

Sandgrouse: models of adaptive compromise

G.L. Maclean

University of Natal, Pietermaritzburg

Sandgrouse (Aves: Pteroclididae) are arid-adapted birds descended from shoreline-dwelling waders (suborder Charadrii). They are highly modified for a diet of seeds and need to drink regularly and quickly. They have no nasal gland for salt excretion, and conserve water by resorption in the kidneys and rectum. Their plumage is cryptically coloured and highly insulative, and the belly region is adapted for transporting water to the young. Their wader-like nesting habits are preadapted to an arid environment. *S. Afr. J. Wildl. Res.* 1985, 15: 1–6

Sandpatryse (Aves: Pteroclididae) is woestyn-aangepaste voëls wat van kuslewende waadvoëls (suborde Charadrii) afstam. Hulle is hoogs gemodifiseerd om sade te vreet en moet gereeld en gou water drink. Hulle besit geen soutafskeidende nasale kliere nie, en bespaar water deur resorpsie in die niere en rektum. Hul verekleed is kripties gekleur en verskaf goeie isolasie teen uiterste temperature, terwyl die pensvere aangepas is vir die vervoer van water na hul kuitens. Hul waadvoëlagtige nese gewoontes is tot 'n woestyn-omgewing vooraangepas.

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Introduction

The principle of preadaptation of waders (Charadriiformes: Charadrii) to an arid environment has been argued by Maclean (1984) and extended to include the sandgrouse which are highly specialized derivatives of the wader stock (Maclean 1967). Sandgrouse are mostly confined to the arid and semi-arid regions of Africa and Asia (Maclean 1976) (Figure 1); in their evolutionary history they have capitalized on certain of those ancestral features which have preadapted them to the arid zone, but they have also evolved some new features, and lost or further modified some ancestral features in their pursuit of a somewhat aberrant diet of seeds and the consequent need to drink water. The purpose of the present paper is to examine possible reasons for behavioural and structural divergences from the ancestral condition and to assess the relative merits of each specialization, based on the principle that every adaptive change brings with it some inherent disadvantages, so that evolution involves a series of compromises. This seems to be especially true of sandgrouse, a group of obligate drinkers in a water-poor environment.

Food

By far the greater majority of waders feed on arthropods and other invertebrates, whether they are inhabitants of shorelines, grasslands or deserts. Only two families, the seedsnipe (Thinocoridae) of South America and the sandgrouse (Pteroclididae) of the Old World have moved away from an animal diet to one consisting almost exclusively of plant material (Maclean 1968, 1969) and they have undergone remarkable convergent evolution (Figure 2); in the case of sandgrouse this material is almost entirely small dry seeds picked up from the ground. The advantage of seeds as a staple food is that they are abundant, although sometimes only locally in space and/or time, but usually predictably abundant after good rains.

An excellent analysis of granivory as an adaptive strategy is given by Wiens & Johnston (1977). Although seeds are small they are rich in energy but usually low in proteins, so that large amounts must be eaten to satisfy the nutritional needs of the birds. Sandgrouse compensate for this in part by selecting seeds of legumes and other protein-rich plants (Thomas 1984). The success of granivore populations may rest on their adaptive responses to patterns of seed availability in time and space, such as high and rapid reproductive rates, regional or seasonal shifts in distribution and abundance (nomadism and migration respectively), and gregariousness at least at some stages of the annual cycle (Wiens & Johnston 1977).

G.L. Maclean

University of Natal, P.O. Box 375, Pietermaritzburg, 3200
Republic of South Africa

