Arid-zone adaptations of waders (Aves: Charadrii)

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Waders (birds of the suborder Charadrii) have radiated into the arid zones of the world through the successful use of adaptations formerly evolved in response to a marine or brackish shoreline habitat. These preadaptations are traced through the major lines of wader radiation, ending in such highly specialized taxa as the sandgrouse (family Pteroclidae), which refined existing adaptations or evolved further adaptations to suit them to a diet of seeds and the need to drink in an environment poor in surface water.

S. Afr. J. Zool. 1984, 19: 78–81

Waadvoëls (onderorde Charadrii) het in die dorre gedeeltes van die wêreld versprei deur die suksesvolle gebruik van aanpassings wat vroeër ontwikkel is in reaksie op see- of brakwater-kushabitat. Hierdie voorafaanpassings kan deur die hooflyne van waadvoëlevolusie nagespoor word tot sulke hooggespesialiseerde groepe soos die sandpatryse (familie Pteroclidae).

Hierdie groep het bestaande aanpassings verfyn, of verdere aanpassings ontwikkel sodat hulle vir 'n dieet van sade en die gevolglike behoefte aan drinkwater in 'n waterarm omgewing aangepas geraak het.

S.-Afr. Tydskr. Dierk. 1984, 19: 78–81

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Several groups of waders (Charadriiformes, Charadrii) have given rise to arid-adapted species, or even entire families. The most notable of these are the coursers (Glareolidae, Cursoriinae), the pratincoles (Glareolidae, Glareolinae), the seedsnipe (Thinocoridae) and the plovers (Charadriidae). The phylogeny of these groups within the suborder Charadrii has been the subject of several major studies (Fjeldså 1976; Jehl 1968; Sibley, Corbin & Ahlquist 1968; Strauch 1978) from which it is increasingly clear that certain features of the suborder are highly significant in the determination of relationships within it.

It is also clear that the Charadrii as a group have an aquatic origin — whether marine or freshwater — and that the arid-zone taxa are more recent offshoots from the aquatic ancestors. It is my intention to show how the basic anatomical and physiological equipment evolved by the waders for the waterside (especially the marine waterside) are the very same features that have preadapted them to the deserts of the world.

Wader phylogeny

The criteria on which family trees of waders have been drawn up include, most importantly, adult and neonatal plumage patterns, osteology, anatomy, behaviour and breeding biology. Relationship with any major order of birds can be established with certainty by an analysis of egg-white proteins (Sibley & Ahlquist 1972), on the basis of which the order Charadriiformes is shown to be a natural one. Osteological evidence points to a major dichotomy into the Scolopaci (or Scolopacoidea) on the one hand and the Charadrii (or Charadrioidea) on the other (Strauch 1978) with a third branch leading to the Alcae (auks) which will not be considered here. Another arid-adapted family of birds, the Pteroclidae (sandgrouse) also falls within the limits of charadriiform egg-white protein patterns, and sandgrouse possess many other charadriiform features (Maclean 1967a). However, their close osteological resemblance with the doves [Columbidae, Columbiformes (S.L. Olson *in litt.*; Stegmann 1969)] indicates that the sandgrouse should be regarded as an intermediate order of their own (Pterocliformes) whose charadriiform affinities are very close, and which will therefore be included in this account.

Of the five taxa to be considered — seedsnipe, coursers, pratincoles, plovers and sandgrouse — the seedsnipe are exclusively Neotropical, the coursers, pratincoles and sandgrouse Afrotropical, Palaearctic and Oriental, while the plovers have representatives in all the world's deserts. The affinities of the seedsnipe within the Charadriiformes have long been open to question, but the weight of osteological evidence points to an
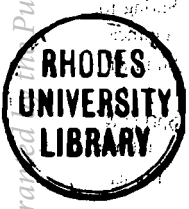
early divergence from scolopacoid stock (Strauch 1978); they are the only arid-adapted taxon on that evolutionary line. The plovers, coursers, pratincoles and sandgrouse are all derived from the charadrioid line.

Basic charadriiform adaptations

Since three of the families under review are derived from a common stock, they can provide evidence for a history of charadriiform evolutionary trends. The plovers (Charadriidae) tend on the whole to be generalized, versatile and cosmopolitan. Most plovers are aquatic shorebirds in the strict ecological sense, some marine, others freshwater. With few exceptions they are characterized by longish legs, rather short anterior toes, reduced or absent hind toe, long pointed wings and shortish bills for surface feeding or shallow probing. Only the marine forms invariably have a supraorbital nasal gland which produces a highly saline secretion and is therefore called the salt gland (Thomas & Phillips 1978). Most other plovers have a supraorbital gland, but some exclusively freshwater forms, like the red-kneed dotterel *Erythrogonys cinctus* of Australia, have no trace of even a supraorbital groove (Maclean 1977), so the gland has either been lost or has moved into a preorbital position within the orbit. The non-aquatic grassland forms like the crowned plover *Vanellus coronatus* and the blackwinged plover *V. melanopterus* have well-developed supraorbital salt glands (Maclean, unpublished), as does the truly desert-adapted Australian dotterel *Peltohyas australis* (Maclean 1976b).

