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AVIAN ADAPTATIONS TO THE KALAHARI ENVIRONMENT: A TYPICAL CONTINENTAL SEMIDESERT

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Abstract – Bird species adapted to the Kalahari are generally either (a) sedentary, insectivorous (or carnivorous) and non-gregarious, or (b) nomadic, granivorous and gregarious even when breeding. Ground-dwelling birds predominate numerically and are cryptically coloured to avoid predation. Many species have nasal glands which secrete hypertonic solutions in response to the intake of fluids with high solute concentrations, as an adaptation to water conservation. Thermoregulation is discussed especially in relation to high ambient temperatures. Breeding is initiated in most species by rainfall or associated ecological effects, correlated with improved body condition of the females; lag periods between rain and egglaying are related to diet and time of year. Nest orientation is also related to season and capitalizes on maximal shade in summer. Parental care in sandgrouse is discussed.

Introduction

The climate, physiography and vegetation of the Kalahari Gemsbok National Park, Republic of South Africa, have been dealt with in detail in this symposium and in previous publications (see reference lists). My own ornithological research has been concentrated in the southern part of the park and has included all the main habitats found there – sandveld (treeless dunes and *Acacia* savanna), calcrete and riverbeds. Early ornithological research in the Kalahari Gemsbok National Park (KGNP) was mainly in the form of checklists (De Villiers 1958; Prozesky 1962), updated by Mills (1976) or incidental observations compiled from short research trips (Labuschagne 1959; Broekhuysen, Broekhuysen, Martin, Martin, Martin & Morgan 1968). Very little scientific work has been done on birds elsewhere in the Kalahari ecosystem so I shall concentrate largely on my own research in this review. I shall emphasize adaptations that seem to be especially suited to a hot arid zone, though even with these I have necessarily been highly selective, partly for reasons of space, and partly to highlight those that I consider most significant.

Populations and movements

Avian populations have been studied in the Kalahari by Maclean (1970b) and by Pianka & Huey (1971). The Kalahari avifauna is divisible into five ecological categories on the basis of movements or seasonal occurrence: residents (or sedentary species), nomads, breeding migrants, nonbreeding migrants and occasional species (or vagrants). Only the sedentary and nomadic species are relevant to this review, since only they are truly arid-adapted in the sense that they do not normally move beyond the limits of the semi-arid ecosystem. Sedentary species are mostly insectivorous (or carnivorous) and not usually gregarious, except in relatively small flocks when not breeding; they are largely or entirely independent of drinking water and are, at best, facultative drinkers. Nomads on the other hand are largely granivorous (seed-eating) and most are gregarious even when breeding (*e.g.* sandgrouse, doves, some larks, ploceids, estrildids and fringillids).

One of the few anomalous species is the Sociable Weaver *Philetairus socius* which is highly sedentary, largely insectivorous and highly gregarious at all times. The Doublebanded Courser *Rhinoptilus africanus* is also somewhat anomalous in being insectivorous and solitary, but at least partly nomadic; it is a ground dweller that needs good visibility, so it is obliged to move out of an area where good rains have brought on a dense growth of vegetation (Maclean 1967). A large proportion of the Doublebanded Courser population will also move out of an area in extreme drought conditions, but some pairs will always remain and even breed regardless of the time of year, so the effect of emigration is merely to reduce the population density to one that the environment can support.

Coloration

Although only about 26 species of birds in the southern KGNP are entirely or predominantly ground-dwelling or at least ground-foraging, and therefore need to be cryptically coloured to avoid predation, they comprise a substantial proportion of the avian biomass – probably well over 50% – since many of them (notably the larks and sparrows) are gregarious nomads that may occur in a given area in very large numbers. Although it is sometimes assumed (Maclean 1974) that specialized desert coloration occurs only among sedentary ground dwellers, the nomadic species also show remarkable adaptation in the colour of their dorsal plumage relative to the soil coloration of their favoured habitats (Maclean 1970a). This shows up clearly in the rufous-backed Blackeared Finchlark *Eremopterix australis* of the red sandveld and the Greybacked Finchlark *E. verticalis* which is confined almost exclusively to the grey calcrete flats, except at times of very high population density when it extends into the dunes and riverbeds also. All the other lark species of the Kalahari show similar division into "red" and "grey" types with corresponding preferences for dunes or calcrete respectively.

Although sedentary species of ground birds often match their substrates very closely indeed, the separation of birds into "specialized" and "generalized" cryptic types (Maclean 1976), which would be sedentary and nomadic respectively, should be viewed with caution. The division is of doubtful validity. Even among nomadic larks, more easterly forms tend to be darker than more westerly forms of the same species, indicating that nomadism itself is probably limited to a relatively circumscribed range of habitats for a given population.