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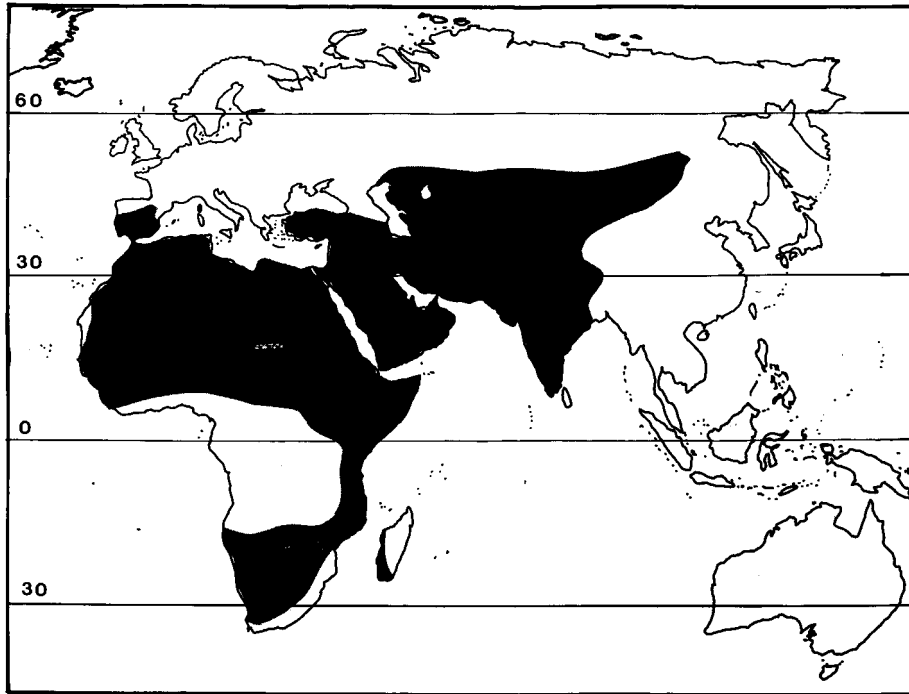


Figure 1 World distribution of the sandgrouse (family Pteroclididae).

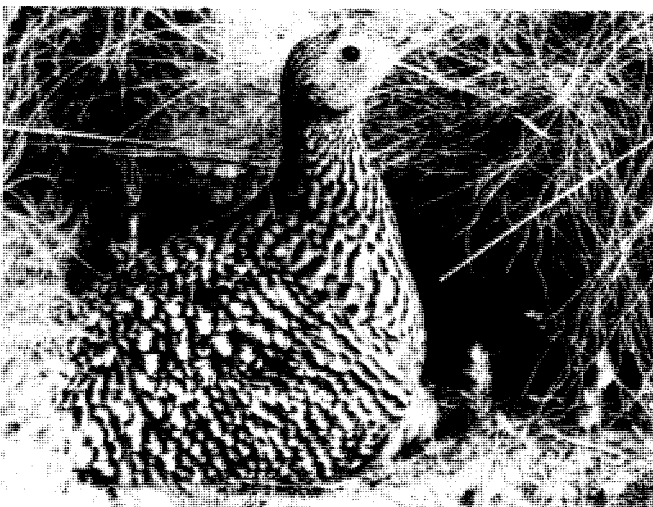
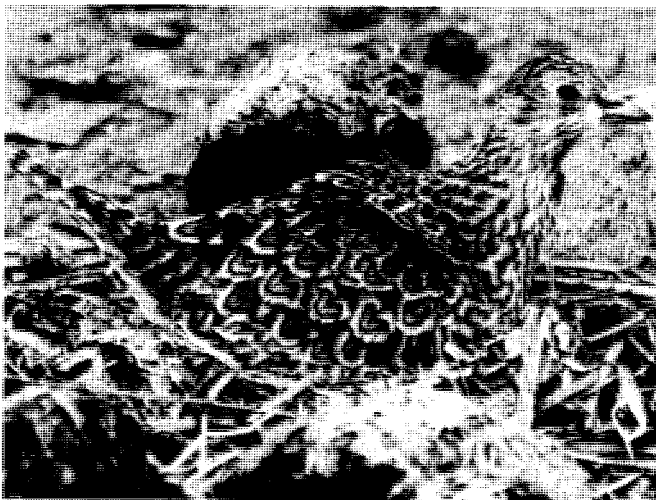


Figure 2 Female least seed snipe *Thinocorus rumicivorus* (family Thinocoridae) of South America (a) and female Namaqua sandgrouse *Pterocles namaqua* (family Pteroclididae) of southern Africa (b) to show convergent features.

Sandgrouse fit most of these predictions, but not that of a high reproductive rate, as will be discussed later.

