YAWNING AND OTHER MAINTENANCE ACTIVITIES IN THE SOUTH AFRICAN OSTRICH

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Behavior functions according to the principles of homeostasis and may therefore be called regulatory. The term "maintenance behavior" is used here to describe activities that help regulate the physiological state of the organism. When given in the presence of another organism, certain maintenance activities may have secondary, communicative effects through "sympathetic induction" causing social facilitation; for example, some complex and derived maintenance activities, such as the collecting of food by individuals and groups for the benefit of all participants or their dependents, have become social events in both primary and ritualized contexts.

Yawning and stretching are examples of basic regulatory behavior for the purpose of maintenance of bodily functions. These activities are stimulated by endogenous metabolic events and serve to regulate physiological processes of respiration and blood circulation. Several endogenous factors can stimulate and trigger yawning and stretching behavior. Insufficient blood circulation in the brain leading to oxygen deficiencies is said to elicit yawning and the accompanying acts of stretching; in turn, this behavior improves circulation as it is associated with deep inhaling and exhaling (Dumpert, 1929). Further, a homeostatic relationship is thought to exist between the neural center for breathing and the extrapyramidal motor system (Selbach and Selbach, 1953). When the stimulation of the breathing center becomes insufficient, an increased amount of carbon dioxide is required to reactivate it. This is accomplished during the act of stretching by muscle contraction that delivers the necessary carbon dioxide (Peiper, 1956). It is also possible to trigger yawning and stretching in cats through electrical stimulation of the brain stem in the region of the diencephalon between the anterior commissure and the infundibulum (Waldvogel, 1945; Hess, 1954).

While the relevant internal events do both stimulate and elicit yawning and stretching, this behavior can be released also by environmental stimulation when the organism is sufficiently and specifically motivated. In man and other mammals, and equally among birds, one can observe a strong social induction of this behavior when it is exhibited within a social group. Therefore, one should ignore neither the existence and releasing values of specific, environmentally controlled releasing mechanisms nor the social implications of yawning and stretching in gregarious species. Tembrock (1964: 211 ff.) while noting certain environmental effects, overlooked these behaviorally, and particularly socially, important

exogenous components in his treatment of this behavior complex. In calling this the *Räkelsyndrom*, Tembrock followed an earlier usage of this term by Selbach and Selbach (1953).

Yawning and stretching frequently follow each other, or they appear together in various combinations. They consist largely of fixed action patterns, which, for the stretching behavior, often achieve a high degree of complexity. The yawning and stretching activities of man are also composed of a set of basic motor patterns, but his behavior appears frequently flexible and modulated by many individual idiosyncrasies. Yawning and stretching are described as phenomena associated with fatigue. The behavior is blocked as long as the organism breathes regularly and sufficiently deeply, and fully exercises its muscles during the periods of activity. Thus, yawning and stretching characteristically appear at the end and at the beginning of activity cycles, i.e., their occurrence is correlated with periods of rest and sleep.

YAWNING IN BIRDS

Maintenance activities are common among all vertebrates, and yawning and stretching are general behavioral attributes of the homeotherms. Among birds, as well as among mammals, yawning is so wide-spread that it is difficult to understand why it has not become better known. Maintenance behavior in birds is easily observed; particularly when the ontogeny of an organism and its behavioral systems are carefully studied, one has no difficulty in identifying the patterns of maintenance behavior. However, students of bird behavior are commonly more interested in other behavior patterns, such as social behavior or migration, and the establishment of ethograms, the complete behavioral catalogues for individual species, is badly neglected. The organic and physiological bases of bird behavior are usually overlooked and also largely unknown. However, a knowledge of these underlying mechanisms is required for a full understanding of maintenance behavior and as a basis for experimental analysis of such behavior.

There is still another reason why yawning is not better known in birds. When Heinroth (1930) focused his attention on species-specific behavior in birds, he compared homologous action patterns in groups of related species. Noting the value of this stereotyped behavior for taxonomic studies, he introduced the use of genetically fixed action patterns in the study of phylogenetic relationships between species. With his superb knowledge of bird behavior and his outstanding contributions to the biology of so many species of birds, Heinroth programmed and influenced for decades the development of the science of ethology in Europe. So authoritative were his views on bird behavior that his statement that

birds do not yawn was accepted without question, and it was even treated as dogma. Once a discussion of ours of yawning in warblers of the genus *Sylvia*, though documented by photographs and many observations, did not pass the first editorial critique for this very reason, and remained unpublished. As recently as 1963 Konrad Lorenz stated that birds and reptiles do not yawn, which he considered a finding of taxonomic importance unknown to any zoologist before Heinroth ("Dass Vögel und Reptilien nicht gähnen, zum Beispiel, ist eine taxonomisch wichtige Feststellung, die vor Heinroth kein Zoologe gemacht hat"; Lorenz, 1963: 153).

