Sandgrouse as models of avian adaptations to deserts

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Sandgrouse have many adaptations whose cumulative effect is sufficient to let them thrive and reach high population densities. The adaptations include: (a) Selection of appropriate micro-environments: movement between sun and shade is reminiscent of heliothermic reptiles, conserving energy and water reserves; (b) Activity (flying and feeding) in the morning and evening, when metabolic heat can be dispersed most easily without invoking evaporative mechanisms; (c) Thermal insulation by feather erection and huddling with conspecifics at both low temperatures (energy conservation) and when ambient temperatures exceed body temperatures (water conservation); (d) Infrequent drinking (in some species at least), allowing exploitation of wider areas around watering points, and saving water and energy on drinking flights; (e) Reduced metabolic rate and selection of energy- and protein-rich seeds reduce food requirements, metabolic heat loads and possibly foraging time; (f) An excretory system apparently well adapted for water and salt conservation; (g) Specialized reproductive biology, reducing the metabolic demands for clutch formation and egg-water loss, and allowing the young to be watered without drawing on parental water reserves.

As a general principle, it is suggested that successful desert animals are also likely to show a similar multiplicity of adaptations, whose concerted effect is to conserve water and energy reserves.

S. Afr. J. Zool. 1984, 19: 113 – 120

Sandpatryse beskik oor baie woestynaanpassings waarvan die kumulatiewe effek hulle toelaat om te gedy en hoë bevolkingsdigthede te bereik. Hierdie aanpassings sluit die volgende in: (a) Uitsoek van geskikte mikro-omgewings: bewegings vanaf son na skaduwee herinner aan heliotermiese reptiele wat water- en energiereserwes bewaar; (b) Aktiwiteite (vlieg en voeding) in die oggend en laatmiddag wanneer metaboliese hitte die maklikste versprei kan word sonder om verdampingsmeganismes te gebruik; (c) Termiese isolering: deur die vere te laat rys en deur saam te bondel by lae temperature (energiebesparing) sowel as hoë omgewingstemperature (waterbesparing); (d) Ongereelde waterinname (by ten minste sommige soorte) waardeur hulle in staat gestel word om 'n groter gebied te benut en om water en energie op vlugte na drinkplekke te bespaar; (e) Verlaagde metaboliese tempo en seleksie van energie- en proteïenryke sade, verlaag die voedselbehoeftes, metaboliese hittelading en moontlik ook voedingstye; (f) 'n Uitskeidingsisteem wat oënskynlik goed aangepas is om water en elektroliete te bewaar; (g) 'n Gespesialiseerde voortplantingsbiologie wat die metaboliese vereistes vir broeisels en waterverlies vanaf eiers beperk en die kleintjies in staat stel om water te bekom sonder om die ouers se liggaamswatervoorraad te benut.

As algemene beginsel word voorgestel dat suksesvolle woestyndiere waarskynlik soortgelyke veelvuldige aanpassings vir effektiewe water- en energiebesparing sal openbaar.

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Birds, even small ones the size of larks, are strikingly conspicuous members of the desert fauna. This contrasts with mammals, the other class of homoiotherms, which are seen there by day only if they are large. The majority of bird-sized desert mammals are nocturnal and avoid daytime conditions in the recesses of a burrow or crevice. Diurnal animals in hot deserts have to deal with high temperatures and heat loads during the middle of the day, and these problems become more severe for animals living nearer the ground (owing to the absolute increase in temperature extremes at that level; Gates 1962) and for animals of diminishing size.

However, heat exchange is only one of a series of problems all arising as consequences of the shortage of moisture in truly desert environments: dry atmospheres allow large upward and downward radiant heat fluxes (Figure 1), which are expressed mostly in extremes of ambient temperature, since there is little moisture in the environment to act as a temperature buffer by absorbing or releasing latent heat of vaporization. Low biological productivity is another consequence of water shortage: other things being equal, primary productivity in arid zones increases in a broadly linear fashion with increasing annual rainfall (at least up to 600 mm/year, as illustrated for grasslands in various continents by Walter 1964). Consequently, arid lands are characterized by a low density of food resources, to which animals must also become adapted. This they may do both by increasing their foraging effectiveness and by conserving energy and nutrients. Thirdly, the water supply itself is limited, or at least only locally abundant, and its quality may vary. As the concentration of dissolved solids increases, the physiological availability of water decreases owing to osmotic effects. This is a problem not only for those animals that drink, because the sap of plants (especially halophytes) and the body fluids of animals also contain significant concentrations of solutes. However, there are certainly desert areas where essential minerals are deficient and herbivores (such as sandgrouse) need adaptations for salt conservation rather than salt excretion (Thomas 1984). Once again, animals may adapt to water shortage as to food shortage, both by increasing their effectiveness at obtaining their needs and by conservative use of what they have.

