THE CONDOR

TRANSPORT OF WATER BY ADULT SANDGROUSE
TO THEIR YOUNG

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In 1896 the English aviculturist Meade-Waldo published an astonishing and seemingly incredible account of how the males of sandgrouse that he successfully bred in captivity carried water to their young in their breast feathers. To quote from his original report:

As soon as the young were out of the nest (when twelve hours old) a very curious habit developed itself in the male. He would rub his breast violently up and down on the ground, a motion quite distinct from dusting, and when all awry he would get into his drinking water and saturate the feathers of the under parts. When soaked he would go through the motions of flying away, nodding his head, etc. Then, remembering his family were close by, would run up to the hen, make a demonstration, when the young would run out, get under him, and suck the water from his breast. This is no doubt the way that water is conveyed to the young when far out on waterless plains. The young . . . are very independent, eating hard seed and weeds from the first, and roosting independently of their parents at ten days old (Meade-Waldo, 1896). See also Meade-Waldo (1921).

Despite the fact that Meade-Waldo (1897; 1921) observed 61 broods from three different species of sandgrouse hatched in his aviaries between 1895 and 1915, and soon received confirmation from another breeder for two species (St. Quintin, 1905), and despite the fact that field naturalists and native hunters have frequently observed wild male sandgrouse wetting their breast feathers at water holes in the way described (Meade-Waldo, 1906; Buxton, 1923; Heim de Balsac, 1936; Hoesch, 1955), the idea that the young do receive water in this exceptional way has met with a great deal of scepticism (Archer and Godman, 1937; Meinertzhagen, 1954, 1964; Hüe and Etchécopar, 1957; Schmidt-Nielsen, 1964). Schmidt-Nielsen, however, had his doubts shaken when Dr. Mendelssohn of Tel Aviv University told him "that chicks of sand grouse that he reared would die from thirst even if drinking water was available to them, but that they would take water from wet cotton (p. 217)."

First of all, the doubters argued that such a method of transport is too inefficient to survive the rigors of natural selection. How could an adult sandgrouse traveling from the water hole at 30 to 40 miles per hour in hot, dry air arrive back on the breeding grounds with sufficient moisture in his feathers to nourish the young? More importantly, some recent authors have assumed—incorrectly as it turns out—that sandgrouse feed and water their young by regurgitation like doves and pigeons. This notion probably first arose as an extension of the equally erroneous belief that sandgrouse drink by "sucking," with their beaks continually immersed like the columbids, and that they are specialized desert representatives of the Columbiformes (but see Goodwin, 1965; Cade, Willoughby, and Maclean, 1966). Only Meinertzhagen (1954) claims actually to have seen watering by regurgitation—in captive *Pterocles exustus* kept in Hampshire between 1895 and 1897.

We believe, for reasons stated elsewhere (Maclean, 1967), that sandgrouse are phylogenetically near the Charadriiformes and that they are not at all closely related

to doves and pigeons. In any case, their young are highly precocial and are not fed by regurgitation or by any other method.

Until recently, field observations on the parental care of young sandgrouse in the wild have been notably lacking. Then Marchant (1961, 1962) reported on some observations he made in Iraq on broods of *Pterocles alchata* and *P. senegallus*. Although he was uncertain about some of the details, the activities that he describes and calls "litter of puppies" behavior clearly support the correctness of Meade-Waldo's original observations. During the 1965 breeding season in the Kalahari Gemsbok National Park, we were also able to confirm, in detail, the fact that the male sandgrouse (*Pterocles namaqua*, in this case) transports water to his young in his belly feathers and that the young extract this water in some way by stripping the wet feathers with their beaks, exactly as Meade-Waldo (1921) said.

OBSERVATIONS AND DISCUSSION

ADULTS DRINKING AND WETTING THEIR FEATHERS AT WATER HOLES

Since October 1964, once or twice weekly, observations have been made on sandgrouse watering at the Houmoed game well located in the Kalahari Gemsbok Park about 10 miles up the dry bed of the Auob River from Twee Rivieren, the park headquarters. Less-regular visits have also been made to other water holes and wells both in the Kalahari and in the Namib Desert of South West Africa. These observations have provided a great deal of accurate information on the times of watering, seasonal changes in numbers watering, effect of rainfall on watering, method of drinking, and seasonal changes in the percentage of watering birds that also wet their ventral feathers, for two locally abundant species, *Pterocles namaqua* and *P. burchelli*. Only information pertinent to the question of water transport to the young is presented here. For details about drinking behavior, see Cade *et al.* (1966).

Table 1 shows seasonal data on the numbers of sandgrouse watering and wetting their feathers at Houmoed. Unfortunately, actual counts of birds wetting their feathers were not made during the period from December through April, but our general impression was that few males soaked their feathers at this time. Although some males of both species are to be seen soaking their feathers right through the year (a few pairs may also be found breeding at any time, too), there was a greatly increased incidence of such behavior beginning in late May and continuing through the winter into early summer. These months correspond with the time when *P. namaqua* was found breeding in greatest numbers in the park. The first nest was found on 1 June 1965, and five nests or broods were found in June, seven in July, eight in August, only three in September, a month in which continuous observations were not made, five in October, seven in November, eight in December, two in January 1966, one in February, none in March, and one again in April, plus one of *P. burchelli*. Presumably the latter species was breeding all through this period, too (collected specimens showed active or recently active gonads), but its nests, which are located in the sand dunes rather than on the outcroppings of calcrete adjacent to the river valleys, the typical nesting habitat of *P. namaqua*, are difficult to find.

Thus, there was a close association between the incidence of males wetting their feathers at water holes and the peak breeding period. It is also worth noting that these peaks occurred in winter, exactly the opposite season to be expected if the wetting behavior were mainly adaptive for evaporative cooling. Further, it is nearly always the males that wet their feathers. Only six times out of hundreds of cases have we seen females wetting their feathers.

TABLE 1

SEASONAL DIFFERENCES IN PER CENT OF WATERING SANDGROUSE THAT SOAK
THEIR VENTRAL FEATHERS

Date	Pterocles namaqua				Pterocles burchelli			
	Number drinking	Soaking males	Soaking females	%	Number drinking	Soaking males	Soaking females	%
11/5/65	300	1	0	0.3	40	0	0	0
14/5/65	500	1	0	0.2	200	0	0	0
21/5/65	550	3	0	0.5	250	6	0	2.4
28/5/65	800	4	0	0.5	600	20	0	3.0
3/6/65	650	0	0	0.0	160	9	0	5.6
18/6/65	300	7	0	2.3	360	4	0	1.1
25/6/65	770	13	0	1.7	650	6	0	0.9
29/6/65	600	15	0	2.5	950	30	0	3.2
6/7/65	340	5	0	1.5	400	8	0	2.0
9/7/65	480	16	0	3.3	900	21	0	2.3
13/7/65	380	30	0	7.9	750	40	0	5.3
16/7/65	270	7	0	2.6	350	8	0	2.2
3/8/65	200	3	0	1.5	340	1	0	0.3
17/8/65	140	6	0	4.3	220	4	0	1.8
1/10/65	100	3	1	4.0	55	1	0	1.8
2/11/65	650	43	4	6.6	670	35	1	5.2

When about to soak, the male sandgrouse walks into the water until it touches his belly. He then squats down on his tarsometatarsals with his feet crossed over each other (a detail which has been observed several times in *P. burchelli* from a distance of nine feet with 8-power binoculars through clear water); he then rocks his body on an axis about the pelvis in short, rapid bursts of five to six rocks at intervals varying from a few seconds to a minute or more. During rocking, the head is held up high, the tail is elevated, the abdominal feathers are raised away from the body, and the body is lifted so that only the tips of the feathers touch the water (see fig. 1). The feathers are shaken about, and the water is thereby thoroughly worked into them. The soaking process lasts from a few seconds (abortive attempts) to more than 15 minutes in some cases. Some individuals remain soaking in the water long after the rest of the flock has departed, and such birds appear to be in a kind of dazed or trancelike state, similar to that often seen in sun-bathing or anting birds (Burton, 1959); however, they immediately fly up if disturbed.