Food and water

As I have already shown, social organization and movements of birds can usually be related to their diet and their need to drink free water. Seed-eating birds in the Kalahari have a locally abundant but erratic food supply, hence their need to be nomadic. This of course is also tied in with their drinking habits, since the presence of food may often go hand in hand with the presence of water, however temporary. The artificial provision of water by man (from boreholes) must have enabled many arid-zone birds to capitalize on food resources which, although good, might have been impossible to exploit in the absence of water.

Birds feeding on animal food usually obtain enough water from their prey to satisfy their normal needs, although the food supply itself is often (if not usually) relatively sparse. Furthermore the body fluids of prey animals usually contain electrolytes which have to be removed in order to conserve water. This is done either by the kidneys (which in birds have a relatively poor concentrating ability), or by the nasal glands (Thomas & Phillips 1978) as found in the raptors (Cade & Greenwald 1966) or in the Charadriiformes (Maclean 1967). Further work on the presence and function of avian nasal glands (or salt glands) in arid zones is urgently needed.

The origins of the avian salt glands are not certain, but their primary function in the ancestral Charadriiformes was undoubtedly to remove excess NaCl from sea water and from the body fluids of marine invertebrates taken as food. This would constitute one of several pre-adaptations to arid zones which, like the sea, are physiologically poor in water because of the frequently high solute load of desert water sources, be they animal body fluids, springs or boreholes (Maclean 1984).

Water resorption occurs in the cloaca of most, if not all, birds and represents the most important site of water conservation, especially in those species, like sandgrouse, which have lost their nasal glands in response to the need to drink large amounts of relatively fresh water, even if only every 3–5 days (Thomas 1984). Sandgrouse have relatively small kidneys and therefore probably produce relatively small amounts of fairly concentrated urine (Thomas & Robin 1977).

Thermoregulation

Closely associated with water balance in homoiotherms is the need to regulate body temperature, expecially at high ambient temperatures. Evaporative cooling is efficient but expensive of water; it is employed by all Kalahari birds, but has not been studied quantitatively. Studies on captive sandgrouse in the Namib (Thomas, Maclean & Clinning 1981) have shown that birds under ambient temperatures above body temperature (about 40 °C and upwards) not only sought shade, drooped their wings, spread their wrists and gular-fluttered, but also huddled closely together, so that they were actually touching one another; all these thermoregulatory mechanisms were intensified in dehydrated birds and began at temperatures as low as 31 °C.

Huddling in sandgrouse is unexpected and quite the opposite of what happens in most homoiotherms at high temperatures, but it is suggested that it enhances insulation against heat uptake and reduces surface areas exposed to radiation and may be associated with the presence of a dense undercoat of dark brown down in sandgrouse. Neither of these features is known in any other birds inhabiting hot climates. However, limited field observations (Maclean unpublished) indicate that huddling may not be usual under natural conditions. A family of Namaqua Sandgrouse *Pterocles namaqua* in the KGNP consisting of the parents and a fully grown juvenile were watched for several hours on a number of separate occasions at temperatures ranging from 37 °C to 40 °C; the birds drooped their wings, spread their wrists, gular-fluttered and stood still in the shade for long periods, but at no time showed any inclination to huddle. Huddling in the wild may indeed occur at higher temperatures than these, however. The behaviour is difficult to observe under field conditions because the birds tend to scatter quietly when disturbed.

Another unconventional thermoregulatory device is the large communal nest mass of the Sociable Weaver. The interior of the nest chambers was found always to be at a lower temperature than that of the outside air during the day in summer (Bartholomew, White & Howell 1976); although ambient temperatures in this study did not exceed 33,5 °C, it seems as if the insulating effect of the nest mass confers a real thermoregulatory advantage on the birds, in both hot and cold weather.

Breeding biology

Initiation of breeding

Because of the temporally and spatially erratic rainfall in the Kalahari, the control of the timing of breeding in its birds cannot be affected primarily by changes in daylength as in the northern hemisphere, because only after a good rain is the food supply adequate enough to allow of breeding in most species. It is therefore not surprising to find that breeding cycles of nearly all Kalahari birds are closely governed by rainfall, directly or indirectly (Maclean 1970c).

Evidence from avian studies in Natal (Earlé 1981) points to the nutritional condition of the female as a major intrinsic factor correlated with the timing of breeding, even in a more mesic and seasonal environment; only if the female's protein reserves have reached a satisfactory level can she respond appropriately to stimuli from the male, and proceed with egg production. This is borne out in the Kalahari by examining the lag periods between rainfall and egglaying in passerine birds in different rainy periods. In one study (Maclean 1970c) there were two summer rains and one autumn rain. The mean lag periods of insectivorous passerines for the two summer rains were 12,7 and 10,1 days respectively, while the mean lag period after the autumn rain was 19,3 days. This indicates that insect emergence after rain was almost immediate, though faster under hot than under cool conditions.