It is difficult to know what to expect in quantitative terms when one looks for animal adaptations to particular environments, although one might suppose that the most extreme environments would evoke the most extreme adaptations. Since differences may also arise between animals owing to differences in phylogeny and to simple scaling effects associated with body size, there are great advantages in looking for adaptive dif-

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ferences among closely related species of similar size, which differ mainly in the different environments in which they live. When it comes to studying the adaptations of birds in deserts, sandgrouse fulfil these criteria rather well: for all the arguments as to whether the family is allied with columbiform or charadriiform birds (e.g. Maclean 1967), there has never been any doubt as to the phyletic uniformity of its member species, and this uniformity is confirmed by recent DNA-hybridization studies (G.C. Sibley, pers. comm.). The size range among sandgrouse is small compared to that in many families of animals (from around 150 g in *Pterocles namaqua* and *P. bicinctus* to 600 g in *P. orientalis*), and they all have a basically similar diet (seeds) for which they forage on the ground in more or less open habitats. On the other hand, the various species occur in a range of habitats, from comparatively mesic ones (reliable rainfall of *ca.* 400 mm/year: e.g. *P. alchata*, *P. orientalis* and *P. gutturalis*) through to extremely harsh desert conditions (very variable and unreliable rainfall of *ca.* 50 mm/year: e.g. *P. senegallus* and *P. coronatus*). Other species, such as the southern African *P. bicinctus* and *P. namaqua* seem somewhat more catholic in their choice of habitat, and are able to thrive in the Kalahari and Namib Deserts as well as in areas with considerably higher rainfall and denser vegetation. Thus sandgrouse have many attributes which make them suitable models for studying avian adaptations to hot deserts.

Sandgrouse have numerous traits which can be interpreted as adaptations for life in arid lands. In some cases this interpretation is reinforced by the observation that the trait is more marked in species from harsher deserts compared to those from more mesic habitats. Indeed, virtually every trait examined seems to show some evidence of adaptive modification and suggests that a general feature of animal adaptation to a particular environment involves many aspects of behaviour, ecology and physiology.

Therefore, this paper will seek to illustrate the premise that sandgrouse succeed in deserts as a result of a large number of appropriate changes suitable to the environment.

The following material is based mainly on work done in Morocco (Thomas & Robin 1977) on sandgrouse living in steppe (*P. alchata* and *P. orientalis*) and desert habitats (*P. senegallus*, *P. coronatus* and *P. lichtensteini*), and on work in the Namib Desert on *P. namaqua* and *P. bicinctus* (Thomas & Maclean 1981; Thomas, Maclean & Clinning 1981). Other subjects touched upon in this paper are discussed more fully in a recent review (Thomas 1984).

Energy balance and temperature regulation

The clear atmosphere of desert environments permits large solar and environmental ('thermal') heat fluxes, downwards mainly by day and upwards throughout the 24-h cycle (Figure 1). Sandgrouse show behavioural patterns by which they exploit the temporal and spatial heterogeneity of their thermal environment. During the heat of the day, birds make use of the best shade available, even if it gives only partial cover. If it is sufficiently extensive, they maximize their exposure to the clear sky (a valuable heat sink: Figure 1) by moving to the edge of the shade (Figure 2). Soon after dawn, however, *P. namaqua* and *P. bicinctus* sun themselves (Figure 3), and this accounts for about half the 2 – 2,5 °C rise in body temperature normally found at this time of day (Thomas *et al.* 1981). This would save a small proportion of their daily energy requirements (since they would otherwise have to generate metabolic heat to produce the normal increase in body temperature which occurs about dawn), but the proportion may be enlarged in starved or thirsty birds by lowering overnight body temperatures even further and by deriving all heat exothermically for the dawn temperature increase.

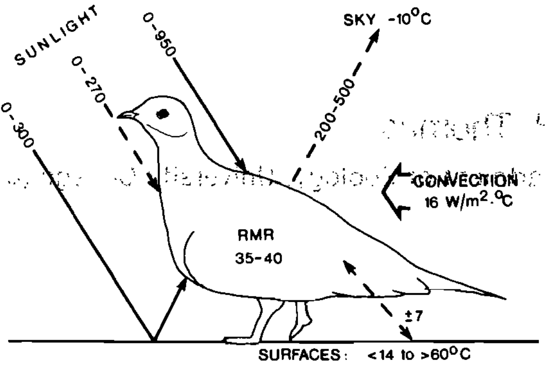

Figure 1 Heat fluxes (W/m^2) estimated for a 150 g sandgrouse in the Namib Desert. Solid lines show visible and near infra-red radiation, and dashed lines show far IR ('thermal') radiation. Note that the clear sky acts as a heat sink at all times, which may be exploited by day when sandgrouse need to lose heat (see Figure 2), and which they may avoid at night by roosting in huddles in the protection of a rock or bush. 'Thermal' radiation exchange with the surroundings is probably small because the well-insulated feather layer allows feather surface temperatures to match those of the surroundings. Convective heat exchange (gain or loss, calcualted here for a mean wind speed of 1,77 m/s: Thomas *et al.* 1981) is potentially large and sandgrouse generally do not expose bare or sparsely covered skin. Resting metabolic rate (RMR W/m^2 skin surface) is probably low for the bird's body mass, in comparison to non-desert birds. (Compiled from Thomas & Maclean 1981; Thomas *et al.* 1981.)