TRANSPORT OF WATER TO YOUNG

In order to observe how the adults bring water to the young, it is necessary to establish contact with a family group before 0630 hours in summer and before 0900 hours in winter, as these sandgrouse visit water in the morning as a rule. Routine surveys of suitable nesting habitat were made in a Land Rover between 0600 and 0900 hours in the hope of seeing sandgrouse delivering water to their young. Four unequivocal instances of such behavior have now been witnessed by Maclean for *P. namaqua*, and the details are presented below.

On 10 August 1965 a male with two chicks was found on the calcrete one and one-half miles south of the Houmoed water hole at 0855 hours, before any of the adults had begun to fly to water.

Figure 1. Adult male sandgrouse (*Pterocles namaqua*) soaking his belly at a water hole in the Kalahari Desert. The bird is resting after a period of rocking.

The chicks were only a foot from the nest where they had hatched and probably were no more than one day old. Even at this age they were feeding themselves and preening in typical adult fashion. The female was not seen at first. The following observations were made from the Land Rover with 8-power binoculars at a distance of 75 feet from the chicks.

At 0920 the male walked to the nest and brooded the empty nest for about 20 seconds; then he went to brood the chicks. At 1010 the male left the chicks and went back to brood at the nest for about five minutes. Then at 1015 the male walked away from the nest for about 12 feet and flew up, but landed about 50 yards away. Soon the male and female flew up together (she had evidently been foraging there), the female landing after about 20 yards, the male continuing alone in the direction of Houmoed. The female began to walk toward the chicks about 80 yards away from her, but then she flew up and landed about 15 yards from the chicks at 1020 hours. At 1027 the male flew in from the water hole, landed at the nest, and then walked to the chicks. He stood upright, showing clearly his wet, abdominal feathers. The chicks ran to him and at once raised their heads to his wet feathers and took the tips of the feathers in their beaks.

On 27 November 1965 at 0745 hours a pair of *P. namaqua* with chicks about three days old was found on the calcrete. The male had just returned from water, and his ventral feathers were soaked to a point well above his chest band. As the parents called to the chicks and led them away, the young birds had probably already taken water from the male's feathers. Another male sandgrouse landed nearby about the same time. His feathers were dry, and he went to a nest with eggs.

On 30 November 1965 at 0630 hours a female with three five-day-old chicks was encountered on the calcrete. The female flew up and joined the male 200 yards away. The chicks crouched at the base of some shrubs, and the following observations were made in the Rover at a distance of 20 feet from the chicks. At 0725 both parents returned from the water hole. Only the male

Figure 2. Young sandgrouse (*Pterocles namaqua*) clustered around the wet abdomen of adult male in the Kalahari Desert.

had wet ventral feathers. At 0750 the parents walked up to the chicks. All three chicks rushed to the male, which uttered the "kelkiewyn" call. To get to the male parent, the chicks actually had to run past the female. The chicks clamored around the male's breast and abdomen, but his feathers were almost dry. As the chicks tried to take water, the male called a low, staccato "kirri, kirri, kirri," and then led them away.

On 11 December 1965 at 0840 hours a male *P. namaqua* landed on the calcrete, and Maclean drove toward it, stopping the Land Rover 30 feet away. Both parents were present with three large chicks about two to three weeks old but as yet unable to fly (almost certainly the same family seen on 30 November above). The male had wet ventral feathers. The chicks came out of cover and rushed to the male, ignoring the nearby female. The chicks at once began to take water from the male's feathers by sharp, downward jerks of their heads, probably a "stripping" action with their beaks to get the water out. The male stood bolt upright, exposing the wet feathers. The chicks worked at the feathers for five minutes and then left to lie in the shade. The male immediately began to dry his feathers by rubbing his body on sandy ground for several minutes.

Although Marchant (1961, 1962) evidently watched his birds from considerably greater distances (ca. 150 meters) than we did and therefore missed some details, our field observations parallel his on *P. alchata* and *P. senegallus* in Iraq very closely. The departing of the male with dry feathers and returning to the brood with wet ones, the early-morning time of water transport, the behavior of the chicks in running from their hiding places to the male and ignoring the presence of the female, the male's upright posture with fluffed out feathers, the clustering of the chicks about his abdomen, and their obvious head movements around his wet feathers are all the same and lead only to the conclusion that the young obtain water in the way first described by Meade-Waldo. Figure 2 shows young *P. namaqua* in the Kalahari clustered about the wet abdomen of the male.

MECHANISMS OF WATER TRANSPORT IN FEATHERS

Physical problems of water transport in feathers. While the method of water transport in wet feathers is now established beyond doubt, all of the questions raised by this unique behavior are by no means answered. The major adaptive question, of course, is how far can a male sandgrouse transport usable amounts of water in his breast feathers? The answer to that question is dependent upon the answers to a number of subsidiary problems. What is the rate of evaporation from the wetted feathers of a sandgrouse flying through the early-morning desert air? How much water can be taken up and held in the ventral feathers of a sandgrouse? Are there special structural features of sandgrouse feathers that aid moisture retention? Are there behavioral specializations for trapping or holding water in the plumage? Let us begin with the more elementary questions and see how far we can develop a reasonably approximate answer to the first, which has important implications for breeding distribution, reproductive yield, and limitations on population size.

Behavioral adaptations for water transport in feathers. The details of feather soaking have already been presented. We have been impressed by the degree to which the ventral feathers—especially those on the belly—are erected as the male sandgrouse enters water, by the vigorous downward rocking action of his belly while soaking, and by the large amounts of water that drip off of the bird in the first few feet of flight—more it appears than can easily be accounted for on the assumption that the shower of drops merely represents excess draining off the surfaces of the feathers. When a sandgrouse lifts out of the water his ventral feathers are already closely appressed to his body. These observations suggested that a sandgrouse may be able to trap and in some way hold excess water in his plumage—more, that is,

TABLE 2

COMPARISON OF WATER-HOLDING CAPACITY OF FEATHERS AND OTHER MATERIALS

Material sampled	g dry wt.	g wet wt.	g H_2O/g dry wt.
Synthetic sponge	8.1	51.3	5.3
Paper towel	4.0	24.4	5.1
Passer melanurus breast feathers	0.35	2.15	5.1
Pterocles namaqua male breast feathers	0.90	8.10	8.0

than the absorbed amount in the feather material itself. This inference led us to examine the water-holding capacity and the structure of sandgrouse feathers and to make comparisons with other birds.