The evolution of large-scale granivory among birds is especially noticeable in arid or semi-arid regions (Wiens & Johnston 1977), so that sandgrouse again fit the general pattern.

It would seem from analyses of various species of birds that the energetics of granivory are comparable with those of any other dietary pattern. Table 1 shows that larger birds are energetically more economical than smaller birds; for example the larger non-passerines up to a body weight of 2 500 g have a mean basal metabolic rate (BMR) of only 0,50 kJ/g/day, while the smallest non-passerines have a mean BMR of three times as much (1,51 kJ/g/day) (Pinowski & Kendeigh 1977). It would also seem that passerines have a slightly higher energy requirement than non-passerines of equivalent body weight, but these differences are probably not significant. The BMR for sandgrouse (0,55 kJ/g/day) predictably corresponds with those of similar medium-sized granivorous non-passerines (pigeons) with a mean BMR of 0,59 kJ/g/day, which is lower than the mean BMR of 0,71 kJ/g/day for passerines of similar body weight, but with a more carnivorous diet. The BMR for sandgrouse is also lower than the expected value for birds of that size range (Thomas & Maclean 1981). If this means that seeds require less energy to exploit than insects as a food source, or that sandgrouse have a relatively low metabolic rate in response to a comparatively unproductive environment, then they have taken a small but probably significant adaptive step towards economizing on their resources. Certainly they outnumber insectivorous arid-zone waders, such as plovers and coursers, by several hundredfold.

Water

Sources

The low water content of seeds is their greatest single drawback as an arid-zone food source. Many desert birds compensate for a predominantly granivorous lifestyle by augmenting their diet with insects; as little as 8% by volume is enough to provide the normal water needs of the greybacked

Table 1 Mean basal metabolic rates (BMR = kJ/g/day) of various species groups of birds [mainly from Pinowski & Kendeigh (1977); sandgrouse data from Thomas & Maclean (1981)]

Species group	Weight range (g)	No. of species	BMR	
			Range	Mean
Larger non-passerines	100–2500	12	0,29–0,80	0,50
Largest passerines (raven)	1203–1208	1	0,40–0,43	0,42
Medium granivorous non-passerines (pigeons)	81–353	6	0,42–0,63	0,59
Namaqua sandgrouse <i>Pterocles namaqua</i>	174	1	–	0,55
Doublebanded sandgrouse <i>Pterocles bicinctus</i>	166	1	–	0,64
Medium omnivorous passerines	100–660	8	0,63–0,88	0,71
Small non-passerines	30–100	7	0,67–1,00	0,84
Very small non-passerines (hummingbirds)	3–20	8	1,13–2,09	1,51
Very small insectivorous passerines	3–20	13	1,38–2,89	1,84
Very small granivorous passerines (waxbills and fringillids)	6–20	11	1,55–2,93	1,93

finchlark *Eremopterix verticalis* (Willoughby 1971). Sandgrouse have taken the seemingly drastic step of becoming obligate drinkers of water, placing them in the ecological cleft stick of needing surface water in an environment whose surface water by definition is one of its most limited and localized resources. Sandgrouse are able to exploit available water because of their excellent powers of flight and their ability to drink 22,5–29,5 ml of water/drink (Willoughby & Cade 1967), although many may take no more than 10–15 ml/drink in 3–10 draughts, at a rate of 1,1–1,5 ml/draught (Cade, Willoughby & Maclean 1966). The relatively large water-storage potential of the crop may allow sandgrouse individuals to drink only every 2–5 days, thereby reducing the number of energetically expensive flights to the waterhole and reducing exposure of the birds to predation (Thomas & Maclean 1981).

Predation

Because of the vulnerability of birds at exposed waterholes in an arid environment where predators like falcons and goshawks have learned to gather daily, selection would favour rapid drinking methods to get the most water in the shortest possible time. Doves have evolved a sucking mechanism which enables them to take an entire drink merely by immersing the bill and sucking up water in several quick draughts until full, obviating the need to raise the head to swallow between mouthfuls, as most birds do. Sandgrouse have developed an intermediate method whereby the bill is immersed, the water sucked up and the head then raised to swallow; one possible advantage of this mechanism is that it allows the birds to scan the surroundings between immersions, while at the same time allowing a rapid intake of water. The draughts are made in quick succession, the whole drinking process taking no more than 5–10 s (Cade *et al.* 1966).

