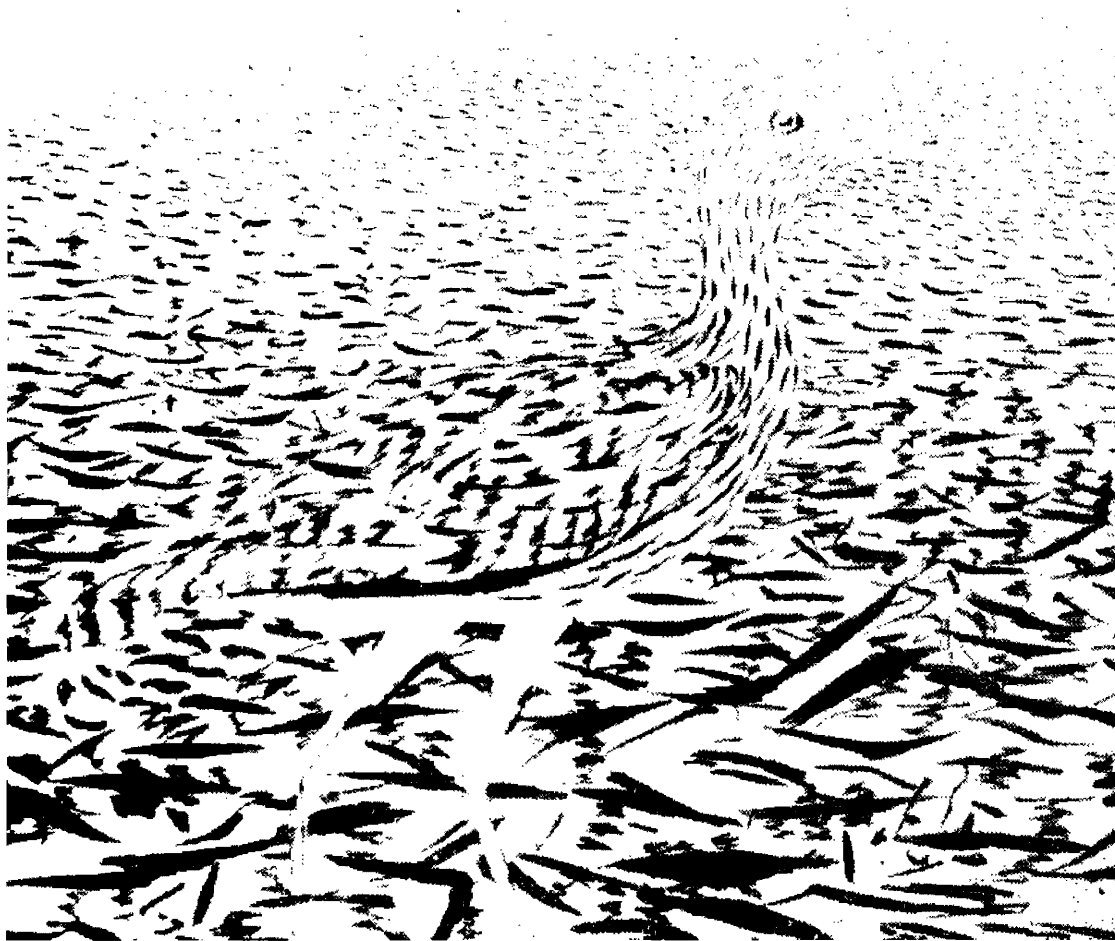


Fig. 1. Curlew drawing from Thayer (1909). Although the Curlew does have plumage that is cryptic against a background of grass, it is possible to infer that almost any plumage pattern is cryptic by presenting the bird against an appropriate background.

transitions are not especially common, but are seen in the black wing tips of the Pied Avocet *Recurvirostra avosetta*, and the white wing patches of the White-tailed Plover *Vanellus leucurus* and Long-toed Lapwing *V. crassirostris*. Transitions that are abrupt and regular, i.e. that involve a sudden change in colour along a straight or smoothly curving border are common in waders; for example most of the head and neck bands of plovers have borders of this type. Indeed, of the nine families of waders, this type of transition is common on the head and body of eight of them (Rostratulidae, Dromadidae, Haematopodidae, Ibidorhynchidae, Recurvirostridae, Glareolidae, Burhinidae (head only) and Charadriidae). Only in the largest family – the Scolopaciidae – are abrupt, regular borders largely absent (with the exception of a few eye stripes). The overall patterns that are separated by borders of these types may depend simply on the shape of a particular area of the body that they highlight, e.g. the rump, or they may have a specific shape – notably stripes and lines on the head and wings, and curved bands on the chin, breast and belly.