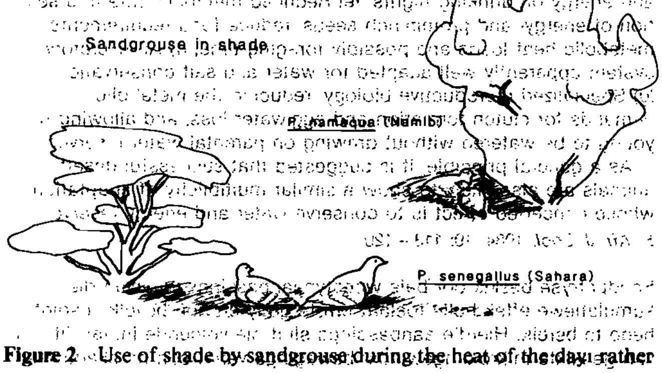

Figure 2 Use of shade by sandgrouse during the heat of the day: rather than remaining right in under a bush, sandgrouse frequently sit out in the edge of its shade. The effect of this will be to retain shelter from direct sunlight while exposing the birds to a clear sky, which acts as a heat sink (see Figure 1). (Traced from the author's photographs of sandgrouse in the wild.)

Sandgrouse activity patterns in the wild and in captivity are closely dependent on air temperatures and time of day (Figure 3; Thomas & Robin 1977; Thomas & Maclean 1981; Thomas *et al.* 1981). Characteristically, strenuous activity (particularly prolonged flights between foraging areas and drinking points) occurs under relatively cool conditions shortly after sunrise or sunset (depending on species), when solar heat loads are small and surplus metabolic heat can be dispersed most easily (by conduction, convection and radiation), thus reducing recourse to evaporative heat dispersal. Timing of such activity varies appropriately: in Morocco, *P. alchata* and *P. orientalis* drank earlier and in larger numbers on hot sunny mornings than on cool misty ones (Thomas & Robin 1977). There are also significant temporal patterns to less strenuous activities: most walking (associated with foraging) occurs in the morning and afternoon, while around midday birds spend much of their time standing or sitting, and this reduction of activity then becomes

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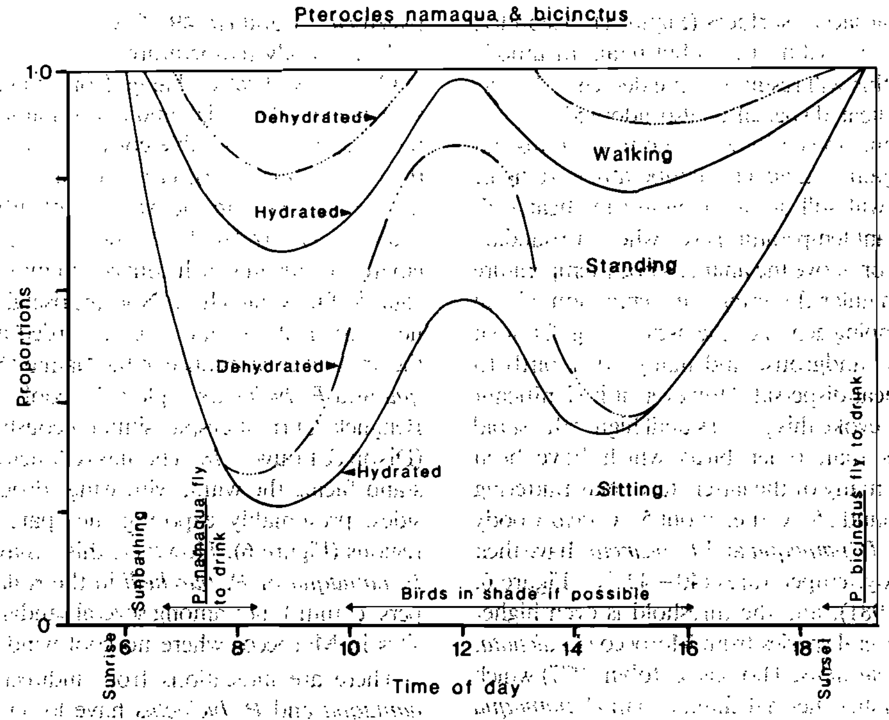

Figure 3 Changing activity patterns at different times of day. The areas between the lines represent the proportions of time spent by birds sitting, standing or walking at any time, for captive birds in an outdoor aviary in the Namib Desert. Solid and dashed lines are for birds with free and without any access to water for up to three days. There is a clear decrease in activity during the heat of the day, which is more marked in dehydrated birds, and which would reduce demands on their body water reserves. Note that birds also sunbathed just after sunrise, and moved into the shade (if available) through the heat of the day. The times of drinking flights by wild birds are also shown. (Compiled and simplified from Thomas & Maclean 1981, and Thomas *et al.* 1981.)

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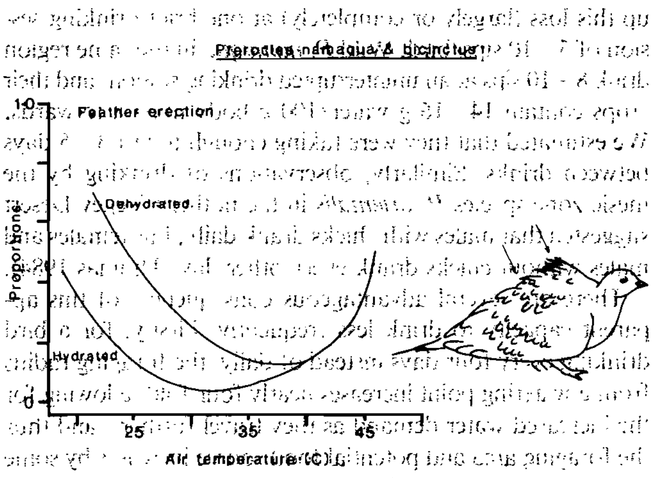

Figure 4 The proportion of time spent insulating by feather erection at different air temperatures. These captive birds in an outdoor aviary in the Namib Desert insulated themselves both at low temperatures and at air temperatures above body temperatures, and the effect was more marked in dehydrated birds. (Simplified from Thomas & Maclean 1981.)