The plovers either modified an already existing nasal gland into a salt gland on contact with marine (or other saline) waters, or evolved it in response to such an aquatic habitat, and later reduced or lost it on becoming freshwater dwellers. It is therefore possible to suggest a marine ancestry for the plovers; indeed the occurrence of salt glands in nearly all charadriiforms indicates a marine ancestry for the group as a whole. Only the sandgrouse among the taxa under consideration have no salt glands (Thomas & Robin 1977); reasons for this will be apparent later. The nasal glands of seedsnipe are exorbital, but not supraorbital (Strauch 1978); whether they function as salt glands has not been ascertained.

Invasion of arid zones

Arid zones can be loosely defined as those land surfaces that receive less than 250 mm of rain/year on average. Rain is not only small in amount, but unpredictable in timing. Surface water is scarce, temperatures and evaporation rates usually high. It therefore behoves a desert animal not to rely on free drinking water as its main supply unless it is able to fly great distances. Since waders almost all feed on invertebrates, and since arthropods have radiated so successfully into all terrestrial habitats including the arid zones (Louw & Seely 1982), those waders that began to colonize the deserts of the world had no major step to take in their feeding ecology, except that they no longer waded or probed for their food in a wet substrate.

How could such a change in habitat have come about? All aquatic waders, except the jacanas, some recurvirostrids, and a few plovers and scolopacids, nest away from water, but within a few hundred metres of it. The basic wader nesting strategy, illustrated typically by the plovers, consists of a small clutch (maximally 4 eggs) of cryptically coloured eggs laid in a simple scrape in an exposed site, with a minimum of nesting material. The sitting parent enjoys good visibility and leaves the nest early in the face of potential danger; the eggs must therefore be inconspicuous, hence their crypsis and the small

clutch.

In such a site the sitting bird is exposed to high insolation and low relative humidity (Grant 1982; Graul 1975; Purdue 1976a, b; Purdue & Haines 1977). Its nesting environment approximates therefore to a desert in many ways, so that even waterside waders nest under conditions that require them to be tolerant of heat loads and desiccation — two eminently arid-zone preadaptations. Thus all the features for meeting the requirements of a desert habitat existed in the waders before they left the waterside for good. Their long legs and short toes were then used for running; their nasal glands processed body fluids of invertebrate prey and halophytic plants, rather than sea water; their nesting habits were tailor-made for exposed ground sites. In short, waders were probably more effectively preadapted to arid zones than any other single group of birds.

History of arid-zone radiation

From what has already been said, it is not surprising to find plovers at almost any waterside, in open grasslands, and in some of the severest deserts in the world. The coursers are superficially very ploverlike; they have a somewhat modified bill, arched and somewhat elongated, which in some species is used for digging for food in soft sand; they have lost the hind toe (which was on the way out among the plovers in any event) and some have developed plumage patterns specifically adapted for camouflage in stony habitats, notably the doublebanded courser *Rhinoptilus (Cursorius) africanus* (Maclean 1967b). The coursers have gone further than the plovers in the direction of nocturnal activity patterns (Maclean in press) which allow them to remain inactive in the heat of the day — a good thermoregulatory economy measure. The bronzewinged courser *C. chalcopterus* is entirely nocturnal or crepuscular and the other species largely so. In this the coursers have followed an evolutionary path convergent with that of the dikkops or thick-knees (Burhinidae), a wader family that has some singularly successful arid-adapted species throughout the tropics and subtropics of the world, including the spotted dikkop *Burhinus capensis* of Africa and the doublestriped thick-knee *B. bistriatus* of the Americas. A similarly convergent course has been followed by the nocturnal Australian dotterel (Maclean 1976b), a plover that was for many years placed in the same subfamily as the coursers.

From a study of their osteology and their neonatal plumage patterns it is fairly clear that the coursers are on the charadrioid line of evolution (Jehl 1968; Strauch 1978). If they did not arise directly from the plovers, they arose from a common ancestor. Similar evidence shows that the sandgrouse and coursers have some fairly close affinities (Fjeldså 1976); their chicks share some plumage characteristics and the curious habit, unique among waders, of crouching with the head up when alarmed; all other wader chicks crouch with the head flat on the substrate.

