Drinking behavior of sandgrouse in the Namib and Kalahari deserts, Africa.

In the past 30 years it has become commonplace to state in general works that sandgrouse, family Pteroclidae, drink by a pumping or sucking mechanism, with the beak continuously immersed during imbibition, as do doves and pigeons, family Columbidae (E. Stresemann, *Handbuch der Zoologie*, vol. 7, Aves, Berlin, W. de Gruyter, 1927–34, see p. 762; E. A. Armstrong, *Bird display and behaviour*, London, Lindsay Drummond, 1947; N. Tinbergen, *The study of instinct*, Oxford Univ. Press, 1951; O. L. Austin, *Birds of the world*, New York, Golden Press, 1961; R. Meinertzhagen, pp. 711–712 in *A new dictionary of birds*, A. Landsborough Thompson, ed., New York, McGraw-Hill, 1964). In fact, this case has become widely accepted as a classic example of the utility of a behavior pattern to indicate phylogenetic relationships in a situation where morphology fails to provide an unequivocal answer to the question. In this instance the result has been relating two families to the same order.

All statements about the phylogenetic implications of this method of drinking can apparently be traced back to K. Lorenz (Verhandl. Deutsch. Zool. Ges., 41 [Zool. Anz. Suppl. 12]: 69–102, 1939) who said, as best we can translate: “For example, one can recognize the order of doves by the exclusive application of morphological characteristics only through a tangled combination of these characters: carinate, insessorial bird, with weak, soft-skinned, blistered beak, medium-long pointed wings, short perching or schizopodal leg, etc. There are exceptions to each of the named characters. *Goura* is not an insessorial bird, and besides has round, generally chicken-like wings, *Didunculus*, a generally different bill, and so forth. On the other hand, one recognizes the order by the single behavioral characteristic, namely that in drinking the water is pumped up by peristalsis of the esophagus, which occurs without exception within the order. The only other group, however, which shows the same behavior, the Pteroclidae, is placed near the doves just by this doubtlessly very old characteristic even more than by many morphological characteristics which point to the same conclusion.”

The phylogenetic significance of this type of drinking went unchallenged until W. Wickler (Zeit. für Tierpsych., 18: 320–342, 1961) called attention to previously published observations which indicate that other groups of birds (Estrildinae and Sylviidae) also contain species which drink by sucking. In addition, Cade and Greenwald (Auk, 83: 126–128, 1966) have found that mousebirds (Coliiformes) drink by exactly the same method.

Wickler (op. cit.) also cited the old statement of Bartlett that the aberrant and apparently primitive Tooth-billed Pigeon (*Didunculus*) drinks, not like other columbids but like geese, by putting its beak down into the water and then quickly raising up its head. Similarly, L. Schönholzer (*Der zool. Garten* [NF] 24: 345–434, 1959) took motion pictures of sandgrouse (*Pterocles quadricinctus*) in a zoo, showing that individuals of this species drink by sucking in a draft and then raising their heads up high to swallow.

In field work carried out in January, 1964, from June to September, 1964, and from October, 1964, through January, 1965, we have had numerous occasions to verify and extend Schönholzer’s observations for two additional species of sandgrouse, *Pterocles namaqua* and *P. burchelli*, which are common inhabitants of the Namib and Kalahari deserts in southern Africa. Most of our observations were made at the Namib Desert Research Station, located at Gobabeb approximately 70 miles inland.
from Walvis Bay, in South West Africa and in the Kalahari Gemsbok National Park, Republic of South Africa. At Gobabeb, an open pit dug down through sand to the water table in the dry bed of the Kuiseb River provides one of the few sources of surface water for thousands of square miles. In January, 200 to 300 Namaqua Sandgrouse came to water every morning, but in July and August the number was usually 50 or less, and flocks did not fly to the water hole every day. A number of game-watering tanks distributed along the Nossob and Auob rivers in the Kalahari Park attract thousands of sandgrouse of both species. Most of our observations in the park were made at the Mata Mata, Craig Lockhart, and Houmoed game wells.

We have observed thousands of sandgrouse drinking at these water holes, often watching from hides or vehicles situated only a few feet away from the birds. In January, Cade spent most of three days in a hide at the Gobabeb water hole observing birds drinking at a distance of about 10 feet, and in July and August, Cade and Willoughby made three dawn to dusk surveillances of this water hole from a hide located about 20 feet from the water. Maclean carried out intensive watches each of several hours’ duration on nine days during October and November at Houmoed water hole, either from a hide or parked vehicle. During all of these periods of observation, we have never seen one of these sandgrouse drink like a dove or pigeon.