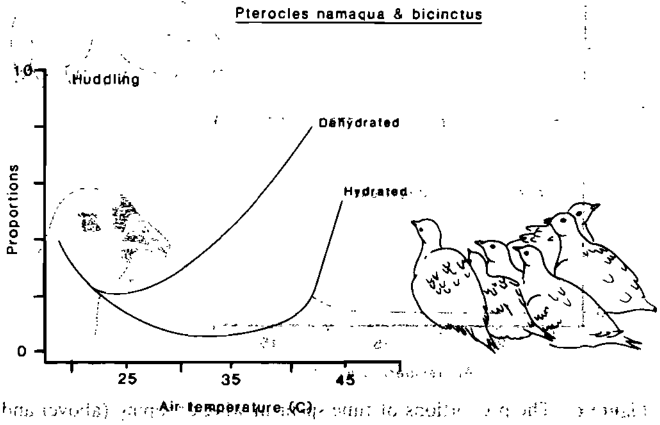

Figure 5 The proportion of time spent insulating by huddling together in groups, among captive birds in an outdoor aviary in the Namib Desert. Huddling occurred in night-time roosts and at high air temperatures during the heat of the day, and was also more marked among dehydrated birds. It would be extremely difficult to observe huddling in the wild, since birds dispersed quickly from huddles on the least disturbance. (Simplified from Thomas & Maclean 1981.)

Other than sandgrouse, few birds have been studied which regularly face air temperatures well in excess of deep body temperatures. For example, sandgrouse are faced with, and can readily survive, air temperatures of over 50 °C for at least 4h/day on a regular daily basis. Insulation (both by feather erection and by huddling together for mutual benefit: Figures 4 & 5; Thomas & Robin 1977; Thomas & Maclean 1981) is an important reponse to both low and high (i.e. > body temperatures of 40 – 42 °C) air temperatures, since it retards adverse heat exchange. Insulation against heat loss is universal amongst homoiotherms, and diminishes as air temperatures rise towards body temperatures. However, few if any animals (with the exception of sandgrouse) seem to have the sensory-motor capacity to perceive the boundary conditions (when air = body temperature), and to reverse the trend of reducing insulation then so that it increases again at higher temperatures as the tendency to gain heat from the environment also increases. Calculations show that conductive heat transfer across the sandgrouse's feather coat is probably rather slow (Thomas *et al.* 1981), which has two principal consequences under hot conditions: firstly, the radiant (outer) feather surface will reach similar temperatures to those of other opaque solids in the vicinity, so that net radiant heat exchange is probably small

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between the bird and adjacent surfaces (Figure 1). Secondly, insulation will not only retard heat gain but retain metabolic heat production, and this will result in some degree of hyperthermia unless active heat dispersal is also adopted.

Evaporation is the only means by which homoiotherms can disperse excess heat against an adverse temperature gradient, although a clear sky will still act as a significant heat sink (because of its low radiant temperature) even when surrounding air temperatures are at or above the animal's body temperature (Figure 1). Gaping and gular fluttering (i.e. ventilation of oral membranes by the pumping action of the oscillating gular area: Figure 6) are used by sandgrouse and many other birds to enhance evaporative heat dispersal. However, it is significant that sandgrouse do not evoke this process until higher threshold ambient temperatures than other birds which have been studied. For example, many of the latter start gular fluttering at air temperatures around 35 °C (i.e. about 5 °C *below* body temperatures), whereas *P. namaqua* and *P. bicinctus* have their thresholds at their body temperatures (40 – 42 °C: Figure 6; Thomas & Maclean 1981), and the threshold is even higher (48 – 50 °C) among several species from Morocco (*P. alchata, P. coronatus* and *P. senegallus*; Thomas & Robin 1977) which experience an even harsher thermal climate than *P. namaqua* and *P. bicinctus* in southern Africa (Thomas & Maclean 1981).

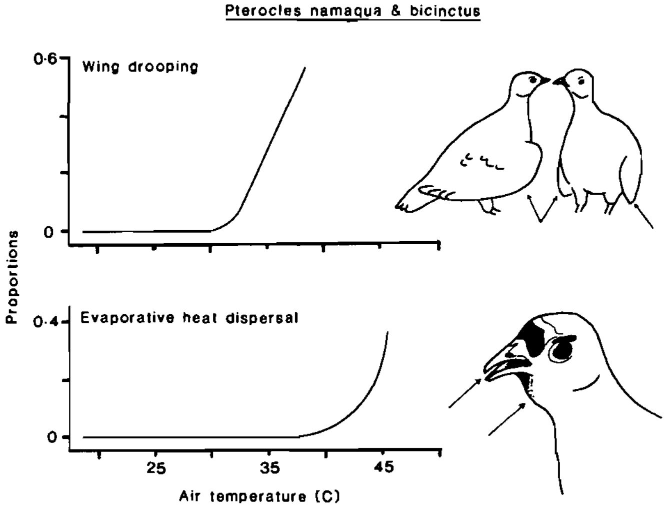

Figure 6 The proportions of time spent in wing-drooping (above) and in evaporative heat dispersal by gaping and gular fluttering (below), by captive birds in an outdoor aviary in the Namib Desert. Wing-drooping appears to be used to enhance convective heat loss, and is seen only during the heat of the day where birds are exposed to wind temperatures lower than body temperatures (as in the Namib Desert during cool onshore winds off the Benguela Current). Unlike other birds, sandgrouse do not start evaporative heat dispersal until air temperatures at or above body temperatures (40 – 42 °C). (Simplified from Thomas & Maclean 1981.)