Other patterns, including those involving streaks and spots cannot easily be categorised in the above way since they do not involve uniform blocks of colour and do not have very precise borders. These patterns are usually associated with crypsis.

## PHYSICAL FUNCTIONS OF COLOUR AND PATTERN

### Thermoregulation

Dark colours increase the absorption and emission of energy from solar radiation, whilst light ones decrease it (Campbell & Norman 1998). For this reason, Fjeldså (1977) has suggested that the dark dorsal plumage of some chicks from damp habitats may be an adaptation to faster warming in the sun, whilst the pale dorsal colours of others from arid environments may protect them by reflecting light and heat. Red-necked Phalarope *Phalaropus lobatus* chicks may be in the former category, and Stone Curlew *Burhinus oedicephalus* chicks in the latter.

### Physical protection

Melanin improves the resistance of feathers to wear in a wide range of species (Barrowclough & Sibley 1980, Bergman 1982). This probably explains why the flight feathers of most waders are dark, even when the rest of the plumage is pale, e.g. most coursers *Cursorius* spp. In the case of variegated feathers, the paler edges wear faster in waders (Hayman *et al.* 1986).



## Radiation protection

Dark colours, especially those produced by melanin, protect feathers from damaging UV radiation that might otherwise accelerate the rate of feather wear (Burt 1978, Hayman *et al.* 1986). Such wear is especially likely in the exposed tips of the primaries (Burt 1978, 1986) and so these are often protected by heavy deposits of melanin, and there is usually a slight decrease in the amount of melanin proximally, e.g. most lapwings and plovers of the genus *Vanellus*.

## Sighting lines

It has been suggested that eye stripes, with their sharp borders, can act as sight lines and hence improve the accuracy with which birds can strike at mobile prey (Ficken & Wil-mott, 1968, Ficken *et al.*, 1971). In waders this is most likely to be of value to plovers and many of them do have conspicuous eye stripes. However, Graul (1973) thought it unlikely that this was the explanation for their presence in this group.

## Glare reduction

Light coloured plumage near the eye could cause glare and thus interfere with vision, leading to an advantage for dark plumage in this area (Ficken *et al.* 1971, Burt, 1984, 1986). Whilst many waders do have the eye surrounded by dark feathers there may be other reasons for this (see below), and several species that forage in habitats with plenty of glare have white head plumage, e.g. Banded Stilt *Cladorhynchus leucocephalus*, Long-toed Lapwing and Sanderling *Calidris alba*.

## FUNCTIONS OF COLOUR AND PATTERN INVOLVING INTERSPECIFIC COMMUNICATION

### Crypsis

Camouflage allows an animal to avoid communicating its presence to predators and prey. It can be divided into several categories – countershading, blending, protective resemblance and disruptive coloration.

Most waders show countershading to some extent, i.e. they are generally darker on the back than they are on the undersides, with a gradual transition between the two. This compensates for the greater illumination to which the back is subjected, supposedly making the bird more uniform in tone and allowing it to blend more easily with its background. The winter plumages of the Greenshank *Tringa nebularia*, Willet *Catoptrophus semipalmatus* and tattlers *Heteroscelus* spp. all provide good examples. Such countershading is habitat dependent, being reduced in birds where the ground is highly reflective, and consequently the undersides are well lit (Herán 1976). This may be the explanation of the reduced countershading shown by some desert dwelling coursers *Cusorius* spp.

Completely white undersides can contribute to more efficient foraging. Gulls painted black underneath catch fish less efficiently because the fish see them sooner (Götmark 1987), and the same might be true of waders with some prey. Common Redshanks *Tringa totanus* have been shown to depress the surface activity of *Corophium* (Selman & Goss-Custard 1988), but it remains to be determined whether being white underneath reduces such disturbance.