The water-holding capacity of sandgrouse feathers. Feathers are not very wettable. The imperviousness of the horny, outer sheath impedes penetration by water molecules, and the surface structure of feathers is admirably constructed to shed water. In addition, the preen-gland oil, which many birds apply to their feathers, provides a further hindrance to the absorption of water, as does the powder down of some other birds. One adaptive advantage of the "dusting" behavior that male sandgrouse sometimes perform before entering the water may be to remove oil from the feathers and thereby render them more wettable.

Once they do become wet, however, feathers have a good water-holding capacity. Table 2 presents data from a preliminary series of experiments comparing samples of feathers with other wettable materials. It can be seen that the breast feathers of the Cape Sparrow (*Passer melanurus*) have as good a water-holding capacity as an ordinary synthetic kitchen sponge or a piece of paper towel. The interesting discovery was that the breast feathers of a male *P. namaqua* held almost twice as much water as any of these other materials. This significant difference encouraged us to examine in detail the water-holding capacity of individual feathers from males and females of four species of sandgrouse (*P. namaqua, P. burchelli, P. bicinctus,* and *P. gutturalis*) and to compare the results with values for six species from other families and orders of birds.

The results are presented in figure 3. Feathers from the sandgrouse held about two to three times as much water when thoroughly soaked and allowed to drip until all surface excess was lost as did the feathers of any other species tested. Male sandgrouse feathers held significantly more water than female feathers. Even after repeated soaking and stripping with the fingers to remove water, the belly feathers of sandgrouse still retained their structural integrity; this was not true of the upper breast feathers, neck feathers, or dorsal body feathers of sandgrouse, or of the body feathers in general of other species tested. After being thoroughly soaked and stripped several times, these latter feathers became frayed, matted, and twisted into a cordlike structure while wet. On drying, it was often impossible to restore their webbing. These differences between the ventral feathers of sandgrouse and other kinds of feathers demand explanation in structural terms.

Structural specializations of sandgrouse feathers. The belly feathers of sandgrouse are elongate, averaging about six times as long as they are wide, with a slight curvature away from the midline of the body. The elongate shape seems to be advantageous for grasping and stripping by the beak of a young sandgrouse—certainly more so than the broader, shieldlike shape of the ventral feathers in many
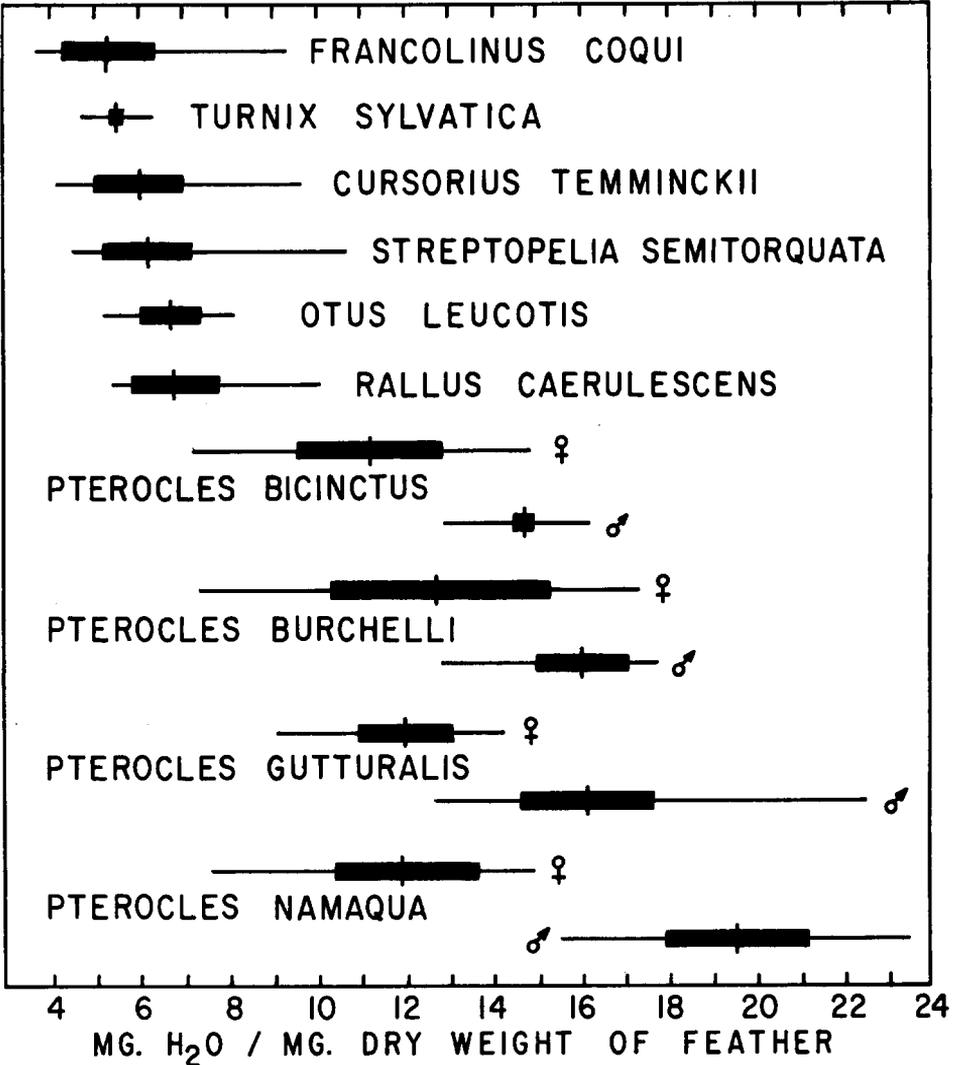
Figure 3. Water-holding capacity of sandgrouse belly feathers compared with that of the belly feathers of the Coqui Francolin (Galliformes), Kurrichane Button-Quail (Gruiformes), Temminck's Courser (Charadriiformes), Red-eyed Turtle Dove (Columbiformes), White-faced Owlet (Strigiformes), and Cape Rail (Gruiformes). Horizontal lines represent the ranges of each sample, vertical lines indicate the means, and the black rectangles delimit plus and minus 2 standard errors of the mean. N equals 10 in all samples. In all cases, individual feathers were allowed to become thoroughly wetted in water, then were removed with forceps, were suspended in air until all excess water dripped off, and then were immediately weighed on a Mettler balance accurate to 0.1 mg.

other kinds of birds. Also, it is interesting to note that female feathers average rather broader in proportion to length than those of males. The curvature in the shaft may help to retard downward movement of water along the length of the feather, or it may be related to the high density of feathers in the belly region and to their manner of overlapping each other so completely that only the distal fifth or less of each feather is exposed to the surface.

The belly feathers of all sandgrouse, as in many other birds, have downy bases. In addition, they bear a fringe of downy tufts on the ends of the barbs on both sides, extending about four-fifths of the way toward the tip. Only the distal fifth—the part exposed to the surface—has a typical body-feather construction with rather loose webbing in the vanes and slightly frayed tips. The webbing of the proximal four-fifths adjacent to the shaft is very strong and springy, and the barbs are not easily separated. The difference in structure between the proximal and distal areas is sharply demarcated and is quite clear to the unaided eye.