By raising the temperature threshold thus, sandgrouse effectively reduce the demands on their body water reserves by reducing the duration of forced evaporation, albeit at the expense of thermal homeostasis. It is to be emphasized that this water-saving strategem is more marked in the species which experience the more extreme climatic conditions. The corollary of this difference is that *P. namaqua* and *P. bicinctus* (which experience generally lower air temperatures) guard body temperatures of 40 – 42 °C in air temperatures of over 51 °C (Thomas & Maclean 1981), whereas the Moroccan species just mentioned evidently tolerate some measure of hyperthermia, since insulation without heat dispersal at air temperatures between *ca.* 41 and *ca.* 49 °C will retain metabolic heat which will raise body temperatures.

Convective heat exchange from uninsulated areas of bare skin can be substantial, and many animals of less hot environments exploit favourable convective losses, as is well known (Calder & King 1974). However, it is conspicuous that sandgrouse have little in the way of unfeathered surfaces, which is doubtless correlated with the temperature extremes of their environments, in which convection may be a serious potential source of unwanted heat. Not surprisingly therefore, convective heat dispersal has only been recorded among sandgrouse in the unusual circumstance of the Namib Desert, where *P. namaqua* and *P. bicinctus* exploit the cool onshore winds off the Benguela Current despite simultaneously high solar heat loads (Dixon & Louw 1978; Thomas & Maclean 1981). These birds stand facing the wind, with wings drooped away from their sides, presumably exposing the sparsely feathered axillary regions (Figure 6). However, this behaviour was not seen in *P. namaqua* or *P. burchelli* in the Kalahari (G.L. Maclean, pers. comm.), nor among several sandgrouse species at inland sites in Morocco, where no cool wind was available.

There are indications from indirect calorimetry that *P. namaqua* and *P. bicinctus* have lower mass-specific resting metabolic rates than would be expected for birds of their size (Thomas & Maclean 1981). Such reductions are well known for other mammals and birds of deserts, and seem to confer several useful advantages: reductions in food requirements, metabolic heat production and demands on body water reserves. It would seem that sandgrouse generally are likely to show this adaptation, but more and better measurements are required to test this supposition.

Water metabolism

There is considerable evidence that sandgrouse are capable of a very parsimonious water economy, although they drink regularly in the wild (as would be expected of seed-eaters with little preformed water in their diet: Fisher, Lindgren & Dawson 1972), and they may drink frequently in captivity when offered water *ad libitum*. Indeed, some species in the wild may normally drink only every 3 – 5 days. Under experimental conditions in an outdoor aviary in the Namib Desert *P. namaqua* and *P. bicinctus* survived three days of water deprivation without any signs of distress, during which they showed only slow loss of body mass, and at the end of which they made up this loss (largely or completely) at one brief drinking session of 5 – 10 sips/bird. Wild *P. namaqua* in the same region drink 8 – 10 sips at an uninterrupted drinking session, and their crops contain 14 – 16 g water/100 g body mass afterwards. We estimated that they were taking enough to last 3 – 5 days between drinks. Similarly, observations of drinking by the mesic zone species *P. orientalis* in the nothern Negev Desert suggested that males with chicks drank daily, but females and males without chicks drank every other day (Thomas 1984).

There are several advantageous consequences of this apparent capacity to drink less frequently. Firstly, for a bird drinking every four days instead of daily, the foraging radius from a watering point increases nearly four-fold (allowing for the increased water demand as they travel further), and thus the foraging area and potential food source increases by some factor approaching 16-fold, which must be extremely important in an environment with low biological productivity. Incidentally, this might explain reports in the literature of sandgrouse travelling great distances to drink: for example, 60 km each way (Meinertzhage 1964) seems uneconomically long as a daily

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journey, but not so unreasonable if spread over four days and thus involving only 30 km travel per day. Secondly, less frequent drinking reduces the daily travelling required between feeding areas and drinking points, and thus reduces the birds' food and water requirements. Thirdly, it cuts down the frequency with which individuals are exposed to predators (such as falcons, *Falco* spp.) which congregate at waterholes to exploit the predictable arrival of flocks of drinking sandgrouse. However, it seems likely that chicks have to be watered daily (although there is no direct evidence for this), so presumably nests would have to be located within the inner portion of the foraging range to be within economical daily reach of water.

Experimental water deprivation results in significant changes in sandgrouse behaviour, all tending to reduce demand on body water. These behavioural changes must explain, at least in part, why the birds are able to drink so infrequently. For example, birds become less active (Figure 3) and insulate themselves more both at low and high temperatures (Figures 4 & 5), thus generating less metabolic heat, conserving energy reserves (so reducing the need to forage) and reducing the evaporative water losses inevitably associated with activity.