Woodcocks *Scolopax* spp. and snipes *Gallinago* spp. provide classic examples of blending coloration in which their mottled plumage makes them virtually invisible against the ground (Darwin 1871). Protective resemblance is no more than blending coloration in which the resemblance to some specific feature of the background environment is particularly notable. The resemblance of Woodcock *Scolopax rusticola* plumage to dead leaves, sticks and other ground vegetation (Thayer 1909, McKelvie 1986), and Ringed Plover *Charadrius hiaticula* plumage to stones (Cott 1940) are examples.

The Ringed Plover is a classic case of disruptive camouflage, with both the chick and the adult cited (Thayer 1909, Cott 1938), and drawings of the chick featuring in the classic work on animal coloration (Cott 1940). Both have black and white bands across the neck, with abrupt and regular borders, that visually separate the head from the body and therefore break up the familiar bird shape. However, for the chicks at least, this functional interpretation is disputed by Fjeldså (1977), simply because the neck is hidden when danger threatens and the chick crouches. On the basis of a comparative analysis of adult plovers, Graul (1973) concluded that the most likely explanation of their head and breast patterns was that they were indeed disruptive. The latter study treated species as independent data points, and therefore really needs repeating using modern comparative methods.

Byrkjedal & Thompson (1998) pointed out that tundra plovers possess sharply contrasting black and white breeding plumage that may serve to break up the characteristic bird shape against a background of lichen covered tundra or alpine habitat. American Golden Plovers *Pluvialis dominica* nesting on such areas suffer lower rates of predation than do those nesting on more uniform backgrounds (Byrkjedal 1989). This does not necessarily conflict with the view that the dorsal breeding plumage of the genus, and of many other waders, is cryptic against similar backgrounds (Darwin 1871, Cott 1964).

The eye is a conspicuous feature of birds and its characteristic outline is often disrupted by being included in a dark stripe running from beak to neck, e.g. Whimbrel *Numenius phaeopus*, or from one eye to the other, e.g. Woodcock *Scolopax rusticola*, Ringed Plover (Cott 1964). The patterns of Woodcock, Ruddy Turnstone *Arenaria interpres* and Killdeer *Charadrius vociferus* have all been cited as further examples of disruptive camouflage (Cott 1940, 1964). The fact that woodcock is cited as an example of so many different forms of camouflage illustrates the difficulty of defining the various types precisely.

### Aposematism

Some forms of conspicuous coloration, involving sharp borders and bright contrasting colours, may serve to warn experienced predators of distastefulness or other danger. For example, some brightly marked waders such as the Red-wattled Lapwing *Vanellus indicus* and Egyptian Plover have been judged to be distasteful (to a tiger cub and man respectively), and others such as the Northern Lapwing and Eurasian Oystercatcher *Haematopus ostralegus* mildly distasteful (to man) (information cited in Cott 1947). Moreover, the Blacksmith Plover *Vanellus armatus* has been observed giving an aposematic display in which the bird reacted to a fast low approach by a Lanner Falcon *Falco biarmicus* by facing it with its wings partly spread and calling loudly (Thomas 1983). The suggestion was that this plover was distasteful.



However, the Blacksmith Plover's wing spurs provide a more obvious source of danger to an attacker.

### Mullerian mimicry

Similar coloration may be shared by more than one aposematic species, and this minimises losses to naïve predators as they learn to avoid distasteful or dangerous prey. All four of the African species of *Vanellus* with wing spurs share bold black and white markings (e.g. Fig. 3d), and this could conceivably be an unrecognised example of Mullerian mimicry.

### Batesian mimicry

Non-distasteful or non-dangerous species may mimic aposematic ones. There are no completely convincing wader examples unless Batesian mimicry is deemed to include mimicry of any unpalatable organism (e.g. Edmunds 1974), in which case it can be regarded as including mimicry of leaves and dead branches, and therefore overlaps with protective resemblance. Eight of the 11 African breeding species of *Vanellus* have bold black and white marks. Half of these lack wing spurs and it is conceivable that they are Batesian mimics of the others. However, they may have bony wing knobs or just be aposematic distasteful species.