In their recent *Auk* review of aspects of avian field ethology, Ficken and Ficken (1966) note the importance of maintenance activities to the survival of the bird and as phylogenetically important components of display behavior. Following closely the traditional ethological concept, procedure, classification, and selection of examples, the authors did not mention yawning. This is not surprising, but it seems desirable to point out that yawning does exist in birds and to note its importance as regulatory behavior and its potential as a social releaser in gregarious species.

METHODS

In this paper yawning and some related behavior patterns are described for the South African Ostrich, *Struthio camelus australis*. We also discuss panting and open-mouthed threat gestures to illustrate differences in superficially similar behavioral expressions; a complete account of the maintenance activities and social behavior of the Ostrich will be published elsewhere. The descriptions are based on observations of the Ostrich in South West Africa in 1957–58 and 1964. For further information see Sauer and Sauer, 1959, 1966 *a, b*. Still and motion picture photography and tape recordings were used to supplement the direct observations. The field studies pertained to wild birds of all age groups and covered all phases of their daily and annual activity cycles. The main study was performed in the inner Namib Desert, in the Erongo Mountains, at Etosha Pan, and in the Omaheke district of the Kalahari region; occasional observations were made throughout the country.

MAINTENANCE BEHAVIOR IN THE OSTRICH

Yawning.—Soon after hatching, having rested and recovered from their tiring attempts to rid themselves of the egg shell and membranes, the chicks yawned for the first time. This indicated that they had either been disturbed while resting or that they were about to begin a new phase of activity. The first yawn, with or without a stretching movement of the neck, appeared in the complete form characteristic throughout the life of an Ostrich. No changes in its expression and motor coordination were noticeable that suggested any postnatal maturation of this behavior. It appeared at the beginning and at the end of the many activity cycles

Figure 1. Nestlings resting, yawning (1, top bird), and panting (2, bird on right). Tinkas Flats, Namib; 13 December. Photographs by the authors in South West Africa, 1964.

during the day, in the functional context mentioned in our introduction and further outlined below.

When uncovered, the dozing nestlings drowsily yawned (Figure 1). A group of chicks exploring the surroundings of the nest quickly became tired from their walk; a few meters from the nest they paused for a rest, squatted, gave deep yawns which were often associated with stretching, and then closed their eyes for a nap (Figure 2). Commonly the chicks yawned deeply; the gular part of the mouth was lowered maximally, and the tongue was withdrawn during the long phase of inhaling. The chicks yawned and might stretch either the neck or the whole body at the same time (Figures 1, 2). The yawning was terminated with a relaxation of the body which began with the short phase of exhaling (Figure 3). Occasionally, a yawn consisted of a short phase of inhaling followed by a long phase of exhaling.

The chick's yawn lasted for about seven to eight seconds, during which it usually erected its head feathers for some two seconds when it was about to have its beak maximally opened (Figure 3, upper and lower). Drowsy chicks frequently kept their eyes closed while they yawned, provided they were not aroused by some environmental event. When a chick was affected by an external stimulus, such as a restless sibling,