Kidney structure is also consistent with good water-conserving capabilities. Medullary tissue (i.e. the portion responsible for generation of zones of hyperosmolality, and hence urine concentration) is extremely well developed, occupying a large proportion of renal volume and having very long arrays of collecting ducts and loops of Henle. Moreover, sandgrouse have relatively small kidneys (59 – 89% of the mass expected from allometric analysis of kidney and body size), as do several other seed-eating birds from arid environments (Thomas & Robin 1977; Thomas, Degen & Pinshow 1982). The reason for this is not known, but I have suggested (Thomas 1984) that relatively small kidneys with a small proportion of extra-medullary tissue can be considered as functionally equivalent to a permanent state of glomerular antidiuresis. Glomerular antidiuresis by preferential shut-down of extra-medullary nephrons (under the influence of arginine vasotocin, the avian antidiuretic hormone) is a normal feature of avian kidney function (Braun 1982). So it seems that during their adaptation to deserts sandgrouse have evolved a preferential loss of extra-medullary nephrons in response to the need for prolonged (and now effectively permanent) antidiuresis. Interestingly enough, among the five species of sandgrouse in Morocco those with the greatest proportional reduction of relative kidney mass are those which are most desert adapted (Thomas & Robin 1977).

The final composition of fluid in bird droppings is determined not by the kidneys but by the lower intestine (i.e. coprodeum, rectum and caeca), except perhaps where birds lack extra-renal salt glands (as do sandgrouse) and need to excrete a large intake of NaCl (Thomas 1982; Thomas, Pinshow & Degen 1984). Normally, however, ureteral urine and fluid from the upper intestine mix in the lower intestine, where the epithelium has a large and homeostatically variable capacity for absorbing water, NaCl and other useful solutes (Thomas 1982). While nothing is known specifically about the function of the sandgrouse lower intestine, the caeca are extremely large and fluid from the rectal lumen has a composition (moderately hyperosmotic and with a significant content of NaCl) which suggests that Na-linked water and solute absorption is possible (Thomas & Maclean 1981; Thomas 1982). Certainly both caecal and non-caecal droppings of sandgrouse have a low water content, consistent with a substantial capacity for recovering water in the lower intestine.

Ecological isolating mechanisms

Sandgrouse are birds with a modest range of body sizes (150 – 600 g), and all feed on seeds which they find in a similar way by searching on the ground. Yet, despite these general similarities, the harshness and low productivity of their habitats might suggest that ecological isolating mechanisms should be well developed between species, particularly since Maclean (1976) has shown that up to six sandgrouse species may occur in a geographical region. However, I have shown recently (Thomas 1984) that when one examines sandgrouse distribution on a local rather than geographical scale, few areas have more than two common sympatric species. Where there is a third, it is often uncommon or a seasonal immigrant. For example, in north-west Africa there is little distributional overlap between the two species in steppe habitats (*P. alchata* and *P. orientalis*) and the three desert species, of which *P. coronatus* and *P. senegallus* are common and *P. lichtensteini* is very local. Similarly, in southern Africa not more than two of the four species seem to occur in any given area, although a species may coexist with one species in one area and another elsewhere. Such sympatric species pairs are *P. namaqua* and *P. burchelli* in the Kalahari sandveld, *P. namaqua* and *P. bicinctus* in the Namib Desert and adjacent areas, and *P. bicinctus* and *P. gutturalis* in mopane bushveld.

Amongst sympatric species there are often considerable differences in body size (e.g. *P. orientalis* 450 – 600 g compared to *P. alchata* 235 – 340 g; or *P. gutturalis* 350 – 400 g compared to *P. bicinctus* 150 – 170 g), but this is not necessarily so. *P. coronatus* and *P. senegallus* are of similar size (*ca.* 300 g) as are *P. namaqua, P. bicinctus* and *P. burchelli* (150 – 170 g), yet two of these species pairs, (*P. coronatus* and *P. senegallus*) and (*P. namaqua* and *P. burchelli*), have even been recorded as feeding on the same foods in the same areas, albeit during times of local abundance of the particular food plants (Thomas 1984). Among these similarly sized sympatric species, ecological compatibility seems to be promoted by some preference for different microhabitats (but with very considerable overlap: e.g. *P. senegallus* and *P. burchelli* prefer sandy substrates, *P. coronatus* and *P. namaqua* more stony ones, and *P. bicinctus* rocky low hills). Somewhat different feeding techniques may also allow them to differentiate their food resources. The latter point has been substantiated partially for *P. namaqua* and *P. bicinctus*, which are similar in size of body and bill, and show overlapping habitat preferences. *P. namaqua* forages extensively, searching a wide area rapidly, while *P. bicinctus* forages intensively, searching restricted areas more carefully. This may allow the two species to exploit different types of seed (segregated by the winnowing effects of the wind, for example) in the way that similar differences in foraging technique appear to allow in some north American species of heteromyid rodents (Thomas *et al.* 1981; Thomas 1984). However, it has not been shown that *P. namaqua* and *P. bicinctus* really do take different diets when feeding in the same area, while instances have been mentioned already where pairs of similar species have been found feeding on the same (possibly superabundant) foods.