### Deimatic behaviour

Predators may be put off by some form of shock or flash coloration or by an intimidatory display that is suddenly revealed when a feeding, roosting or incubating bird is disturbed. For example, the Willet displays its conspicuous underwing pattern when it lifts its wings prior to taking flight (Baker & Parker 1979).

### Deflective coloration

Some marks and displays may deflect attacks towards harmless or less harmful areas of the body. Brooke (1998) suggests that this is an unlikely explanation of flash marks in waders since they are not obviously located at the less vulnerable extremities. However, the tips of the outer tail feathers are just such a location, and Forbe's Plover *Charadrius forbesi*, Killdeer, Common Sandpiper *Actitis hypoleucos* and snipes do have conspicuous marks situated there.

### Pursuit deterrence

Some marks and displays may be used to attract the attention of predators, but to discourage attack, and perhaps direct it towards less fit individuals. The white rumps and wing bars of waders may fall into this category, e.g. Red Knot (Baker & Parker 1979).

Unpredictable behaviour may make it more difficult for predators to catch prey. The jinking flight of snipes and some sandpipers probably falls into this category (Piersma 1996a). This behaviour occurs mainly in species that both rely on cryptic plumage to avoid detection, and flush late; consequently they may need to take pre-emptive evasive action.

### Pursuit invitation

Similar marks and displays may be used to attract predators, and invite attack, thereby diverting attention away from eggs

and young. The broken wing trick, rodent run, incubation feigning and the fly-away trick (Simmons 1985) all fall into this category. It is conceivable that particularly conspicuous parts of the plumage, e.g. white rumps and wing bars, might have evolved for this reason – they are certainly displayed to good effect during some of these distraction displays – but, of course, each species may simply be taking advantage of conspicuous colours and patterns evolved for other reasons.

## FUNCTIONS OF COLOUR AND PATTERN INVOLVING INTRASPECIFIC COMMUNICATION

### Aggressive mimicry

Animals may mimic potential hosts or prey to facilitate parasitism, predation, or to gain some other advantage. Male Buff-breasted Sandpipers *Tryngites subruficollis* closely resemble females (unusual in a lekking species), perhaps because this allows them to disrupt mating pairs more easily and obtain sneaky mating opportunities (Myers 1979). Satellite Ruffs *Philomachus pugnax* do not mimic females but have less bright breeding plumage than other males and to some extent kleptoparasitise the mating opportunities afforded by other males' breeding territories at leks (van Rhijn 1991).

### Sexual selection

Colours and patterns designed to attract mates or increase the likelihood of obtaining them through success in intrasexual competition are both included within the sphere of sexual selection. For example, it has been suggested that the silvery white tips of the undersides of the tail feathers of all five species of woodcocks may be used in courtship (Davison 1976), and may thus be a consequence of sexual selection. Great Snipe males at leks with more white in their tails are apparently more attractive to females (Höglund & Lundberg 1987, Höglund *et al.* 1990, but see also Sæther *et al.* 2000). Wood Sandpipers *Tringa glareola* and other waders display their white rumps towards rivals during aggressive encounters (Chojnacki & Stawarczyk 1981).

Piersma & Jukema (1993) have suggested a very good reason why it would be advantageous for Bar-tailed Godwits to select breeding partners with the spectacular bright red breeding plumage exhibited by this species. These feathers appear during a moult that takes place on the northward migration to the breeding grounds. Although the cost of producing the feathers is small, some individuals of low body mass are apparently unable to afford it because of the simultaneous need to store reserves for the migration itself. Thus bright red individuals encountered on the breeding grounds demonstrate both a sound migration strategy and efficient foraging during the course of it. If migration strategy has any genetic basis (as it does in species such as Blackcaps *Sylvia atricapilla*), red individuals demonstrate that they possess good genes in this respect. Efficient foraging might allow more time to be devoted to parental duties and therefore be of direct benefit to those choosing red mates (Hoelzer 1989).

Hasson (1991) suggested that feather decorations, such as spots, notches and differently coloured tips could act as amplifiers of feather wear and damage. For example, the white tail tips of the Great Snipe wear more quickly than coloured ones, making the difference between high quality individuals with low rates of wear, and low quality individuals with high rates of wear, more apparent. As pointed out



by Fitzpatrick (1998a), such accelerated wear is also a handicap, since it constrains flight. Male Great Snipes offer only mating opportunities to females, so the benefit of choosing unworn individuals in this case is most likely to be that they offer good genes.