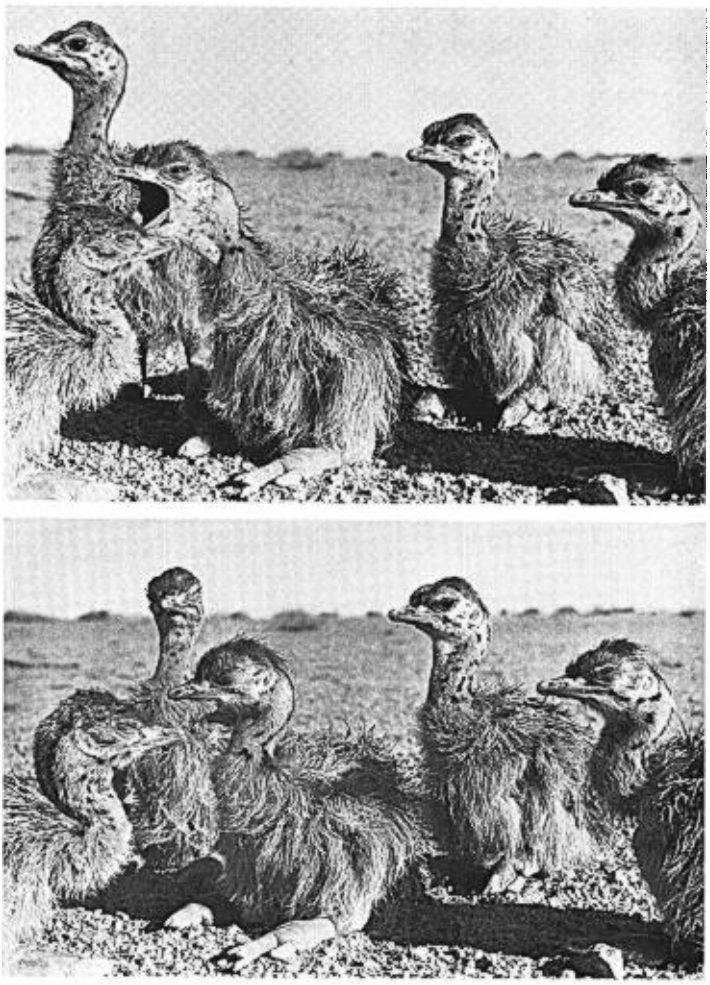

Figure 2. Chicks at rest during exploration of the surroundings of the nest site. One chick yawns and stretches its neck (upper), and subsequently relaxes to sleep (lower). Tinkas Flats; 5 December.

the call from another chick, or the call of a parent, it might open its eyes slightly or fully during yawning. The act of yawning, however, was not oriented toward the source of disturbance or attraction, but remained directed as always in the mid-sagittal body plane. When terminating a yawn, a chick might return to the same resting posture or, quite commonly, change the position of the head and neck slightly. The latter indicated some discomfort or fatigue from the earlier resting posture.

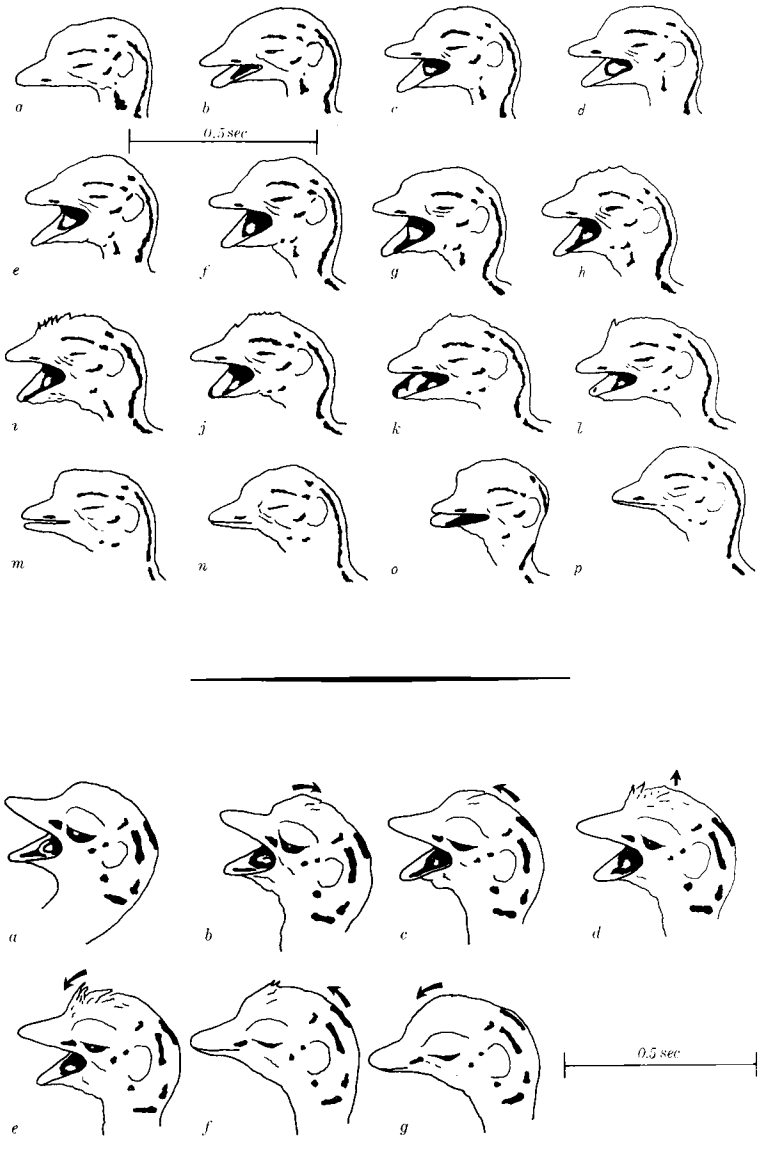

Figure 3. Sequences of yawning drawn from 16 mm motion picture film. Upper. Exhaling begins with *g*, erection of head feathers with *h*; yawning is terminated with *n* and followed by a brief opening of the mouth during inhaling *o*, whereupon the chick sleeps. Lower. Sequence beginning with the phase of exhaling at *b*. The arrows indicate the completed movements of the head relative to the preceding phase. Erection of head feathers from *b* to *f*.