Lag periods for granivorous passerines averaged slightly more than twice as long (28,5 and 23,9 days for summer and 43,8 days for autumn) as for the insectivorous species. The selective advantage of this is that young are leaving the nest when food plants have set seed. The greater lag period may be a result of the longer time it takes to accumulate protein reserves on a diet of seeds than on one of animal foods; the female would also have to wait longer for seeds to ripen than for insects to emerge after reasonable rains had fallen.

Minimum lag periods among insectivorous passerines were only 6–10 days, depending on the species, indicating not only that their gonads were almost at a reproductive level of activity, but also that the food supply and consequently the birds' body condition responded very quickly to the rain. More detailed studies are needed on gonadal physiology, insects eaten, insect emergence, and the physiological response of birds to improved food supply in arid zones. It is clear that temperature, at least, has little effect on the timing of reproduction in Kalahari birds, since they can breed throughout the winter after good autumn rains (Maclean 1970c).

Nest building and orientation

Nest building may start within five days of a rainfall of 20 mm or more (*e.g.* in the Yellow Canary *Serinus flaviventris*). The Sociable Weaver has an advantage over other Kalahari birds in that it lives in a permanent nest and does not need to build afresh at each breeding attempt, thereby cutting down the lag period between rainfall and egglaying still further; its minimum lag of six days is the shortest yet recorded for any arid-zone bird. Its nest is also a perfect shelter against extreme temperatures and insulates eggs, young and adults against insolation.

Nest orientation may be critical, especially in summer and especially among ground-nesting birds subjected to high insolation and high radiation. It is therefore not surprising to find that larks and buntings in the Kalahari place their nests at the side of an object (grasstuft, stone, shrub, etc.) that receives most shade for the greatest part of the day, *i.e.* the sector of the compass between east and south (Maclean 1976). In a winter breeding season this orientation breaks down and nests are often in the open, away from any shelter at all. No doubt the improved visibility of an exposed site offsets any minor discomfort from the heat at midday.

The principle of good visibility is employed by ground-nesting birds such as coursers, plovers, bustards and sandgrouse, but their relatively larger body size gives them a thermal advantage over the smaller birds like larks and buntings. Sandgrouse in the Kalahari tend to nest mainly in the winter months anyway, which may be thermally adaptive.

Parental care

Most patterns of parental care in Kalahari birds are typical of those of the taxon concerned, although parental protection of eggs and young against overheating and direct sunlight in particular are enhanced, but by no means peculiar to the arid zone. Only the sandgrouse seem to show patterns of parental care that differ substantially from those of more "typical" birds.

In most sandgrouse species the female incubates by day and is therefore periodically subjected to great heat loads. It has been shown in North Africa, where sandgrouse nest mainly in summer, that the female has to withstand air temperatures at ground level of around 50 °C or more (Thomas & Robin 1977). The thick undercoat of down characteristic of sandgrouse is said to exercise some control over the uptake of heat from the environment, but studies on the way in which this may occur still have to be done. Certainly sandgrouse seem to be able to withstand direct sunlight for longer periods than most birds of similar size, and would reward further investigation in this direction.

The provision of water by sandgrouse to their young is of especial interest in the arid-zone context (Maclean 1983). Their ventral feather structure is uniquely adapted for water transport and sandgrouse chicks are the only ones known to drink from their parents' belly plumage. Usually only the male parent is involved in water transport; he soaks his belly plumage at the waterhole at his species-specific drinking time, flies back to his young and allows them to drink from the wet feathers. Such a mechanism of water transport obviates the need for the parent to sacrifice any of his own internal water supply, as would happen if he were to provide water from his crop.

Clutch size and brood reduction

Clutch size in some arid-zone birds is directly proportional to the food supply as deduced from circumstantial evidence in the Sociable Weaver (Maclean 1973); the higher the rainfall, or the better the food supply, the larger the clutch size. However, an increased brood size is adaptive only as long as the food supply remains good. If, as happens in semideserts like the Kalahari, high summer temperatures quickly dry up green vegetation and lead to a rapidly diminished food supply for the birds, it is advantageous to reduce the brood size correspondingly quickly. One way in which this occurs is demonstrated by the Sociable Weaver which, unlike most small passerines, starts incubating with the first or second egg of the clutch, leading to slightly discrepant ages between young in the subsequent brood. The larger the clutch size, the greater the discrepancy in age between youngest and oldest of a brood and, since the larger chicks are the strongest and therefore most able to beg for food from the parents, it is highly likely that, in times of food shortage, only the older chicks will survive. This ensures that at least some young in a brood will leave the nest successfully, rather than all dying of starvation if they were all equally competitive.

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