

Foot-movements in plovers and other birds

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WADERS SHOW many striking adaptations in behaviour and structure which enable them to obtain their food. In particular, several types of foot-movements have been evolved and this short paper sketches, informally, something of what is known about these, with special reference to the activities of plovers. There is much scope for study of the various feeding movements of waders; especially, we need more information on the precise function of individual movements.

FOOT-MOVEMENTS IN PLOVERS

“Foot-trembling”

This behaviour has been recorded in at least four species of plover, being especially well known in the Lapwing (*Vanellus vanellus*) (see, for example, Portielje 1922 and Spencer 1953). Contrary to the impression given in the editorial comment to Coleman (1960), “foot-trembling” (or “foot-tapping” or “foot-pattering”) when feeding is well known in the Little Ringed Plover (*Charadrius dubius*), having been recorded as long ago as 1915 by Heinroth. I have myself quite recently reported (Simmons 1953b) that this species shares with the Lapwing and the gulls (*Larus* spp.), among others, “one curious habit apparently connected with food-seeking—that of making pattering movements of the feet on mud. In the two plovers this is a trembling action of one foot only while the gulls mark time with both feet.” Sluifers (1938) also referred to this behaviour in the Little Ringed Plover, calling the trembling action “leg-shaking” (after Heinroth and Heinroth 1928) and noting that, when trembled, the foot may be lifted up to half an inch above the ground. Sluifers remarked also that, while a somewhat similar habit had been recorded in the Ringed Plover (*Ch. hiaticula*) and in the Kentish Plover (*Ch. alexandrinus*) by Verwey (1926), he himself had never seen obvious foot-trembling in Ringed Plovers though these birds did make some sort of one-leg movement while standing still and before seizing prey. In fact, however, Verwey was referring to the quite definite records of Astley (1923) for the Ringed Plover (“very rapid vibration of one foot on the wet sand”) and of Medlicott (1923) for the Kentish Plover (bird stops after a run, taps and “always seems to obtain a morsel”). The Heinroths (1928) observed foot-trembling only in the Lapwing and Little Ringed Plover (captive individuals of which would even perform on hard surfaces, such as linoleum and wooden floors), and their Ringed and Kentish Plovers were not seen to perform any comparable foot-movements. There seems little doubt, however, that these species do foot-tremble (see above and, also, Tucker 1940).

Other foot-movements

The relationship between the one-legged foot-trembling and the various two-legged movements of the Little Ringed Plover and related species also needs to be examined. Most (probably all) plovers use two-footed movements in forming the nest-scape and in egg-uncovering ("scraping"), and also in the pre-copulatory display ("marking-time"), the latter activity perhaps being rarer in the Kentish Plover (J. Walters *in litt.*). A few species, notably Kittlitz's Sandplover (*Ch. pecuarius*), also cover the eggs with sand on leaving the nest, using special leg-movements (see, particularly, Hall 1958).

When scraping, the male Little Ringed Plover (for example) forms or enlarges a hollow "by leaning forward and rotating on his breast, body and tail slanting up, feet scratching backwards" (Simmons 1953b). The same scraping movements are done by both sexes of the Little Ringed and Kentish Plovers when retrieving buried eggs, though they usually probe with the bill first (Walters 1956). The relation between these scraping movements and those used by Kittlitz's and other plovers in hiding the eggs is less clear. Superficially they seem to be similar but the egg-covering ones have a sideways orientation apparently lacking in normal scraping and there are other differences (see Hall 1960). The marking-time actions are quite distinct from foot-trembling and from the various scraping movements. When marking-time, the male Little Ringed Plover (for example) approaches the female, his footsteps getting "progressively shorter and shorter, and higher and higher until, when he stands over her . . . he is 'marking-time' vigorously on the spot, sometimes with such exaggeration that he may actually strike his breast with the alternately raised feet" (Simmons 1953a).

There have been attempts to equate foot-trembling with some or all of these two-legged movements (e.g. Tucker 1940, Armstrong 1950, Milon 1951), but these seem ill-advised. Armstrong and others have suggested that marking-time derives from foot-trembling, "entering" courtship as a displacement-activity. There has obviously been confusion here with the superficially similar foot-paddling of gulls (as there was also, in a different context, in Simmons 1950). I put forward an alternative explanation (Simmons 1953a), namely that marking-time was "more likely an inhibited locomotory movement". It may be added that such behaviour is now ritualised and that it is equally likely that, instead of being derived from inhibited approach movements, marking-time is based on inhibited mounting movements.

FOOT-MOVEMENTS IN OTHER BIRDS WHEN FEEDING

As indicated by Portielje (1922) and Verwey (1926), foot-trembling seems confined to the true plovers. Portielje did not observe it in other wader species watched by him, including the Ruff (*Philomachus*

pugnax), Black-tailed Godwit (*Limosa limosa*), Redshank (*Tringa totanus*) and Curlew (*Numenius arquata*). However, some other movements have been recorded and may be mentioned briefly.