Yawning appeared in Ostriches of all age classes in the very same context as described for the young chick: just before falling asleep or beginning to rest, when a rest was interrupted, and again when the bird awoke and initiated a new phase of activity. Typically, a bird that yawned had been immobile for some time, either resting on the ground or standing. Quite commonly, a flock or herd of Ostriches, coming to a halt in their communal area near a water hole, crowded and rested before they would approach the water. Many of these birds, enjoying safety and protection in the group and having come a long way from their "family" territories might begin to preen and rest or sleep. Those that appeared exhausted from their long walks might immediately reveal their tiredness with a few deep yawns; then they would nod a few times in the manner familiar to everybody of one who falls asleep while planning to do something else. Closing its eyes, a tired Ostrich would slowly tilt its head downward and, after a while, jerk it up just to droop it again. Nodding in this manner a few more times, and often giving a few more yawns, the bird in the end dozes off, holding its neck typically locked in the sigmoid resting posture. When waking after some time an Ostrich would come into action usually with a deep yawn (Figure 4), often associated with a stretching of the neck and followed, or sometimes preceded, by a complete stretch. Birds that slept and rested with their necks and heads lying on the sand yawned when waking even without lifting their heads.

In general, yawning was seen in the communal areas when the birds rested or waited their turns at the water holes, and in their territories when they guarded their nests, when they incubated eggs or brooded chicks, when they settled for their night's sleep or awoke from it during a disturbance in the night or in the morning, or when they were disturbed during any of their short resting and sleeping periods in daytime. It never occurred when the birds were very active and alert. The periodic appearance of yawning was observed in individual birds studied over long periods of time. A hen, for example, temporarily deserted by her mate, remained on the nest and incubated for several days and nights in a row. Quite regularly she began to yawn extensively in the late afternoon at the time when her mate formerly appeared to relieve her. The deserted hen then yawned several times every half hour and toward the evening more frequently, until she finally fell asleep for the night after several deep and long-drawn yawns.

In the evening about sunset, and regularly up to some 40 minutes thereafter, solitary and flocking Ostriches, having gathered the last bits of food, arrived at their individual sleeping places for the night. Commonly the birds of a flock stood for a while before squatting; they would