It has been suggested that the uniformity of an iridescent colour reflects developmental stability (Fitzpatrick 1998b). This is because precise control of development is needed if an individual is to lay down the melanin layers with sufficient regularity to produce bright iridescent colours. It is possible that a similar argument could be applied to phaeomelanin, but it is less likely to apply to eumelanin, since the latter merely requires a mass of pigment granules to produce an even dark colour. Even better known is the idea that the degree of asymmetry of a bilaterally symmetrical character could indicate developmental stability (Møller & Swaddle 1997). Some of the plumage characters already discussed, such as the breast bands of plovers, could play a role in this respect, especially since many of them are displayed in a way that make any departure from symmetry obvious (Fig. 2). The advantage of selecting evenly coloured and symmetrical mates could be that they have a harmonious genome, and one that is more resistant to the disruption of development through such factors as parasitism and poor nutrition.

### Social selection

This form of selection includes colour and plumage patterns selected by a wider range of conspecifics than just sexual partners (West-Eberhard 1983). Such plumage may serve to inform other individuals of safety or danger, or help to establish rank or territory ownership outside the breeding season. For example, the white tipped outer tail feathers of the Killdeer and other waders emphasise the opened tail that is a prelude to movement or departure and therefore may help co-ordinate group movements and also act as a warning of danger (Davison 1976). Wing-raising in advance of take-off may serve a similar function, e.g. in Red Knot (Cott 1964).

Any signals of this sort need to be of demonstrable benefit to, and improve the survival of, the signal giver as well as the signal receiver if they are to be produced and maintained by social selection. Brooke (1998) has argued that this is true of flocking species in which flash marks, especially wing bars, are common. The first individuals to take off, when a terrestrial predator approaches, benefit by recruiting other individuals to join them (thus protecting their rear), while those who respond to the signal, benefit by not remaining behind.

Stawaczyk (1984) suggested that displays of the rump in waders serve to reduce aggression between birds feeding together, and that species feeding in similar habitats have similar rump patterns. For example, those with "*Tringa*" type rumps prefer feeding in the water and those with "*Calidris*" type rumps at the water's edge. There is no doubt that many species do display their rumps during such encounters but this seems much more consistent with selfishly obtaining personal feeding space than with signalling species identity and hoping for an altruistic response. Moreover, they may simply have inherited a common rump pattern from a common ancestor. An alternative explanation for such wing bars and rump patterns is that they help co-ordinate flock movements (Potts 1984), allowing tighter turns and thus reducing predation, or simply allow energy saving flight formations to be maintained more easily.