It is undoubtedly the case that sandgrouse are highly selective feeders, and it is remarkable how certain plant genera and families from rather a few orders recur in the diets of different sandgrouse species in widely different geographical regions. I have dealt with this in detail elsewhere (Thomas 1984) and the point is illustrated in Figure 7. Some outstanding features are the recurrence of leguminous seeds (with species of

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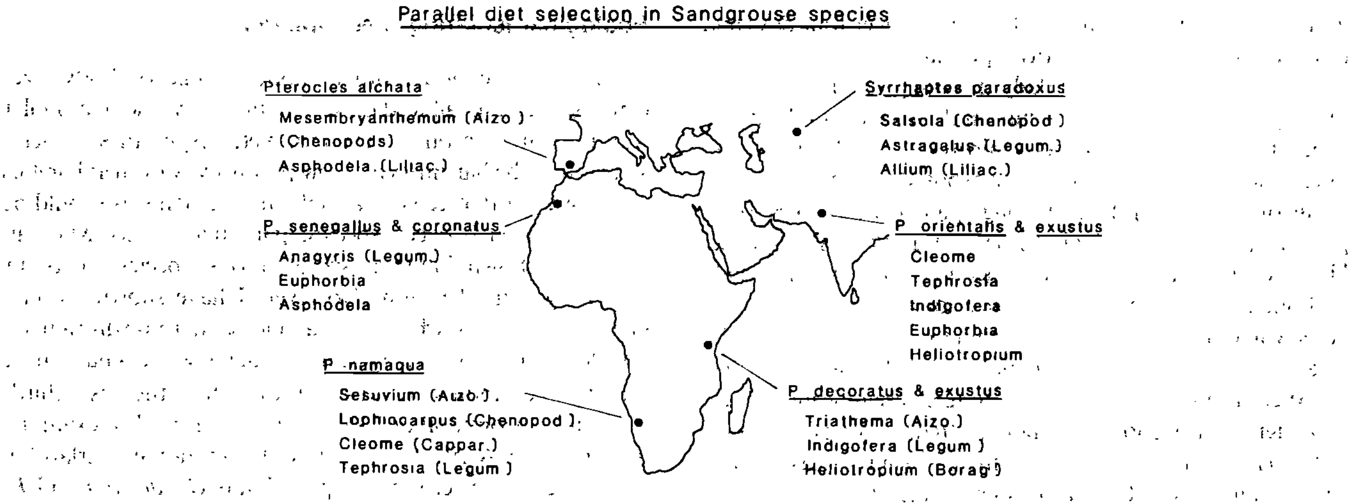

Figure 7 Different sandgrouse species in different geographical regions nonetheless show a remarkable parallelism in their use of seeds from a comparatively restricted range of plant genera and families. The possible reasons and significance of this observation are discussed in the text.

Tephrosia and *Indigofera* being eaten in south-western and eastern Africa and in north-western subcontinental India), of families in the order Caryophyllales (Aizoaceae and Chenopodiaceae with several genera of halophytic plants) and in the order Capparales (including Capparaceae and Cruciferae, many of whose seeds have a high oil content). Bearing in mind the diversity of the flora in the regions covered by Figure 7, and that reports of sandgrouse food items are mainly haphazard with very few thorough studies, the comparative restriction of the foods selected seems particularly noteworthy and in need of explanation.

I believe the explanation involves both positive and negative elements in the selection process, with the key to the former being based on the observation by Dixon and Louw (1978) that *P. namaqua* selected seeds high in crude protein and energy content and low in crude fibre. This type of diet (if repeated in other species) may explain the recurrence of legumes (high in protein) and of oleaginous and other seeds high in energy, for which one can think of many advantages: there may be a general advantage in energetic terms to forage and digest a small number of high quality items rather than the necessarily larger number of low quality ones required to meet the birds' nutritional requirements. Furthermore, there is an unavoidable loss of moisture held mechanically in the bulk of solid excreta, so that the moisture losses associated with the lesser bulk of a high quality diet will be less than those associated with a low quality one with much residue. The repeated use of the seeds (and sometimes leaves) of halophytes may be associated with the generally low salt content of other seeds and of many water sources, which is further substantiated by records of some sandgrouse actually eating crystalline salt (Bannerman 1931; Thomas 1984). Turning from the positive features of a potential dietary component, negative features may include any of the protective devices evolved by plants against seed-predators, such as toxins, hard or spiny seed coats, etc. Many leguminous seeds are known to contain potent toxins, yet the genera of legumes used by sandgrouse tend to be those with a low complement of toxins (M. Wink, pers. comm.).

Thus the comparatively restricted range of foods taken by sandgrouse may be due to the fact that rather few seeds meet the joint requirements of high nutritive value, low content of indigestible residues and toxins, and physical characteristics which allow the birds to handle them effectively. Whatever the reason, sandgrouse do indeed seem to use a limited variety of seeds (in comparison to what is available), which may in turn prevent very much ecological isolation based on diet. This, taken in conjunction with the low productivity of desert environments, may easily explain why there are rarely more than two sandgrouse species common in any given locality.

Adaptations for breeding

Special problems of heat balance and the supply of water, energy and nutrients all have to be faced by breeding sandgrouse. It seems paradoxical, yet it is well substantiated that they nest out in the open, away from shade. There is much to recommend George's (1969) intuitive explanation that this is to avoid predators which may be more numerous in the washes and wadis where shade occurs. In the absence of shade, the incubating bird presumably loses more water: we have shown that an incubating female *P. namaqua* spent more time gular fluttering during the heat of the day than other birds with access to shade. However, this may not matter so much if birds are restricted to nesting within comparatively easy reach of water because of the chicks' requirements, as discussed already. Another apparent paradox is the way in which females invariably seem to incubate through the heat of the day, after all the demands of producing the clutch beforehand. However, this situation may allow her at least two energetic advantages which would be useful in helping her to recoup her previous metabolic outlay on the eggs: she is thus freed firstly to feed in the cool of the morning and late afternoon, and secondly to protect herself more from heat loss to the night sky by getting under a bush and/or by huddling together with other birds, both of which are observed features of roosting behaviour (Thomas *et al.* 1981).