Most importantly, the ventral surface of this proximal zone is densely covered with fine, hairlike extensions of the barbules. This pubescence occurs on all the belly feathers, extends anteriorly into the lower breast feathers, to a reduced extent in the upper breast feathers, and disappears in the neck feathers. It does not occur on any of the dorsal body feathers, nor does its exact counterpart occur on any body feathers of other birds which we have examined, including species representing 10 orders, although the body feathers of some other species do bear a pubescence of a different structural arrangement on their ventral surfaces. Figures 4 and 5 compare sandgrouse feathers with the feathers of four other species, as they appear when thoroughly soaked and floating on water. All of the structures described above are clearly visible.

After a sandgrouse belly feather is fully wetted, a downward stroke of the feather in water, as when the male rocks his belly during the soaking process, fluffs out and expands the barbs, and the downy fringes are maximally spread. The ventral, fuzzy area appears turgid. Then, as the feather is removed from the water, the downy tufts are drawn inward toward the shaft on the ventral side, and in so doing they form a kind of groove or trough in which a column of water is trapped. The pubescence forms a matrix that aids in this retention, probably by supplying a large surface area for adhesion by interfacial tension between the droplets of water and the hairs. If the hairlike barbules are also hollow, as seems likely in conformity with the general structural plan of feathers, then they may also hold some of the water by capillary attraction. At any rate, while the dorsal surface of the feather only appears damp and bears no droplets after withdrawal, the ventral, proximal surface holds a sizable body of water enmeshed in the hairs and further held in along the sides by the downy tufts.

The exact mechanism of water retention is more clearly seen under a microscope with magnifications of 50 to 100 power. On a dry feather it can be seen that the proximal zone is made up of highly specialized barbules completely unlike those at the distal end of the feather, where the barbs have the typical overlapping arrangement of hooks on the distal barbules and grooves on the adjacent proximal ones. The proximal barbs bear a series of barbules that are flattened and riblike along their basal portions and that are coiled along the ventro-lateral sides of the barb to form a series of overlapping helices. Each helical portion consists of two or three open coils, after which the barbule becomes attenuated into a long, straight, hairlike structure. None of these specialized barbules bears hooks or grooves; instead, adjacent

barbs are held together by intertwining of coils between the distal barbules on one barb and the proximal barbules of the adjacent barb. The hairy ends extend distally along the axis of each barb for one millimeter and lie in a flattened position against the ventral surface of the feather. The general appearance under the microscope is of a series of double coils formed around each of the barbs. The basic structures of a single barb are shown in figure 6. It is this coiled construction that gives the inner proximal zone of the feather its springy character, and the interlacing of coils between adjacent barbs produces a strong web that is highly resistant to mechanical disruption.

When a drop of water is applied to the distal end of a sandgrouse belly feather on its under surface, the water is drawn up into the hairs, probably by capillarity or interfacial tension. As the water penetrates to the basal, tightly coiled portion of the barbules, the latter suddenly spring open and extend their hairy ends perpendicular to the plane of the main feather surface, thereby forming a dense stand of upright hairs about two millimeters deep in which the body of water becomes enmeshed and held by interfacial tension. Additional drops of water can be added until the entire specialized proximal zone is loaded, after which any excess drains off along the distal end. We are uncertain what causes the barbules to spring open and project their hairy ends at right angles to the plane of the feather, but it may result from the force of turgor built up inside the coiled, basal parts of the barbules when they imbibe water, or to some differences between the two flattened sides of the barbules in their expansional response to wetting. In the basal parts of the barbules there are some curious grooves that show as dark striations in figure 6 and which may be involved in the mechanics of opening. In any case, as the barbs dry out, a certain point is reached when the recoiling mechanism is set off, and the barbules rapidly reform tight coils around each other, reuniting adjacent barbs into a firm web as they do so.

We have found nothing like the coiled construction of these barbules in the feathers of any other African birds examined, but the ventral feathers of all four species of sandgrouse in southern Africa have barbules of this type. These peculiar structural modifications of sandgrouse belly feathers are undoubtedly what gives them their great water-holding capacity.

Female sandgrouse feathers have essentially the same structure as those of males, except that the area of specialized barbules is not as large on female feathers, and they tend to have a more highly developed, downy, basal area. Also, as one progresses anteriorly along the venter, there is a greater tendency for the female feathers to bear after-shafts than in males. Only a few of the female feathers hold as much water as the highly specialized male belly feather. The area of specialized feathers is smaller on the female than on the male and is mainly restricted to the upper belly, whereas it covers the entire belly area of the male and also extends well up into the breast. The feathers of the juvenal male are also much less specialized for holding water than in the adult.

Thus the highly specialized water-transporting behavior of the adult male sand-

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Figure 4. Above. Wet sandgrouse belly feathers floating on the surface of water (ventral aspect). Left, female *Pterocles namaqua*; middle and right, male *P. gutturalis*. Below. Feathers from male *P. bicinctus*. The specialized proximal zone stands out as a light, fuzzy area fringed by darker, downy tufts.
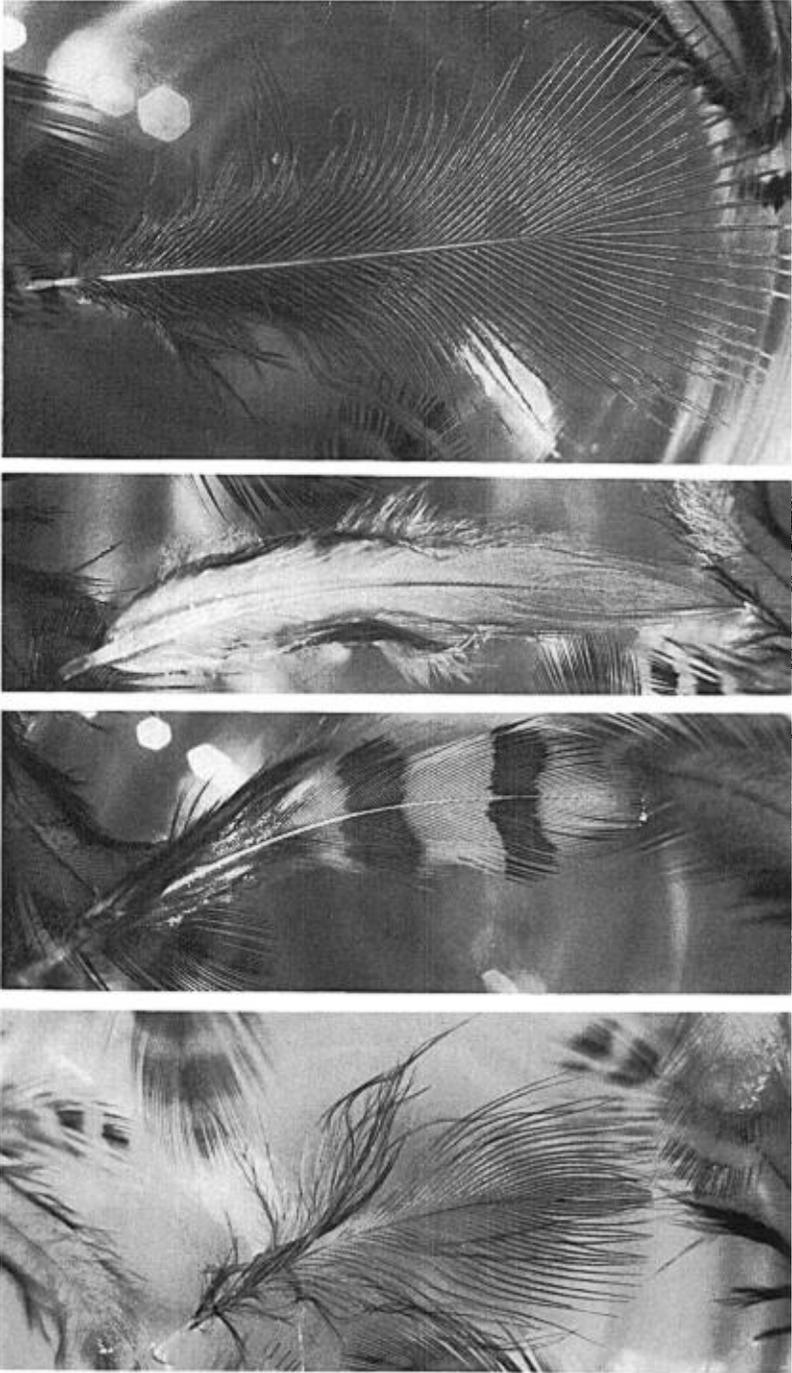
Figure 5. Wet belly feathers of the Cape Rail (uppermost), Red-eyed Turtle Dove (upper center), Coqui Francolin (lower center), and Temminck's Courser (lowermost), floating on the surface of water (ventral aspect). None of these feathers shows a specialized proximal zone like that of sandgrouse feathers.