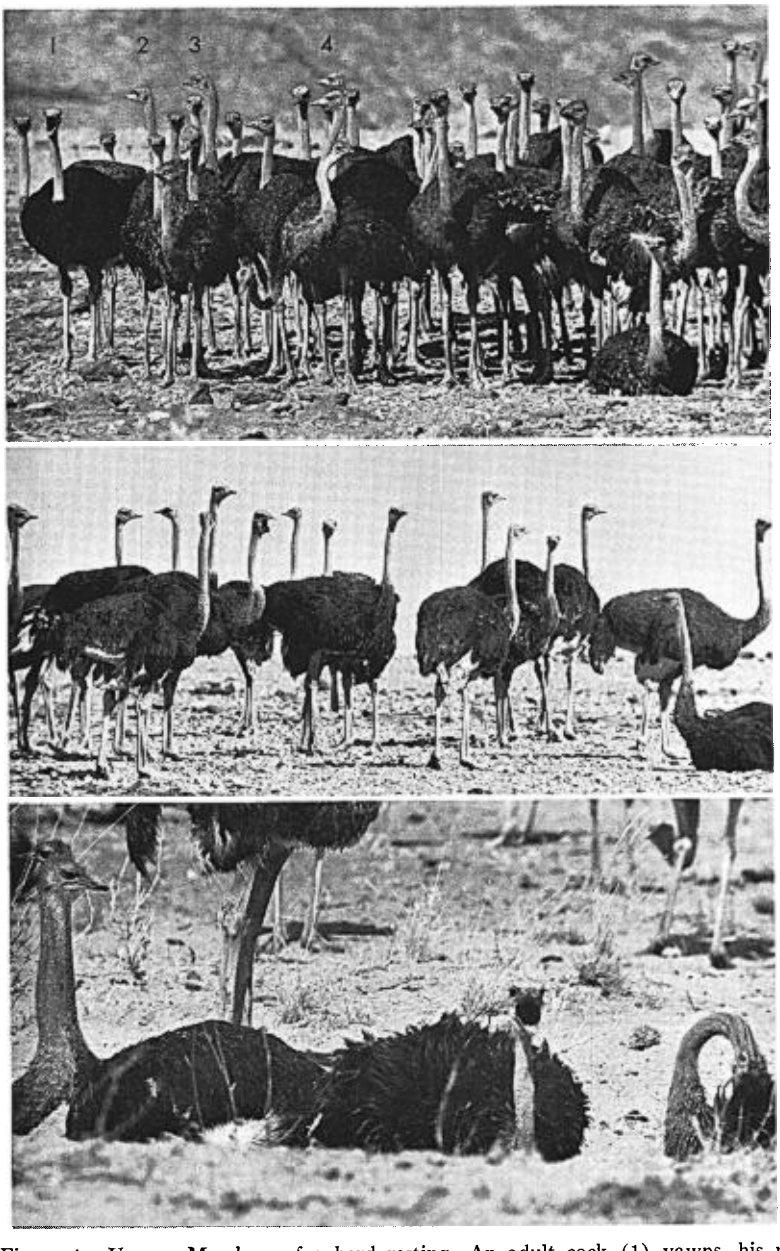

Figure 4. Upper. Members of a herd resting. An adult cock (1) yawns, his rest being terminated as three birds (2, 3, 4) of his flock advance toward the water. Ganab, Namib; 17 July. Middle. Resting Ostriches alerted by an approaching flock; waking adult hen yawns. Ganab, Namib; 14 July. Lower. Immature bird with erected feathers yawns. Ganab; 19 July.

look around, listen, turn their backs up the wind, and begin to preen. While preening would frequently be interrupted by yawning, the birds would continue their toilet behavior for some time after having settled on the ground. The preening was then interrupted more often and for longer intervals during which the tired birds repeatedly yawned or simply stared without moving. Finally preening ceased altogether; the more alert birds in the flock would still hold their heads up for a while, then one after the other would close its eyes and nod its head. Then their necks and heads were lowered to the ground; individual birds would blink a few times, yawn once or several times, and fall asleep. The Ostriches commonly maintained a wide field of view and open space at least to one side of their sleeping places and, therefore, made it easy for us to observe this characteristic sequence of behavior daily after sunset. In the morning, usually up to 40 minutes before sunrise, the wakening birds would yawn, get up and stretch themselves a few times, excrete, and preen briefly, and shortly begin to graze and leave the sleeping place very quickly.

Behavior associated with yawning.—No other behavior was obligatorily associated with yawning, but a number of activities were performed before, after, or at the same time as a yawn. Yawning was sometimes begun during defecation, or the one activity followed the other. Resting and dozing birds from time to time jerked their heads laterally to shake off excess mucus from the nasal cavity and sometimes from the mouth. This head-jerking was frequently followed by a yawn before the birds dozed or slept again. A dozing Ostrich suddenly disturbed by a passing companion or stranger would initiate an open-mouth threat, and, becoming aware of the harmlessness of the situation, switch directly into a deep yawn before closing his mouth and his eyes again. This is a spontaneous displacement of the open-mouthed threat gesture through yawning, both of which, in part, make use of the same motor patterns.

Various acts of stretching were associated with yawning. Most frequently a stretching of the neck or the body was synchronized with yawning, while the unilateral stretching of wing and leg (Figure 5) quite often immediately followed, but might also precede, the act of yawning.

Panting.—In the open and arid veld, heat dissipation by panting was of common occurrence in Ostriches of all age groups. Small chicks sought shelter from solar radiation by standing or walking in the shadow cast by the bodies of the guarding hen and cock. Standing in the open with young chicks, adult Ostriches enlarged their shadows, providing thereby increased heat dissipation for themselves, by lowering the wings and holding them away from the body. The hen was also seen to signal her brood to assemble under her when the group was disturbed, for example, by a group of noisy Burchell's zebras (*Equus burchelli*) passing nearby. The