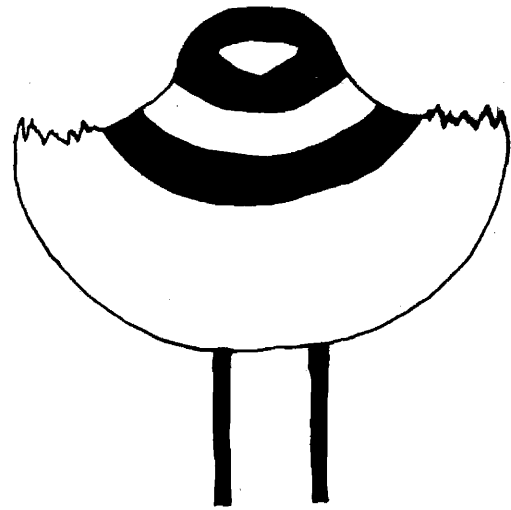


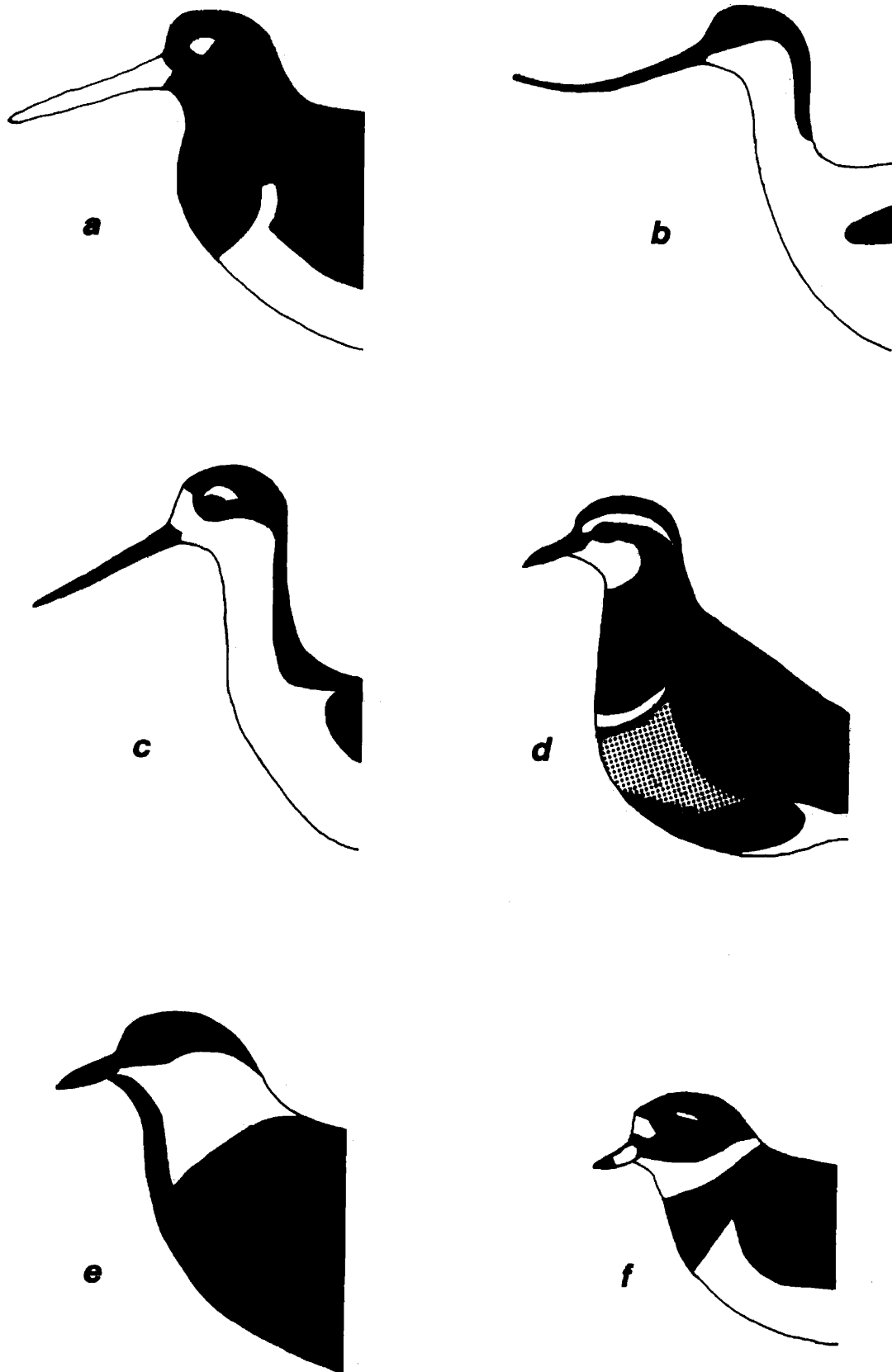
Fig. 2. Displaying Little Plover *Charadrius dubius* with flank feathers erected, showing the prominence and symmetry of the head and breast bands, as viewed by a potential mate.

The contrasting neck collar of young Ringed Plovers, Lapwings and Egyptian Plovers may help in the relocation of the young (Cott 1964, Fjeldså 1977), i.e. facilitate the recognition of young when providing parental care. It has also been suggested that individual recognition of adults could evolve through frequency dependent selection of plumage patterns if the advantages of such recognition were strong enough. Experiments conducted with both breeding and wintering Ruddy Turnstones are consistent with this, though do not prove it (Whitfield 1986, 1988).