The only desert-adapted glareoline, the Australian pratincole *Stiltia isabella* nests on stony ground within 2 km of water, usually temporary pans filled by localized rains (Maclean 1976a). The adult birds drink, but the chicks are fed on insects and process hypertonic body fluids by means of a supraorbital salt gland (Jesson & Maclean 1976). This species represents an evolutionary stage intermediate between that of the true pratincoles (*Glareola*) and that of the coursers (Maclean 1976a).

Dietary divergence

The two most highly specialized (in a derived sense) wader taxa

of the arid zone are the seedsnipe and the sandgrouse. From different ancestries (though within the charadriiformes) they have converged remarkably in habitat, structure, plumage and habits. Both feed largely on plant material, mostly seeds (Maclean 1969; 1976c). This has led to profound structural modifications: short legs and bills, robust bodies, small heads — indeed an altogether dovelike appearance and method of feeding, and another case of evolutionary convergence.

A diet of seeds means a low intake of water, with a resultant water deficit in birds, since their kidneys are generally poorly adapted for water conservation when compared with the kidneys of mammals. This deficit must be made good by the uptake of water in some other form, either as drinking water or as preformed water in succulent food. Seedsnipe eat the water-rich leaves of succulent or subsucculent green plants. Sandgrouse drink. Seedsnipe are therefore restricted to fog deserts on the west coast of South America, or to montane deserts where precipitation, though small, is frequent enough in the form of condensed fog or light snowfalls to support a relatively substantial growth of water-rich plants.

Sandgrouse are not restricted to such desert types and can range widely over the inland continental deserts, provided that drinking water is available within comfortable flying distance of food resources. This in turn imposes its own kinds of restrictions which are not the subject of this review, and have been dealt with elsewhere (Maclean 1976c). But it is necessary to mention the loss of the salt gland in the sandgrouse; by drinking comparatively dilute water and feeding on a salt-poor diet of seeds, sandgrouse encounter problems of salt deficit, rather than salt loading. The need for a salt-secreting gland falls away, and so does the gland itself. Water conservation remains a high physiological priority and sandgrouse employ an efficient method of cloacal water resorption (Thomas & Maclean 1981), a process common to many birds so far studied, and therefore another preadaptation to an arid habitat.

One further preadaptation to the sandgrouse's lifestyle deserves mention, namely transport of water in the belly plumage. Transport of drinking water by male sandgrouse to their young is done by soaking the belly feathers in water until saturated (belly-soaking), then flying to where the young have been left crouched and letting them drink from the wet plumage (Cade & Maclean 1967; Maclean 1983). Belly-soaking as a means of water transport is confined to the Charadriiformes and Pterocliformes and has been extensively reviewed by Maclean (1974) and further discussed by Grant (1982).

As a means of cooling or humidifying eggs and/or young in a shoreline habitat, belly-soaking is an obviously suitable mechanism. The feathers of waders are somewhat modified to hold water in their filamentous barbules. As a means of water transport in an arid environment, belly-soaking is advantageous only if the adults have to drink frequently (daily or nearly so). It is therefore not surprising that sandgrouse have not only retained and refined belly-soaking as a behaviour pattern, but have undergone considerably greater modification of feather structure, especially in the belly region, for just this purpose (Joubert & Maclean 1973), to the extent that a sandgrouse feather can now hold more water per unit weight than a sponge (Cade & Maclean 1967).

One might say that, in sandgrouse, the waterside habits of the ancestral waders have, in some respects at least, come full circle, but answer slightly different needs of the evolutionary end products.

Conclusions

Adaptations (including preadaptations) of waders to the arid zone can conveniently be listed as follows:

(a) Long legs for running; later shortened by highly specialized sandgrouse and seedsnipe for feeding on the ground on small seeds, by taking quick short steps.

(b) Short toes for progression over firm substrates (in the pratincoles and seedsnipe long toes facilitate running over stony ground).

(c) Hind toe reduced or absent (typical cursorial adaptation in birds).

(d) Long wings for strong flight, especially important in nomadic and migratory species, and those that fly frequently to water to drink (like sandgrouse).

(e) Salt-secreting nasal gland for processing saline or hypertonic water or body fluids of prey animals (this gland has been lost in sandgrouse which drink large amounts of relatively fresh water).

(f) Diet of arthropods; highly specialized forms like seedsnipe and sandgrouse have become largely seed-eating to capitalize on a locally abundant food source.

(g) Open nest site with small clutch of cryptically coloured eggs.

(h) Nocturnal or crepuscular activity patterns.

(i) Secondary dependence on drinking water as a result of a diet of seeds (sandgrouse).

(j) Transport of water to young in belly plumage of male parent sandgrouse.

(k) Cryptically coloured dorsal plumage, probably originally an adaptation to nesting in exposed sites.

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