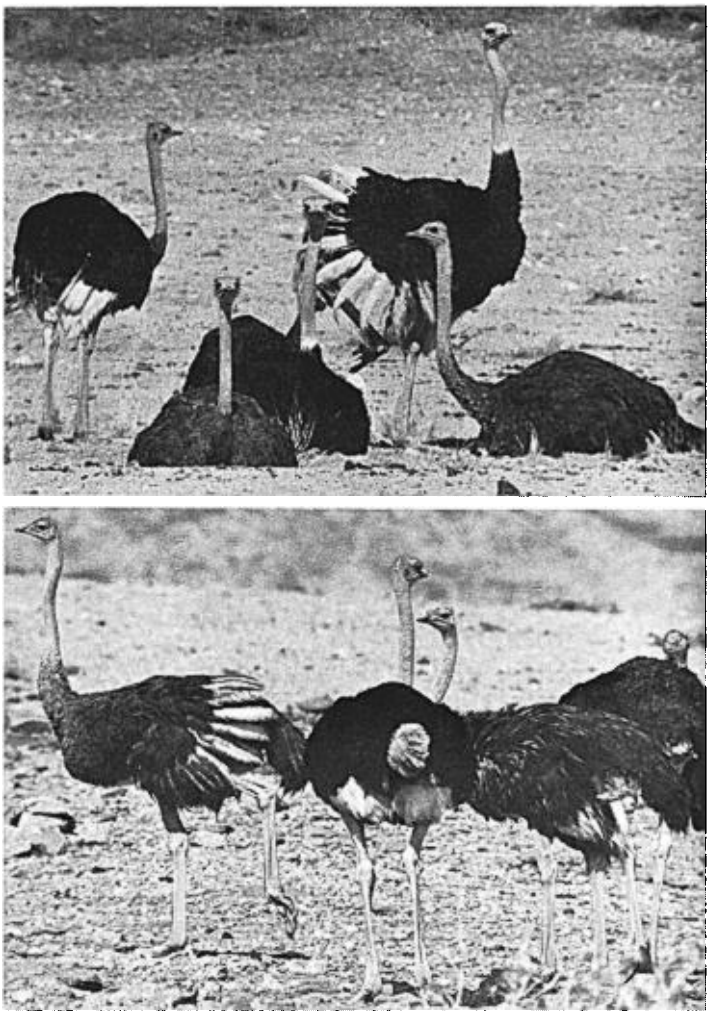

Figure 5. Upper. Waking cock initiates unilateral stretch of the extremities by opening its wing and flexing its leg. Hotsas River; 14 September. Lower. Advanced phase of the unilateral stretch by a maturing hen. Ganab; 19 July.

hen signaled with a rhythmic beating of her wings while she called the young and held her head near the ground. Upon perceiving the signal the resting chicks interrupted their panting and gathered immediately in the shade of her body, where they remained clustered while the group walked slowly to a new resting place. Families with offspring occasionally stood in the shade of trees or large bushes, but every so often the parents did not share this shade with their brood. Chicks were also seen crouching in

Figure 6. Panting chick (inset) on Etosha Pan, 10 November, and adult hen at Erindi Ura, Omaheke, 7 October.

the shade of low bushes or mere depressions in the ground. Many tests at the nests and in the open veld indicated that the chicks sought very actively any available shade-producing object, even our research equipment and the human observer himself.

These observations reveal the chicks' need for shade, but the older Ostriches seldom sought shade, and on the vast Namib flats many of them had none. There they habitually rested and did everything in the open and remained fully exposed to the intense sunlight and heat even during the noon hours. They were, however, very inactive at noon, which prevented accumulation of excessive body heat, and their panting was almost continuous when the birds were not engaged in minor activities such as preening.

While panting, but not when yawning, both young and old Ostriches exposed the triangular submalar apteria (Figure 6); it is reasonable to assume that this aided heat dissipation. When panting the Ostriches held

Figure 7. Open-mouthed threat of an adult cock directed toward immature hen that responds in fear with a weak open-mouthed threat away from the aggressor. Hotsas River; 8 September.

their heads horizontally or tilted slightly upward, which assured maximum air ventilation and a maximum distention of the submalar region. When an Ostrich changed from panting to yawning, the former was usually terminated with a swallowing motion, followed by a yawn.

OPEN-MOUTHED THREAT COMPARED WITH YAWNING

The open-mouthed threat gesture of the Ostrich.—To show the differences between yawning and superficially similar behavior, panting was described above, and now the gesture of the open-mouthed threat is briefly noted. This form of social defense and aggression was given in encounters of the Ostriches with conspecific partners, birds of other species, and with any sizeable mammal or reptile. During this threat an Ostrich might give a variety of threat calls. A hissing note was most commonly associated with the slight threat of a defensive bird. The voice of an aggressive Ostrich, however, changed rapidly with increasing excite-