Another factor that may help to explain the abundance of abrupt, regular borders between blocks of colour in plovers, and their rarity in sandpipers (see earlier, and Fig. 3d-f), is that they may serve to show up feather damage and wear. Such damage could occur during feeding, but is most likely to be caused during fights with other individuals. Plovers are equipped with effective weapons in the form of strong, short bills, powerful legs and in some cases spurs or bony knobs on the wings. Intraspecific encounters are much more likely to lead to feather damage in plovers than in sandpipers, since the latter have only long, sensitive bills and feet to use as weapons. On the whole, territoriality and aggression (both during the non-breeding and breeding seasons) are more intense in plovers than sandpipers (based on information in Hayman *et al.*, 1986, Piersma 1996a,b). This is perhaps because their short bills mean that they can only forage efficiently in areas where other birds have not reduced the surface activity of prey, and so they invest more effort in keeping intruders away.

The regular borders of the head and breast bands of plovers effectively reveal any feather damage caused during fighting by becoming irregular. Birds of low status may acquire irregular patterns as they are excluded from the best feeding and roosting places through interactions with conspecifics. Other individuals may then recognise and avoid them, or take advantage of their patent inferiority. Such inferior individuals are also unlikely to make good breeding partners. This is certainly the case with Common Shelducks *Tadorna tadorna*, in which only those individuals with the most immaculate red breast bands manage to produce any surviving young (Ferns & Lang in press).





**Fig. 3.** Examples of waders with abrupt, regular borders between different blocks of colour on the head and neck, capable of revealing feather damage incurred during fighting. (a) Eurasian Oystercatcher – black chest band, (b) Pied Avocet – black head and nape patch, (c) Black-winged Stilt *Himantopus himantopus* – white eye patch, black head and nape, (d) Eurasian Dotterel *Charadrius morinellus* – white eye stripe, throat patch and breast band, (e) Spur-winged Plover *Vanellus spinosus* – black crown, throat and chest, (f) Ringed Plover – white forehead patch, eye stripe, neck ring and chest. The beaks of oystercatchers are their most formidable weapon, whilst plovers may use their beaks, feet and wings. Despite having delicate-looking beaks, both Black-winged Stilts and Pied Avocets employ them when fighting (Cramp & Simmons 1982).



## CONCLUSIONS

Experimental tests of the efficacy of camouflage, most of them involving birds preying on insects, were carried out in the 1950s (Tinbergen 1974). These included tests of the efficacy of blending coloration (Kettlewell 1956), counter-shading (Ruiter 1956), protective resemblance (Ruiter 1952) and deimatic behaviour (Blest 1957). It is therefore not surprising that such ideas have become widely accepted, and attention has turned to new issues. A search of the expanded Science Citation Index from 1991 to the present (>12 years) yielded only two papers on animal camouflage, neither of them on birds. Much more attention has been paid to conspicuous coloration, including how warning coloration evolved (e.g. Harvey & Paxton 1981), why it is often associated with gregariousness (e.g. Gagliardo & Guilford 1993) and the complexity of its interactions with distastefulness (e.g. Rowe & Guilford 1999). These are not areas in which studies of wader coloration are likely to be especially productive, though the potential role of distastefulness and wing spurs in the conspicuous coloration of some plovers and lapwings remains intriguing.

Although sexual selection is currently under intense investigation, waders have been a relatively neglected group, with the single exception of the Great Snipe. This is despite the fact that they furnish some of the best known examples of marked sexual dimorphism, e.g. Ruff and Reeve, of reversed sexual dimorphism in bill length, e.g. curlews (recently reviewed by Sandercock 2001), and of sexual role reversal, e.g. phalaropes. The wide variety of plumage colour and pattern exhibited by waders means that they are well-suited to comparative investigations, and as their phylogenetic relationships are becoming better known, modern comparative methods can be used (e.g. Székely & Reynolds 1995, Sandercock 2001).

Conspicuous small marks that remain hidden when a bird is feeding are widespread in birds, yet we have little idea of their true function. So many explanations have been proposed for the white rumps, wing bars and tail markings of waders (deflection marks, interspecific pursuit invitation and deterrence signals, intraspecific social signals), that considerable care will be required in designing experiments to distinguish between them. Nevertheless, it is relatively easy to both increase and decrease the size of such marks, and the fact that waders both feed and breed in open habitats where their behaviour can be observed clearly, makes them ideal candidates for studies intended to reveal the true function of these signals.

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