The usually extreme gregariousness of sandgrouse, especially at the watering places must operate as a further defence mechanism against predation, since many eyes are present to detect disturbances. The deterrent effect of a large flock must also be significant in this regard. Largely insectivorous desert waders like the doublebanded courser *Rhinoptilus africanus* and the crowned plover *Vanellus coronatus* are usually grega-

rious only when not breeding, and then in relatively small flocks or family groups; they are also independent of water (pers. obs.) even under the most severe conditions of drought and heat.

Salt balance

Because sandgrouse need to drink relatively large amounts of water, they avoid highly brackish or saline waters, possibly so as to avoid increased physiological stress, but this in turn means that they risk a salt deficit. This is compensated for in part by the absence of a salt-secreting nasal gland (or salt gland) which is found in most waders as part of their basic physiological equipment for excreting excess salt from water or body fluids of prey animals, and therefore a key preadaptation to the arid zone (Maclean 1984). The problem of salt excretion in sandgrouse falls away and that of water and salt conservation becomes correspondingly more important; Thomas & Robin (1977) and Thomas & Maclean (1981) have shown that sandgrouse resorb both water and salts in the kidneys and rectum. It is unusual, if not anomalous, to find a desert vertebrate that is not faced with a salt load.

Thermoregulation

The production of heat during flight is a potential hazard to endotherms on hot summer days. Metabolic heat production by sandgrouse, however, is lower than that expected for birds of equivalent body weight (Thomas & Maclean 1981). Sandgrouse flights to water also occur almost entirely in the cooler morning hours, or after sunset and even in complete darkness (Maclean 1976). Evaporative water loss for thermoregulatory purposes is effectively reduced by these metabolic and behavioural adaptations.

Most birds lose excess body heat in part by conduction and radiation from unfeathered areas of the body, which are termed thermal windows, for example, bill, legs, eyes, underwing apertures and possibly facial wattles. Long-legged birds like storks, coursers and plovers have a particular advantage in this respect because of the increased surface area on the legs over which heat may be exchanged with the environment. In the course of adapting to a diet of seeds, sandgrouse underwent a great shortening of the legs; the

consequent reduction in thermal window area is further reduced by feathering on the anterior surface of the legs and over the nostrils and base of the bill. The body apteria are also insulated by a thick undercoat of brown down, so that thermal windows are almost eliminated. There is no doubt that this insulation is effective against heat uptake from the ambient air, but the question of heat loss in sandgrouse is unresolved and poses one of the most challenging prospects for future research on this interesting family of birds.

Experiments in captivity have shown that Namaqua sandgrouse *Pterocles namaqua* and doublebanded sandgrouse *P. bicinctus* huddle together at high ambient temperatures, which is totally unexpected, and contrary to thermoregulatory behaviour in most other birds (Thomas, Maclean & Clinning 1981). Instead of increasing the overall surface area of the flock by separating individual birds so as to lose heat most effectively, the huddled group functions as a much larger animal with theoretically more efficient thermal properties by reducing overall surface area for heat uptake, although individuals do increase their surface area by wing-drooping. Huddling has not been observed in wild sandgrouse; huddled groups may quickly break up when disturbed, or huddling may be a psychological phenomenon induced by captivity.

Structural features

Although sandgrouse can run well, their short legs necessarily reduce their speed relative to that of coursers or plovers. When danger is observed at some distance, sandgrouse will walk quickly between shrubs and stones until at a safer range, or out of the path of the intrusion; when more closely approached they crouch on the ground before finally taking wing at the last moment. Crouching behaviour is not typical of long-legged waders, and is undoubtedly correlated with the small steps and short-legged gait of sandgrouse. Also correlated with crouching is the extreme crypsis of sandgrouse plumage patterns and coloration, concealing them most effectively even at very close range. This camouflage is of course also highly adaptive when the birds are nesting.