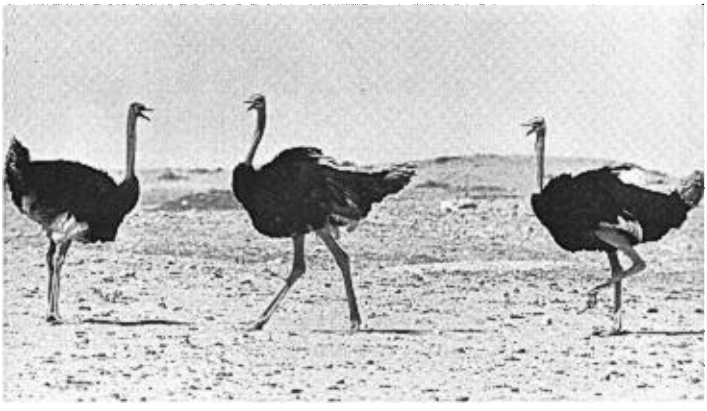

Figure 8. Open-mouthed threat gestures in fighting cocks. An adult chases a maturing male which, in turn, threatens a young male at rest. The last gives a defensive threat; its confidence is indicated by its tail-up posture. Hotsas Flats; 6 September.

ment, from hissing to loud and harsh snorting and to one- and two-syllabled calls with pronounced tonal qualities.

During the open-mouthed threat the gular tissue is pressed upward, quite in contrast to its maximally lowered state during a yawn. Further, the tongue is thrust upward and slightly forward. These characters remain the same regardless of the degree of the opening of the beak and the intensity and quality of the threat (Figures 7, 8). The open-mouthed threat gesture, therefore, cannot be mistaken for yawning, even when a bird faces danger with an immediate threat at the moment of awaking from sleep (Figure 9) when one expects the bird to yawn.

DISCUSSION

The primary function of maintenance behavior.—Maintenance of the organism through homeostasis is commonly based on both physiological and behavioral mechanisms. Yawning, stretching, and panting are described as examples of maintenance or economic behavior in the Ostrich. While Cannon (1932) introduced in biology the term homeostasis to designate primarily feedback and regulatory mechanisms of humoral and visceral processes that maintain constancy of internal body conditions, Jacob von Uexküll in 1909 had already applied clearly the principle of homeostasis to behavioral activities. This principle was later emphasized by Richter (1942) in his analysis of animal and human behavior. Though it is now generally understood that maintenance behavior that regulates various

economic requirements of an organism is activated by homeostatic needs, quantitative analyses of all but the few known kinds of maintenance activities, such as eating and breathing, have been hampered by a lack of an understanding of the physiological correlates as well as by a lack of a qualitative description and analysis of the associated behavior. Yawning has not yet become well known in birds. Using the Ostrich as an example, this preliminary report emphasizes its existence as well as the importance of this behavior in these homeotherms. It should be noted once more that yawning in birds is by no means restricted to the Ostriches with their large bulk, but that it occurs in small birds as well (pp. 572–573), and we have noticed it in many bird species of very different taxonomic position where it occurs in the same functional context, correlated with periodic fatigue. We have seen it also in lizards and geckoes, and it is common in the Florida gopher tortoise. Indeed the "so-called yawning" in fish may be true yawning, triggered for the same common reason and serving the same purpose. It is conceivable that yawning is a phylogenetically old behavior pattern among vertebrates and common to most if not all of them.

Yawning as a social stimulus.—While yawning serves primarily as a regulator of physiological conditions, its secondary function as an involuntarily presented social stimulus becomes obvious when it is studied in a group of Ostriches. A bird that yawns quite often makes one or several neighboring birds yawn too, and yawning in an Ostrich herd can spread out like a "snowball-effect."

Yawning in the Ostrich is not given as a signal for the purpose of social communication; it is not a social display. The effect that it exerts on the conspecific partner is not easily assessed, because the latter commonly responds only with a minute change in expression, posture, or with an intention movement. A clear identification and evaluation of this requires a profound knowledge of the action system of the species. Some of the important social functions are as follows. At the beginning of a period of rest it assures members of a group of momentary safety or absence of danger. This is particularly significant in view of the fact that the socially higher-ranking birds customarily relax and yawn before the lower-ranking and more nervous birds calm down to rest. Thus, yawning does induce a general relaxation of tension in a group and trigger sleepiness. This prevents a scattering of the flock and disturbance of the group life, which is easily caused by lower-ranking birds that are not assured of safety by their dominant companions. Indeed, nervous Ostriches run from many a harmless event if they are not assured of safety. The