“Foot-paddling” and “jumping”

“Foot-paddling” (or “foot-trampling” or, when done in water, “puddling”) is apparently common in scolapacine waders. The Woodcock (*Scolopax rusticola*) tramples before probing (Heinroth, quoted by Tucker 1940; Portielje, quoted by Tinbergen 1953). The Dunlin (*Calidris alpina*), together with its allies, “will sometimes patter on the mud or sand with its feet or jump up with both feet together” (Tucker 1940), similar “jumping and dancing” on the sand being mentioned by Ticehurst (1923). The Redshank, also, will “jump” up and down on the mud when feeding (Tucker 1940). Recently, Meyerrieks (1959) described a Semipalmated Sandpiper (*Calidris pusilla*) seen foot-paddling in a small pool formed by the incoming tide. It alternately lifted and depressed its legs very rapidly for about ten seconds before peering at the surface and then stabbing (not probing) rapidly with its bill, making brief swallowing movements afterwards.

Two-footed paddling is also very well known in gulls (see Portielje 1928 and Tinbergen 1953; also, for example, Colthrup 1923, Savage 1923 and Robinson 1923). It also occurs in the ducks, geese and swans, in the flamingos and in the herons.

Other movements

The “pirouetting” of phalaropes (*Phalaropus* spp.), chiefly in shallow water, is too well known to require further description (see Tinbergen 1935, 1953, Tucker 1940) but the “rushing” behaviour in shallow water of certain other scolapacine waders, e.g. Green Sandpiper (*Tringa ochropus*) and Greenshank (*T. nebularia*), has been much less fully documented. Greenshanks have been seen running about quite fast with high steps, sharply and abruptly changing direction, before settling down to quiet, normal feeding (Simmons 1951). While an element of fear could be involved in such behaviour, it seems more likely that such movements help in uncovering prey (see below).

THE FUNCTION OF FOOT-TREMBLING AND OTHER
FEEDING MOVEMENTS

Worms

Burrow-haunting, segmented worms (Annelida) figure frequently in the diet of many waders and gulls, and the foot-trembling of plovers and the analogous paddling and jumping of other birds are widely supposed to have reference to worms as prey (see titles in the list of references; also, for example, comments in Tucker 1940). Both

Portielje (1922) and Spencer (1953) stressed this in the case of the Lapwing (Portielje mentioning earthworms of the genera *Lumbricus* and *Allolobophora*), while Sluiter (1938) described foot-trembling in the Little Ringed Plover under the heading "worm-drilling". It is clear, however, especially from the discussion in Tinbergen (1953), that this particular interpretation of the function of foot-trembling and paddling is far from settled. These movements are said to exploit the innate escape reaction of the earthworm to soil disturbance caused by the Mole (*Talpa europaea*) but, as Tinbergen points out, only a few species of worm have this reaction. On land, especially in fields (where Lapwings and gulls feed to a large extent), terrestrial earthworms (Oligochaeta) are the main prey and, of these, *Lumbricus* has not got the response to the Mole, whereas *Allolobophora* has. Yet the former apparently figures more frequently in the diet of the birds concerned than does the latter. On the sand and mud of the shore, marine bristle-worms (*Nereis*) and lugworms (*Arenicola*), both polychete worms (Polychaeta), are frequently eaten by birds, yet neither has any reaction to the Mole. As it seems likely, however, that worms are exposed in some way by the various foot-movements (how anecdotal much of the evidence is, is not clear), obviously other phenomena besides a response to the Mole must be involved, including some sort of reaction to vibration from above. Spencer (1953) suggested that the worms may react to the birds' leg-movements as they do to the patter of rain, while Portielje (1928) mentioned that Herring Gulls (*Larus argentatus*) are especially likely to paddle on grass after rain. Earthworms are known to lie nearer the mouths of their burrows in wet weather and thousands appear on the surface after heavy rain. The precise connection (if any) between the effect of rain and of pattering (etc.) on the behaviour of earthworms remains to be investigated. It may well be that the various foot-movements have reference to a wider range of prey and may be of only incidental value in capturing worms (see below).

Other prey

The suggestions which follow all have much to recommend them. Sluiter (1938) thought that the behaviour of Little Ringed Plovers (which are not great worm eaters, apparently) and Lapwings caused "insects" (presumably quite a variety of invertebrates) that were hidden beyond the range of the birds' short bills to come nearer the surface (though the mechanism of this response goes unexplained). In the editorial comment to Coleman's note (1960), it was thought possible that the "more common function of both tapping and paddling is to cause minute organisms to move and thus show themselves". Spencer (1953) also suggested that the pattering of the Lapwing, besides raising worms, "may dislodge other organisms,

bringing them into the Lapwing's view". Pirouetting, rushing and puddling in water all probably function both to whirr up organisms from the bottom or suspended in the water, or to make these move and show themselves (Tinbergen 1935, 1953, Tucker 1940, Simmons 1951).

It may well be, too, that in causing worms of all types merely to move, and thus reveal themselves or the site of their burrows, the pattering and other movements fulfil their function and that one need not seek more complicated answers.

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FOOT-MOVEMENTS IN PLOVERS

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