The good flying ability of sandgrouse is also adaptive in the face of possible predation, since they are able to take off suddenly and accelerate to speeds of up to about 60 km/h in just a few seconds. The sandgrouse wing is based on the wader pattern. It is long and pointed with long tertials and outer primary remiges (Maclean 1967); it is adapted not only to speed, but also to sustained flight for anything up to an hour or more in order to cover the often long distances between their feeding grounds and the watering points (Maclean 1968). These structural adaptations of sandgrouse are remarkably convergent with those of the seedsnipe of South America (Figure 2), which fill a similar niche.

Breeding adaptations

As descendants of the Charadrii, sandgrouse have many features of breeding biology that eminently preadapt them to the arid zone (Maclean 1984). These include principally: an exposed nest site on the ground, a small clutch (usually three eggs), cryptically coloured eggs, and precocial young.

Nest site and breeding season

Nesting on the ground like the ancestral Charadrii still do, means that sandgrouse are adapted to an environment where open ground is freely available, free of vegetation and therefore free of visual obstructions. Good visibility allows the incubating bird to retain its ancestral pattern of early nest departure in the face of predator disturbance, thereby avoiding

potential danger, and capitalizing on the retention also of the small cryptic clutch. Good visibility on the other hand applies also to potential predators, except that sandgrouse, especially the females, are exceedingly well camouflaged, small enough to blend in with the most commonly encountered objects in the arid zone (stones, shrubs, stubby grasstufts, etc.) and, when necessary, close sitters, such as in the presence of flying birds of prey or small foraging carnivorous mammals.

The high insolation experienced by an exposed bird in an arid zone has to be tolerated to a large extent, particularly in the northern hemisphere where sandgrouse nest in spring and summer. Most waders nest in such habitats anyway, so that their descendants would be preadapted to such conditions, either by tolerating a heat load when necessary, or by using thermoregulatory mechanisms to keep the body temperature below an upper critical temperature, or both. Probably the dense undercoat of down on the apteria of sandgrouse already mentioned above enhances heat tolerance, and undoubtedly insulates the birds against low night temperatures in winter. In southern Africa all four sandgrouse species — Namaqua, yellowthroated *Pterocles gutturalis*, doublebanded and Burchell's *P. burchelli* — nest mainly in winter (April to October, with a peak in July) and avoid the hottest summer months for the most part (Maclean 1985). Whether this is primarily due to food supply or not, nesting in the cooler months removes some of the environmental stresses to which the birds are otherwise subjected. In any event, the supply of seeds must be greater in winter than in summer (even if only locally) over most of the sandgrouse range in southern Africa (Figure 3), since this covers largely a summer to autumn rainfall area whose ephemeral plant production is greatest shortly after the rains, to be followed soon after by dropping of abundant seed.

Reproductive rate

A clutch of three well-camouflaged eggs has the great advantage of being much harder to see than a larger clutch, even when lying exposed on the desert floor. Conversely it means a low reproductive rate, especially considering that (a) incubation takes about 21 days, (b) fledging of the young takes about 4–5 weeks, (c) independence of the young takes at least another 4–6 weeks, (d) seldom does a pair of sandgrouse rear more than one or two young/brood, (e) no species of sandgrouse is known to rear more than a single brood in one breeding attempt, (f) water must be available within a few kilometres of the food supply and must last to the end of the juvenile dependent period and (g) seeds, though abundant, are not unlimited and the food supply in a given area must last the full duration of the breeding cycle, a period of roughly 3–4 months.

How sandgrouse maintain their large numbers with such a low reproductive rate is unknown. The answer must surely lie in a low adult mortality rate, which would be surprising in view of the apparently high predation rate on sandgrouse. However, the intensity of predation may well be low relative to the numbers of birds in a given area or at a waterhole. The relationship of the dynamics of predator vs sandgrouse populations is quite unknown.