grouse is associated with equally specialized structural modifications of his ventral body feathers. We conclude that these modifications are anatomical adaptations for holding large amounts of water in the plumage and for resisting structural breakdown from repeated wetting and "stripping" by the young sandgrouse.

A recent examination of all the skins of sandgrouse in the American Museum of Natural History revealed one curious exception. All 14 species of *Pterocles* have the highly specialized belly feather described above; so does *Syrrhaptes paradoxus*, but the closely related *S. tibetanus* does not. This high montane species is also exceptional in that the sexes are only weakly dimorphic in plumage. The ventral feathers are soft, extremely dense, with highly developed, downy bases, after-shafts, and other auxiliary downy tufts and edgings, and with no trace of the specialized proximal zone found in all other sandgrouse. Instead, the feathers of *tibetanus* give the appearance of being specially modified for maximum insulation. This species breeds at 12,000 to 16,000 feet and winters at only slightly lower elevations. It seems that the environment of this species has placed such a premium on the evolution of a ventral feather structured for maximum insulation that the specialization for water transport has been secondarily lost. (Alternatively, *tibetanus* may represent the survival of a primitive line of sandgrouse.) It would be most interesting to know whether the water-transporting behavior has also disappeared. Perhaps the young are led to water, or perhaps they eat food of high moisture content. All that seems to be known is that this species does not fly to water as regularly as other sandgrouse (Meklenburtsev, 1951:90).

Total amount of water held in the belly plumage. The amount of water that a male sandgrouse takes up in his ventral feathers depends not only on the maximum holding capacity of his feathers, but also on the length of time he soaks his plumage. Most individuals do not soak for more than five minutes. Several dead specimens of male *P. namaqua* whose bellies we soaked in water for a period of five minutes took up and held between 25 and 40 ml of water; however, it is difficult to arrange the feathers on a dead sandgrouse in the same way they are held and manipulated by a live bird. Experiments on pelts of belly skin are not much better but yielded the following results for water-holding capacity: average for four adult male skins, 22.1 ml, with a range from 18.4 to 27.5 ml; average for four adult female skins, 8.4 ml, with a range from 7.5 to 9.1 ml; average for three immature males molting into adult plumage, 12.1 ml, with a range from 6.7 to 14.9 ml. It appears from these data that an adult male sandgrouse usually carries about 25 ml of water in his plumage, depending on the condition of his feathers and on how long he soaks at the water hole.

Evaporation from feathers during flight. The rate of evaporation from any wet material is dependent upon the difference between the vapor pressure at the evaporating surface and that of the surrounding air. The vapor pressure in the air is determined by temperature and by the vapor density—the absolute amount of water vaporized in the air. The rate of evaporation is also greatly affected by wind velocity. The general relationships can be summarized in a simple equation (as presented by Rohwer, 1931, and adapted by Kleiber, 1961):

$$E = (0.44 + 0.118W)(e_s' - e_a'),$$

where E = evaporation in inches of water level per 24 hours, W = wind velocity in miles per hour, e_s' = water vapor pressure in saturated air at the surface temperature in inches of Hg, and e_a' = vapor pressure in surrounding ambient air.
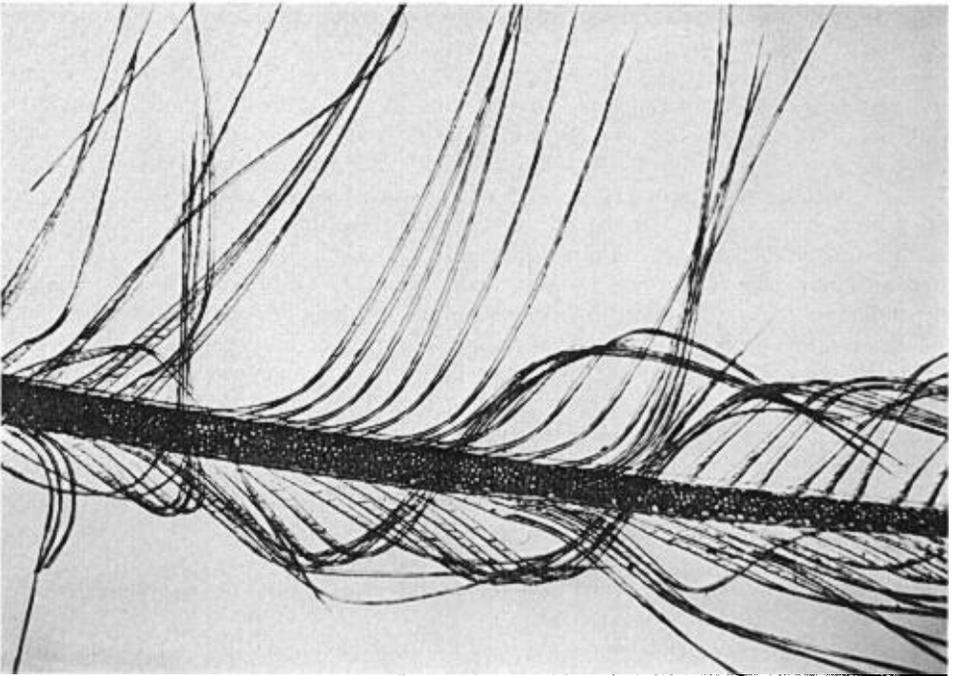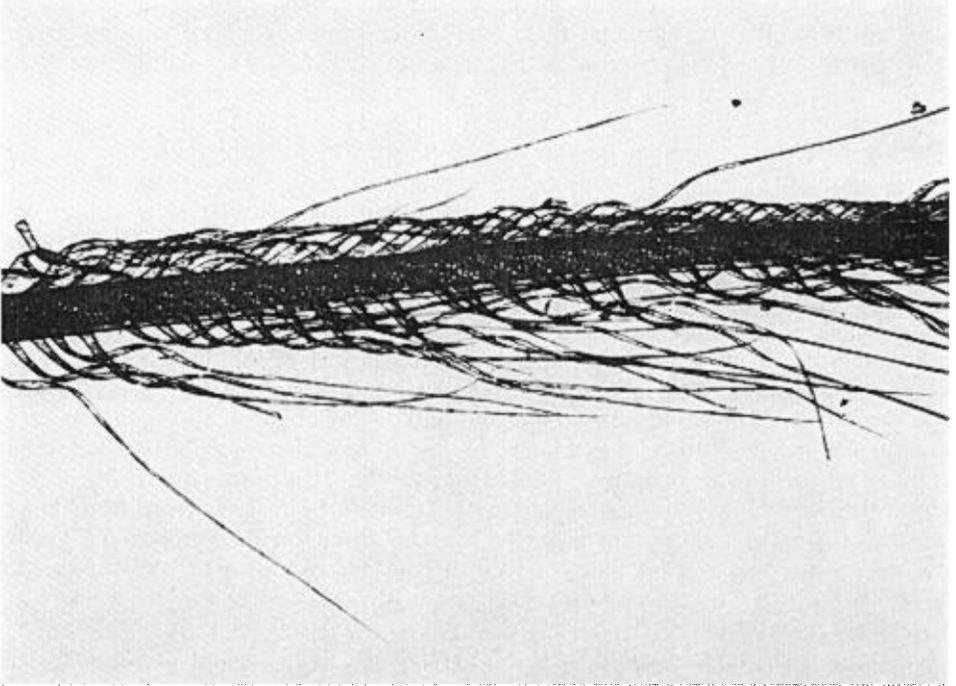
For our purposes it is convenient to convert inches of water level per 24 hours to grams of water per cm² per hour. This is done by multiplying the first part of the equation by 2.54 and dividing the answer from the whole equation by 24. Knowing or approximating the wet surface area of a sandgrouse's venter, the amount of water contained in the feathers, and the bird's flying speed, we can then make estimates of the rate of evaporation for a hypothetical bird flying from the water hole to his chicks under various environmental conditions.