In our areas of study, the difference in drinking between sandgrouse and doves is at once obvious, because frequently three species of doves, Streptopelia capicola, Stigmaphila senegalensis, and Oena capensis, and the Speckled Rock Pigeon, Columba guinea, come to drink at the same water holes with the sandgrouse. Thus, the behavior of sandgrouse and doves can often be compared as they drink side by side. All of these columbid species stick their beaks into the water and suck to satiety before raising their heads.

Drinking by the sandgrouse studied is a brief act requiring no more than 5 to 10 seconds for completion after the water is reached. At Gobabeb, a typical sandgrouse would suck and raise its head 4 or 5 times (range 3 to 10) before flying away. In the Kalahari, Maclean obtained the following figures: for 141 counts of male Pterocles namaqua the average number of drafts per drink was 9.6; for 145 females, 9.4; for 136 male P. burchelli, the average was 7.4 drafts; for 133 females, 7.0. The range was from 1 to 24 drafts. (We use “draft” here to mean one immersion of the beak followed by raising the head and swallowing.) Cade (in press) discusses the probable adaptive significance of this rapid drinking in connection with predation by diurnal raptors around water holes.

It has been reported in the Russian literature that individuals of P. orientalis shot at watering holes in the Soviet Union held up to a “cup” of water in their alimentary tracts, and G. W. Salt and E. Zeuthen (pp. 363-409 in Biology and comparative physiology of birds. vol. I, A. J. Marshall [ed.], New York: Academic Press, 1961) have estimated this amount to be about 150 ml. P. namaqua and P. burchelli apparently drink much smaller quantities. Individuals netted at Houmoed after drinking had an estimated 5 to 10 ml of water in their crops. At Gobabeb, we measured the amount of water consumed at one time by three Namaqua Sandgrouse which had been deprived of water for many days. A male, which had been kept in a small outdoor cage in the shade without water for 25 days, drank 12 ml at once, raising his head 7 times in the process; four minutes later he drank 3 more ml, raising his head 3 times. The average amount of water consumed per draft was 1.5 ml. A female, which had been subjected to the same condition, drank 15 ml, raising her head 14 times, for an average of 1.1 ml per draft. A second female held for 17 days without water consumed 12 ml in 6 drafts. These figures probably represent near maximum
consumptions for this species, but the possibility that breeding birds with chicks drink more should not be ruled out.

We have been unable to find a published account of actual observations of any sandgrouse drinking by holding its beak in the water and sucking continually like a pigeon or dove, although Meinertzhagen (op. cit.) says that "as many as 44 gulps have been counted." On the other hand, three species are now known definitely not to drink in this way. Until some information on other genera or species of sandgrouse becomes available, we feel compelled to abandon the long-held notion that the family Pteroclidae can be related to the family Columbidae on the basis of a common, distinctive method of drinking.

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Drinking behavior of mousebirds in the Namib Desert, southern Africa.—Both the White-backed Mousebird (Colius colius) and the Red-faced Mousebird (Colius indicus) occur in wooded sections of the Namib Desert, usually along dry river courses. In field work carried out between 18 and 23 January 1964 and between 5 July and 11 August 1964, we had frequent opportunities to observe flocks of these two species foraging in the riparian acacia woods (A. giraffae and A. albida) associated with the dry bed of the Kuiseb River. Our observations were made around the Namib Desert Research Station located at Gobabeb, approximately 70 miles inland from Walvis Bay, in South West Africa. The riparian vegetation allows a number of avian species to extend their ranges into the desert region from the more extensively wooded highlands flanking the east side of the Namib.

In the vicinity of Gobabeb these mousebirds fed extensively on the young leaves, flowers, and green or ripe berries of the widespread, vinelike shrub, Salvadora persica. Since this plant appears to undergo at least two cycles of fruiting a year in this region, the mousebirds are able to exploit a more or less constant source of food. Ripe Salvadora berries are the preferred parts of this plant; these have a high water content. For example, a sample of 30 freshly picked ripe berries weighed 7.75 g; on oven drying to a constant weight at 80°C the weight was 2.45 g, of which the seeds, which are not digested by mousebirds, accounted for 0.38 g. Thus, the water content of these berries averages about 66 per cent of the wet weight.

Because of the high water content of their food, mousebirds are not greatly dependent on drinking in order to maintain water balance even in the desert, and except for one brief period they were never seen at the isolated water holes in the bed of the Kuiseb River where many other forms of birdlife gathered in large numbers to drink. In January, when daytime temperatures ranged above 35°C, we never saw mousebirds at water. This period corresponded with a time when the Salvadora bushes were in full fruit, and both species were feeding heavily on the ripe berries. Again, in July and August when temperatures were moderate to cool, we never observed White-backed Mousebirds drinking, but between 30 July and 2 August...