A small clutch is adaptive also in that it represents a relatively small energy output and can be fairly easily replaced if robbed. Sandgrouse undoubtedly lay replacement clutches early in the breeding season, but there is no direct evidence for this, nor any information about the number of replacement clutches a given female is capable of. Maclean (1968) calculated that about 32% of sandgrouse eggs in the Kalahari

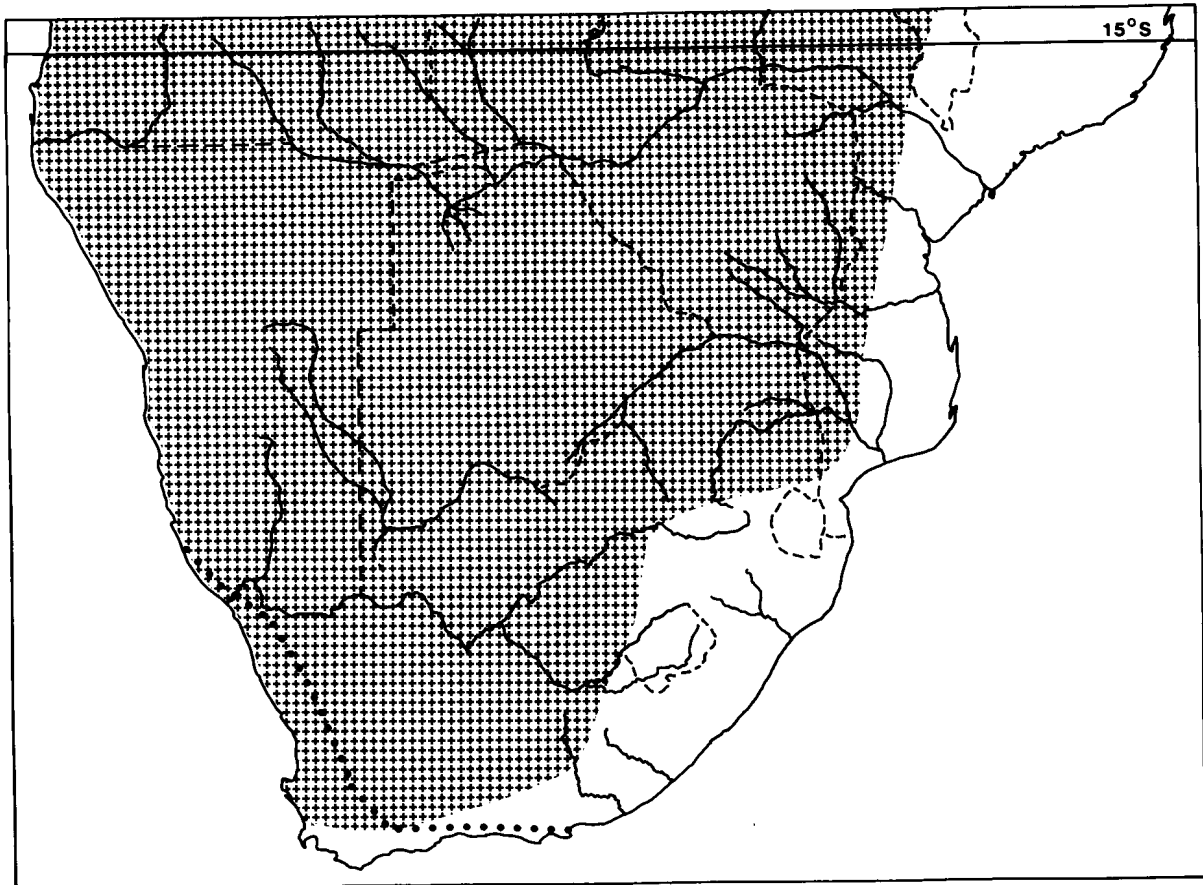


Figure 3 Range of sandgrouse in southern Africa. Heavy stippled line in south-western area shows approximate eastern limit of winter rainfall region.

sandveld were lost to predation, but was unable to offer figures for survival of young. These are in any case difficult to obtain for precocial birds. Even if as many as 50% of hatched young survived to adulthood, only 34% of eggs laid would produce adult birds. This low reproductive rate is not what one would expect from arid-zone granivorous birds which should have a 'large clutch size, multiple broods, rapid developmental rates, early sexual maturation' (Wiens & Johnston 1977). The survival rate must depend in large measure on a high degree of parental care. Reproductive rates in sandgrouse are clearly in need of closer investigation.