Partly erroneous assumptions involved in these calculations are: (1) That water is continuously supplied to the surface of the belly from the wet feathers underneath to maintain a constant saturation vapor pressure over the area considered. Because of the way the feathers overlap, exposing only the distal fifth or less, and because of the special structures described above that hold most of the water in the proximal parts, water may not move freely to the tips of the feathers to provide a constantly wet surface. Attractive forces, such as capillarity and interfacial tension, associated with the fine hairlike barbules on the ventral surfaces of the feathers, may further retard movement to the exterior and allow for considerable drying of the surface while moisture is retained within. These are points that require checking. (2) That the temperature of the surface is the same as the ambient temperature. In fact, because of the cooling effect of evaporation, it will probably be less, although the body heat should warm the underlying moisture before it arrives at the surface. We know of no easy way to integrate these two opposing influences on the surface temperature; therefore, for simplicity we have assumed no temperature difference between the surface and the ambient air.

Table 3 presents some calculations of water loss for different flying conditions. Assuming a wet surface area of 50 cm²—about right for adult male *P. namaqua*— and a moisture content of 25 g of water in the feathers, if the sandgrouse flies for half an hour at 40 miles per hour under ambient conditions of 30° C and relative humidity of 15 per cent, it will have lost 14.6 gm of water; under ambient conditions of 30° C and 30 per cent relative humidity, 12 g of water; 20° C and 15 per cent relative humidity, 9.5 g of water; 20° C and 30 per cent humidity, 6.6 g. From these data, it appears that a male sandgrouse flying under the relatively moderate conditions of the early-morning desert atmosphere should be able to deliver from 10.4 to 18.4 g of water for a distance of 20 miles, starting with an initial amount of 25 g. Since it is quite easy to squeeze out 5 or 6 ml of water from a sandgrouse pelt that has soaked up 10 ml, it is reasonable to believe that young sandgrouse can obtain significant amounts of water from feathers carrying between 10 and 18 ml of water.

These data also demonstrate how necessary it is for sandgrouse to transport water under the most favorable physical conditions of the desert year and of the 24-hour daily cycle. Winter is the most favorable season, and early morning is an advantageous time; the air temperature has not yet reached a maximum, and humidity is likely still to be high from the night-time effect of cooling and condensation. For species such as *Pterocles bicinctus*, which water at night, when temperatures are still

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Figure 6. Photomicrographs of the basal part of single barbs from the specialized proximal zone of the belly feather of a male sandgrouse (*P. namaqua*). The ventral surfaces are oriented toward the plane of view; some barbules have been disrupted by slide preparation. Upper figure shows the tightly coiled barbules of a dry barb; the lower shows barbules extended after contact with water. Note dark striations in basal parts of barbules. Total length of one barbule equals about one millimeter.

TABLE 3

RATES OF EVAPORATION FROM A WET SURFACE EXPOSED TO A WIND VELOCITY OF 40 MILES PER HOUR

Air temp. °C	Relative humidity %	Saturation vapor pressure, inches Hg	Vapor pressure at given R.H., inches Hg	Mg H_2O evap./ cm²—hour
30	15	31.82	4.77	582
30	30	31.82	9.55	480
20	15	17.54	2.63	377
20	30	17.54	5.26	264

lower and humidity higher, the problems involved in water transport in wet feathers are greatly reduced. It would be most interesting to know whether such species do, in fact, water their young, as well as drink, at night.

Although the rate of evaporation increases drastically with wind velocity (air speed of the bird), it is nevertheless advantageous for a sandgrouse to fly fast in terms of the amount of water lost per distance traveled, as shown in figure 7. The greatest percentage savings per unit increase in speed occur at speeds under 20 miles per hour, and above about 50 miles per hour there is little further decrease in the amount of water lost for each 10-miles-per-hour increase in speed. Sandgrouse are notably fast fliers, and we believe that 40 miles per hour is a conservative average speed for flocks seen flying to and from water. Perhaps this fast flight has evolved in association with the mechanism of water transport in feathers; or it may have been one of the pre-existing, permissive attributes that have made this rather ineffi-cient mode of water transport possible.