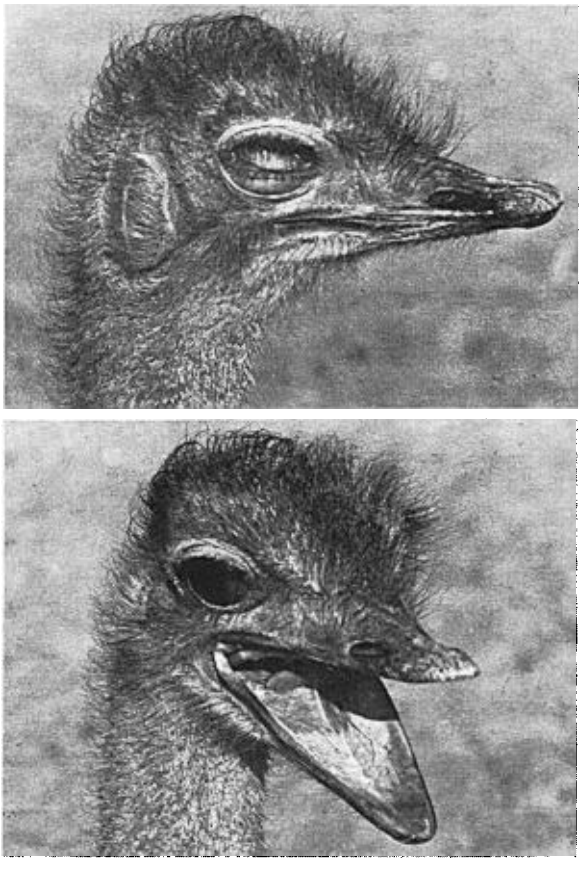

Figure 9. Adult hen disturbed in her sleep by the author. Upper. She opens her eyelid; the nictitating membrane is still drawn over the eye. Lower. Opening the eye fully, the waking bird turns at once toward the observer with an open-mouthed threat and a hiss. Erindi Ura; 2 August.

calming effect functions whether tension had been building up by either intra- or interspecific contacts. Further, after any disturbance during a resting period, yawning does again assure nervous birds that danger has passed and stimulate them to continue their rest or sleep. At the end of a period of rest, yawning would stir up the group. It initiates and even helps to synchronize the new activity cycle that the birds share with one another. The latter function becomes particularly significant after a long rest or sleep on the ground, whereby preening behavior, too, aids in synchronizing the birds' activity before they depart as a group from the place of rest.

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SUMMARY

Yawning, associated stretching, and panting are described for the south African Ostrich, *Struthio camelus australis*, which was studied in its natural habitat in South West Africa in 1957–58 and 1964. These behavior patterns are characterized as maintenance activities that, as their primary function, assist in regulating the physiological state of the Ostrich. While stretching and panting are frequently mentioned in studies of bird behavior, it is a little known fact that birds do yawn (it was even assumed erroneously that yawning does not exist in birds).

Yawning, stretching, and panting are primarily activated and released by endogenous stimulation, but they can also be facilitated and triggered by environmental stimuli when the organism is sufficiently motivated.

Yawning and accompanying stretching behavior are correlated with the periodic appearance of fatigue in the Ostrich, and they occur typically in birds whose motor activities have been reduced to a minimum.

In the Ostrich these maintenance activities secondarily can exert social influence in the form of social facilitation when they are given in the presence of other members of the flock or herd. Yawning induces a relaxation of tension in a group and triggers sleepiness, assuring excited birds of the absence of danger.

Panting and the social behavior of the open-mouthed threat are described and compared with yawning, and differences in these three patterns are noted.

ZUSAMMENFASSUNG

Das in der Ethologie der Vögel vernachlässigte, unter Vögeln jedoch weit verbreitete Gähnen wird anhand von Beobachtungen am Südafrikanischen Strauss, *Struthio camelus australis*, als stoffwechselbedingtes Verhalten beschrieben. Gähnen, Strecken und Hecheln unterstützen auch bei Vögeln im Sinne homeostatischer Regelungsvorgänge die Beibehaltung und Einstellung physiologischer Gleichgewichte im Organismus. Das stoffwechselbedingte Regelungsverhalten wird primär durch endogene Reize aktiviert und ausgelöst. Sekundär kann es stimmungsübertragend wirken, wenn es in Gesellschaft geäussert wird. In dieser Situation ist beim Strauss das Gähnen als Aussenreiz eine sozial bedeutsame Informationsquelle. Es beeinflusst die Gruppenmitglieder zu Beginn oder bei Fortsetzung einer unterbrochenen Ruheperiode im Sinne einer Beruhigung durch ranghöhere Vögel; zu deren Ende aktiviert es die Gruppe und trägt zur Synchronisation des Gruppenverhaltens bei.

Das Gähnen ist im Tageslauf mit den Verhaltenszyklen der Strausse korreliert und erscheint typisch am Ende und zu Beginn von Aktivphasen. Es ist häufig mit verschiedenartigen Bewegungen des Sich-Streckens synchronisiert und assoziiert.

Hecheln und das Drohen mit offenem Schnabel werden kurz erläutert, um auf die Unterschiede im Gebrauch und Ausdruck der diesen Verhaltensweisen gemeinsamen Elementen hinzuweisen.

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