Parental care

Certainly the most dramatic and probably the best-known feature of sandgrouse biology is their habit of carrying water to their young in their belly plumage. Because sandgrouse chicks feed from their first day of hatching on the same small dry seeds as do their parents, they must be provided with water. By carrying water in the feathers, the parent does not deplete its own internal water supply; wet feathers, however, do not make for efficient brooding of the young or insulation of the adult's ventral surface, but two factors compensate for this. Firstly it is usually only the male parent that carries water to the young, leaving the female's belly plumage dry for brooding the chicks. Secondly, because of the apterial down in adult sandgrouse, the male's belly region is adequately insulated against cold, even when the contour feathers are wet; indeed the down is highly water-resistant and remains dry at all times.

In the event that the female parent has to carry water, perhaps because the male has been taken by a predator, or because the amount of water carried by the male becomes

inadequate to supply a brood of three young in their later stages of growth, she is capable of doing so since her belly feathers are also provided with the specialized water-carrying structures, but to a lesser degree than those of the male (Cade & Maclean 1967).

The nature of the structural modifications of sandgrouse belly feathers has been the subject of detailed investigation (Cade & Maclean 1967; Joubert & Maclean 1973) and the whole subject of water transport in sandgrouse has been thoroughly reviewed by Maclean (1983).

In order to put the story of sandgrouse water transport into evolutionary perspective, it is necessary to look at the overall picture of wader parental care and then examine the ways in which sandgrouse have used ancestral features in their own parental strategies. All wader chicks are precocial and cryptically coloured, although dorsal plumage patterns differ between families; generally, however these patterns are fairly constant within a family or subfamily and are useful indications of relationships. Sandgrouse chicks have a unique dorsal pattern of coloration which can be derived from that of coursers of the genus *Cursorius*. Further evidence of a cursoriine ancestry for sandgrouse is that they are the only two taxa of birds in the charadriiform complex whose chicks crouch with the head up and not flat on the ground. This may be an adaptation to keep the head away from the hot desert substrate, but it is equally useful in a systematic context.

Parental feeding of young among true waders is highly variable and not consistent even within some families, but all glareolids (coursers and pratincoles) feed their young to flying age, while sandgrouse do not. This undoubtedly has something to do with their diets of insects and seeds respectively, but sandgrouse do show food to their young by pecking at it.

Several kinds of waders soak their belly feathers in order to moisten or cool their eggs in hot weather (Begg & Maclean 1976; Maclean 1975); the barbules of their belly feathers are somewhat twisted at the base when dry, and straighten out when wet, so as to form a bed of hairs in which water is trapped. The barbules of sandgrouse belly feathers are also coiled at the base, but much more strongly than those of wader feathers, and the hooked barbicels that give most feathers structural cohesion have been entirely lost. Each barbule ends in a terminal filament about 0,3 mm long which stands up at right angles to the feather vane when the wet barbule uncoils; the resulting bed of hairs is dense and capable of holding a substantial amount of water. The belly plumage of a male Namaqua sandgrouse can hold an average of 22 ml, that of a female about 9 ml (Cade & Maclean 1967).

Structural cohesion in sandgrouse belly feathers is conferred in the dry state by the intertwining of the coiled bases of adjacent barbules (Figure 4a). When uncoiled on wetting (Figure 4b), this cohesion is lost with a concomitant loss of insulative properties and may, as already mentioned, be one reason why sandgrouse have evolved a dense water-resistant underdown. After the chicks have drunk, the male sandgrouse usually rubs his belly plumage thoroughly in sandy soil in order to dry it; this is probably especially important in winter to insulate the belly region against excessive heat loss. Most sandgrouse drink and water their young in the first part of the morning (Maclean 1976) when ambient temperatures are



Figure 4 Photomicrographs of part of (a) dry and (b) wet Namaqua sandgrouse *Pterocles namaqua* male belly feathers. The barbule bases in the dry feather are interlocked and hold the barbs firmly together; in the wet feather they are uncoiled, so that their terminal filaments stand upright to hold water.

rising, so that the problem of heat loss is less serious than would seem to be the case in the night-drinking species — Lichtenstein's *P. lichtensteini*, doublebanded, fourbanded *P. quadricinctus* and Indian sandgrouse *P. indicus* — whose parental biology is still poorly known.

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