Sandgrouse are probably phyletically distinct at the ordinal level, and have the Charadriiformes as their closest relatives (G.C. Sibley, pers. comm.), with which they show many parallels, especially in breeding biology (Maclean 1967). The clutch size of sandgrouse (3 eggs) is typical of many waders, yet their egg size (6 – 9 g/100 g body mass) is small compared to those of Charadriidae (12 – 17 g/100 g body mass) of comparable body mass (Lack 1968). Notwithstanding this difference, sandgrouse hatchlings are fully precocial, yet the relatively smaller eggs allow the clutch to be completed with much less investment of resources (nutrients, minerals, energy sources and water), which is an obvious advantage in a desert environment. Incubation time is correlated with egg mass (Rahn & Ar 1974),

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so evolution of smaller eggs may also have been associated with a slight but beneficial reduction in the period for which the incubating adults are exposed to especially high heat loads, and are made more vulnerable to predators by their need to return repeatedly to the nest site.

In addition to their size, sandgrouse eggs are also adapted with respect to their porosity and rate of development. During incubation, birds' eggs lose a remarkably constant 15% of their fresh-laid mass by evaporation, regardless of size or incubation period (Ar & Rahn 1978). This suggests that there are strong selective constraints in operation, and one might therefore expect sandgrouse eggs to be adapted to counteract the desiccating nature of their environment. This is indeed the case: eggs of *P. namaqua* have a water vapour conductance (a measure of porosity, that is, the ease with which water vapour can be lost by diffusion) which is only 76% of that expected on the basis of allometric analysis (Thomas & Maclean 1981). Moreover, they have shells only 81% of the expected thickness (presumably another adaptation, reducing the mineral requirement for shell formation), which would in itself tend to increase water vapour conductance by reducing the diffusion pathway through shortened pores. Consequently, water vapour conductance is reduced by a disproportionately large change in the other possible variable: the total pore area of *P. namaqua* eggs is reduced to only 63% of the expected value (Thomas & Maclean 1981).

Presumably embryonic development starts soon after the eggs are laid if ambient temperatures are at or above incubation temperatures, since sandgrouse can not defer warming the eggs then until the clutch has been completed (Dixon & Louw 1978). Indeed, their problem is often to prevent the eggs attaining lethally high temperatures (Dixon & Louw 1978). Therefore they probably can not usually synchronize hatching by synchronizing the start of embryonic development, yet some other synchronizing mechanism appears to exist because a clutch may take five days to complete, but hatching of all three young may take place within one day (Thomas 1984).

It is well known now that sandgrouse carry water trapped on specially modified belly feathers, from which the flightless young drink (Cade & Maclean 1967; Maclean 1968), but this story has proved to involve yet further subtleties. Not only do the belly-feathers have specialized hair-like barbules with a helical twist at the base (Cade & Maclean 1967), but the keratin imbibes water more rapidly and to a greater extent than that of other bird feathers (Thomas & Robin 1977). Imbibed water is not available to the chicks, but imbibition is a necessary prerequisite to water-carrying, since it is associated with uncoiling of the helical twists in the barbules, which then stand up at right angles to the feather plane (instead of lying flat on it when dry) in a conformation which traps and holds the water droplets for the young birds. An advantage of rapid imbibition must be that it reduces the time that the adults must spend at watering places where predators often congregate. A further but not unexpected refinement is that the water-carrying capacity of belly feathers is greater in sandgrouse species adapted to deserts than in those from less arid habitats.

Although fascinating, belly-soaking may seem a tortuous solution to a straightforward problem, but its value becomes more obvious when one considers possible alternatives. If the young were given regurgitated water they would be competing with the adults for parental water reserves, whereas water taken from the belly feathers does not compromise the adult's normal capacity to resist desiccation because it represents a supplement to the adult's normal physiological stock.

Conclusion

It can be seen from the foregoing material that sandgrouse have many traits which show adaptations for life in deserts. Moreover, it is most unlikely that the examples given are a comprehensive list of all such adaptations. Some of these adaptations may be somewhat more important quantitatively than others, but when they are taken together they provide no evidence to support the possible notion that adaptation to deserts has involved major changes in a few 'key' attributes. On the contrary, they do support the view that the success of sandgrouse in arid lands has to be explained by the cumulative (and often mutually reinforcing) effects of a great range of adaptations influencing all aspects of their biology.

There is no reason to suppose that sandgrouse are unique amongst desert animals in this respect, or that adaptations to life in arid environments has involved patterns of evolution which are in any way special. Based upon the evidence now available, it seems reasonable to offer the much more likely generalization that adaptation to any particular environment has involved modification of many functions and features, the nature and degree of which depends upon the severity of the environment for survival. Therefore, one must beware of conclusions which claim special importance for one or another functional adaptation to explain an animal's (or a plant's) success under particular circumstances, unless they are based on a broad study of many of the organism's attributes.

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