Physiological aspects of the problem. How much free water does a young sand-grouse require each day? Unfortunately, we do not know the answer to this question, but we suspect it may not be very much. It has generally been assumed that sand-grouse require relatively large amounts of water—like doves and pigeons, which are also obligate drinkers—to compensate for the fact that their food consists almost exclusively of air-dried seeds with little moisture content. There are some records in the literature that indicate large consumptions of water by sandgrouse; see, for example, the translation from a Russian source in Salt and Zeuthen (1961:403), where it is stated that individuals of *Pterocles orientalis* shot at watering holes held up to "a cup" of water in their crops. We found, however, that adult *P. namaqua* drank no more than 15 ml of water after having been deprived of water for 25 days (Cade *et al.*, 1966). We further noted that the average amount of water consumed in one draft (one immersion of the beak followed by raising the head) is about 1.5 ml. Out of several hundred observations on individual sandgrouse, 24 drafts was the highest number counted, a figure that equals about 36 ml of water. The average for *P. namaqua* was 9.5 drafts, or 13.3 ml; for *P. burchelli*, 7.2 drafts, or 10.8 ml. These quantities amount to less than 10 per cent of body weight per day, about what one would expect for the body size of these birds (Bartholomew and Cade, 1963). Three adult *P. namaqua* shot by E. J. Willoughby just after they had drunk at a water hole in the Namib Desert on 12 March 1966 gave the following values: a male weighing 183 gm held 30 ml of water in his crop; another male weighing 162 gm held 26 ml; a female weighing 167 gm had 23 ml in her crop. These values range between 16.4 and 13.7 per cent of body weight. Certainly these data do not suggest any unusually high consumptions of water by adult sandgrouse.
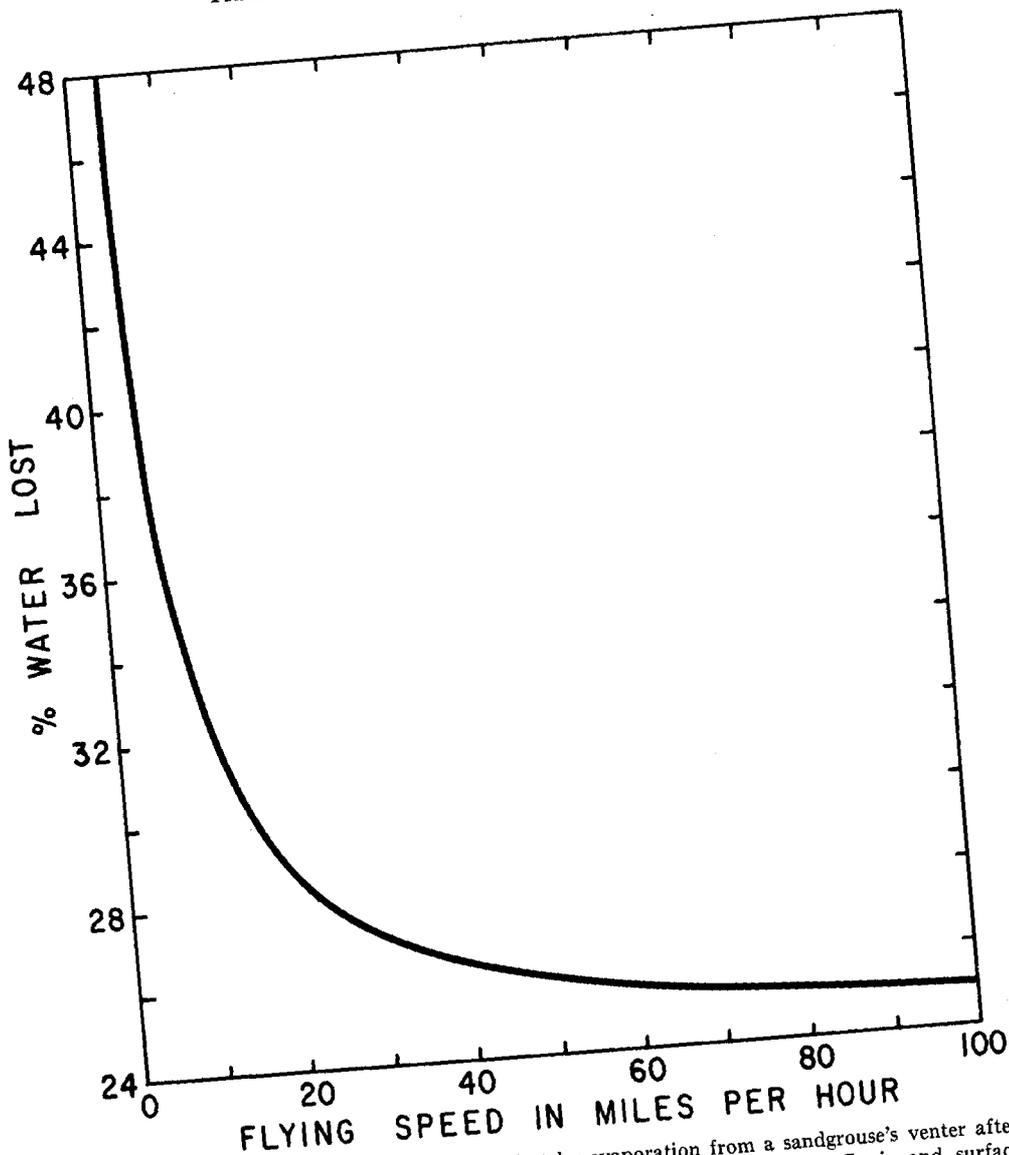
Figure 7. Calculated percentage of water lost by evaporation from a sandgrouse's venter after flying 20 miles at different air speeds, under the following conditions: 20° C air and surface temperature, 30 per cent relative humidity, 50 cm² wet surface area, and 25 g of water in the plumage at beginning.

Moreover, we have noted that many individuals arriving in the flocks at water holes depart without drinking. Some of these undoubtedly return in later flocks, but many do not. For instance, at Gross Tinkas, a natural water hole at the head of an intermittent tributary draining into the Swakop River in Game Reserve No. 3, in the Namib Desert of South West Africa, on 5 December 1965 Cade and E. J. Willoughby watched sandgrouse from 0730 to 1000 hours. An estimated 2000 to 3000 P. namaqua assembled in flocks of 10 to 100 on the knolls and hillsides surrounding

the water hole, but less than 700 came down to the water, and of these not more than half actually drank. During this time the flocks were continually harassed by a pair of Lanners (*Falco biarmicus*), and once they were disturbed by a jackal (*Canis mesomelas*), which came to drink. Possibly some of the assembled birds drank elsewhere, but we doubt it. We believe that an individual sandgrouse does not need to water every day and that species of sandgrouse are much better adapted to conserve water than are pigeons and doves. When deprived of water in captivity, sandgrouse lose body weight gradually and continue eating seeds (Cade and Willoughby, unpublished), whereas doves reduce food consumption or stop eating entirely and lose body weight precipitously (MacMillen, 1962; McFarland, 1964; Willoughby, 1966).

Thus, it seems likely to us that even if a young sandgrouse eats only air-dried seeds—a point which requires further checking—its water requirement may be proportionately less than it is for the young of many other comparable-sized birds. If so, this would be another permissive characteristic allowing for the evolution of water transport in wet feathers.

CONCLUSIONS

Water transport in feathers as a limiting factor on populations. For the reasons given above, we believe it is possible for a pair of sandgrouse to nest at least 20 miles away from surface water and still allow the male to transport sufficient amounts of water to nourish the young. Field observations on this point are rather meager, as Marchant (1961) pointed out. None of the nests he located was more than 6.5 miles from water, and some were less than two miles away. Similarly, all of the nests we have located in the Kalahari have been close to water, the farthest distance being about nine miles; however, we believe *P. burchelli* must nest considerably farther away. O. P. M. Prozesky (personal communication) found a brood of *P. bicinctus* in the Kruger National Park about 15 miles from the nearest water hole, and Willoughby found a nest of *P. namaqua* in the Namib between 15 and 20 miles from water. Little else has been reported.

It is obvious, however, that the dependence of young sandgrouse on water transport in feathers places a definite limitation on the effective breeding range of these species. Regardless of how far out into the desert away from water adult sandgrouse can forage, the breeding pairs must settle within the range of the male's ability to transport adequate amounts of water to the young. We suspect that only a small portion of the total sandgrouse population of a given region breeds at any one time —even during the peak season—and that the water transport mechanism to the young—greatly restricting the area available for breeding—may be the major limiting factor on population growth.

The present great abundance of sandgrouse in the Kalahari Gemsbok Park and in other arid, settled parts of southern Africa has almost certainly been influenced by the presence of man-made sources of water. Before the bore holes and dams were in existence, sandgrouse must have occurred in far fewer numbers and have been much more restricted in their distribution. In regions such as the Kalahari where natural, permanent sources of surface water do not exist for tens of thousands of square miles, the breeding of sandgrouse must formerly have been entirely dependent upon the infrequent heavy rains that fill pans and other depressions sufficient to last through the period of rearing the young.

Evolutionary considerations. Being seed-eaters, sandgrouse are obligate drinkers. Neither their beaks nor their digestive systems are adapted for the regurgitation of

food or water, and the adults do not produce any substance like the "pigeon's milk" of columbiform birds. The sandgrouse have probably evolved from an insectivorous or omnivorous charadriiform ancestor that produced precocial young (Maclean, 1967). How the seed-eating habit evolved we do not know, but it is interesting that there is a South American parallel in the seedsnipes (family Thinocoridae of the Charadriiformes), which also produce precocial young. In any case, the evolution of the seed-eating habit in a line of desert-inhabiting charadriiforms with precocial young, which also eat seeds, necessitated the concurrent evolution of a mode of water transport by the parents to the young. Having no mechanism for regurgitation— itself a highly specialized mode of parental care—soaking a part of the plumage seems to be the only other recourse. Buxton (1923) has suggested that the short legs of sandgrouse, bringing the abdomen in contact or near contact with water when the adults drink, may have been responsible for the evolution of this mode of water transport. It seems more probable to us, however, that water transport in the belly feathers represents a transformation of the bathing response, which is nearly universal among birds.

It would be highly enlightening to know how young seedsnipes obtain water. The problem of water transport to the young in these birds must parallel very closely that of the sandgrouse, and in view of the limited number of possibilities open to birds for watering their young, it would not be surprising to find that seedsnipes have reached the same solution. In this connection, we were most interested to discover that the ventral feathers of seedsnipes have a pubescent area similar to that of sandgrouse, although not so well developed. Furthermore, this pubescence is formed by barbules that are coiled at their bases; but in seedsnipes there appears to be no intertwining of barbules between adjacent barbs as there is in sandgrouse. We have had no opportunity to test the response of seedsnipe feathers to water.

Sandgrouse and the science of ornithology. There is a moral to be read in the literature that has developed about sandgrouse in the last 70 years. We have found it strange—and a little disconcerting—that points of fact, such as how sandgrouse drink and transport water to their young, should so long remain in question. How does one explain the curious acceptance in the literature for more than 30 years of the myth that sandgrouse drink like doves and pigeons, in the complete absence of any published, substantiating data? Yet the fact of water transport in the belly feathers, well documented by direct observations on captives and indirectly corroborated by field observations of adult males wetting their feathers, has been labeled a myth and is categorically stated to be "not so" in *A New Dictionary of Birds* (1964:712), the most recent, "authoritative" compendium of our knowledge about birds.

SUMMARY

Seventy years ago Meade-Waldo described the unusual method by which the male sandgrouse delivers water to his young in his wet abdominal feathers. Although many subsequent authors have doubted the accuracy of Meade-Waldo's statements, our observations on the sandgrouse *Pterocles namaqua* in the Kalahari Gemsbok National Park in the Republic of South Africa confirm them in every detail, and also correspond very closely to descriptions of the water-transporting behavior of *P. alchata* and *P. senegallus* in Iraq.

In short, the adult male flies to a water hole in the morning, soaks his ventral feathers in a special way, and then flies back to the nesting grounds, where he alights,

walks to the hiding brood, and presents his abdomen by standing in an upright
posture with his feathers fluffed out. The young run from their hiding places, cluster
around the male's belly, take the wet feathers in their beaks, and remove the
absorbed water by a "stripping" motion.

Although feathers are not very wettable, they do have a good water-holding
capacity when saturated. The belly feathers of sandgrouse are superior to all other
kinds of feathers tested for this property. Male sandgrouse feathers typically hold
from 15 to 20 mg of water per milligram of dry weight, and female sandgrouse
feathers hold about 11 to 13 mg per milligram of dry weight. Feathers from seven
other species representing six different orders ranged around 5 to 6 mg of water per
milligram of dry weight, which is about the water capacity of paper towel or syn-
thetic sponge. Sandgrouse belly feathers retain their structural integrity after re-
peated wetting and stripping with the fingers to remove water, whereas other kinds
of feathers quickly become frayed, matted, and twisted out of shape.

The unusual water-retaining characteristics of sandgrouse belly feathers are cor-
related with structural peculiarities of the proximal four-fifths of the feather. The
structure of the barbules in this specialized zone is unlike that recorded for any
other species of bird. The barbules have no hooks or grooves, but are flattened at
their base and coiled into helices along both sides of the barbs. The ends of the
helices terminate in straight hairlike tips, giving the ventral surface of the feather a
peculiar pubescence in the proximal zone. The helices of barbules intertwine, forming
a network of coils that is very resistant to mechanical disruption.

When water is dropped on the ventral surface of the feather, the coiled parts of
the barbules spring open and project their hairy tips at right angles to the plane of
the feather. Water is held in this meshwork by interfacial tension, and possibly also
by capillarity. When the water evaporates, the coils spring back, reuniting adjacent
barbs into a strong web. These attributes of sandgrouse feathers are interpreted to
be adaptations for holding large amounts of water and for resisting structural break-
down from repeated wetting and "stripping" by the beaks of the young.

Measurements made on dead sandgrouse and on pieces of belly skin and plumage
indicate that 25 to 40 ml of water can be absorbed and held in the belly plumage of
an adult male sandgrouse. Assuming that the wet venter acts as a simple physical
evaporating system, and applying realistic values for flying speed, environmental
conditions, and water capacity of the plumage, we have estimated that a sandgrouse
should be able to deliver from 10 g to 18 g of water for a distance of 20 miles. These
quantities should be sufficient to enable young sandgrouse to obtain significant
amounts of water from the wet feathers.

The dependence of young sandgrouse on water transport in feathers, by greatly
restricting the area available for breeding, may be a major limiting factor on popu-
lation growth. Before the occurrence of man-made sources of water in the arid parts
of southern Africa, sandgrouse probably were less abundant and were more restricted
in their distribution.

The evolution of the seed-eating habit in a line of desert-dwelling birds with
precocial young has necessitated the concurrent evolution of a mode of water trans-
port by the parents to the young. Lacking a mechanism for regurgitation, soaking
a part of the plumage seems to be the only other recourse short of some major
anatomical innovation. It seems likely that water transport in the belly feathers
represents a selective adaptation of bathing behavior.

The seedsnipes of South America show many parallels with sandgrouse. In view

of the limited ways available for adult birds to carry water to their young, it would be most instructive to know how young seedsnipes obtain water.

ACKNOWLEDGMENTS

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