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ABERRANT SEXUAL BEHAVIOR IN THE SOUTH AFRICAN OSTRICH

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DURING our studies of *Struthio camelus australis* in the South West African arid veld (Sauer and Sauer, 1959, 1966a, 1966b, 1967a, 1967b, 1970; Sauer, 1970; 1971) the year 1969 was marked by exceptional ecological conditions. Unusual rains fell in the central Namib during March and April and yielded an abundant and rich vegetation. The herbivores found excellent grazing until the end of the year. It boosted the local populations and attracted immigrant species from the mountainous hinterland and other neighboring districts that had received little or no rain.

The impact on the Ostrich was a mass reproductive activity which, in turn, triggered social stresses and incompatibilities among these cursorial and largely gregarious birds. The plentiful food supply allowed the Ostriches to produce many offspring several months before they normally reach a reproductive peak. Large numbers of chicks hatched from July through December 1969 and well into 1970. Normally the offspring do not appear in any significant numbers before late November or early December. Many sexually motivated adults did not start nesting, but remained in the communal areas where they performed sexual displays continually day after day. This not only prevented them from assuming their parental tasks, but also incited other birds to participate in the sexual displays even at the expense of their small chicks whom they abandoned. One of these strange and unusual activities was the males' display of homosexual behavior, the main subject of this report on a rare event affecting a whole population of wild birds.

Homosexual behavior is defined as a sexual display directed toward a member of the same sex. Such behavior is known in a number of vertebrates. Morris (1952) reports it in sticklebacks and cichlid fishes, anatid birds, rats, monkeys, and man. Nonhuman primates often display homosexual behavior not as an outlet of sexual tension, but as an expression of social dominance or subordination. In an evolutionary sense

this ritualized form of homosexual behavior is thought to have become severed from the original functional context of sexuality (for examples see Wickler 1967). It is therefore necessary to distinguish between homosexual behavior displayed as an occasional or habitual individual outlet of sexual excitement and its derived pattern presented in a different functional context. Homosexuality in its primary form can serve different purposes, for example a relief of individual tension or social stimulation. I attribute the Ostriches' infrequent demonstration of homosexuality only to the primary mode of an occasional outlet of sexual tension.

Though both sexes may, in homosexual social contacts, perform sexual behavior patterns typical of the other sex, Morris (1952) thinks the female more commonly acts like a male than vice versa. Among the Ostriches I noted homosexual behavior only in males. When they initiated it they acted always as males and never elicited a sexual or agonistic response from their chosen male counterparts. These birds simply ignored them or walked away. Occasionally males played homosexual when they were attacked by other males.

In discussing the question of terminology, Morris (1952) sees several ways in which homosexual behavior may occur. A homosexual may not be able to distinguish a male from a female; suboptimal stimuli may be sufficient, or the animal may show a clear preference for its own sex. The second and especially the third category apply in the case of the homosexual male Ostriches. They never reversed their sexual pattern but played their role as sexually strong males in front of other males.

In brief, this report is on the aberrant sexual behavior of Ostrich males that made male sexual overtures toward other males and did so even in the presence of females. Occasionally a male performed courtship behavior when alone, thereby indicating a need for an outlet of strong sexual motivation. The normal sexual behavior of Ostriches is described as far as it is needed for a comparison with the aberrant performances.

THE ECOLOGICAL AND SOCIAL SITUATION

The inner section of the central Namib within the Namib Game Reserve (Figure 1) is dominated by vast flats of sand, gravel, and surface limestone. The plains are intersected by many, usually dry streambeds of various sizes and depths ranging from shallow courses (the "omurambas" in the Herero language) on top of hard granitic bedrock to marked riverbeds and to several gorges cut deep into calcareous rock. A few granitic monadnocks (Inselberge), basalt, and marble ridges interrupt the starkness of the plains.

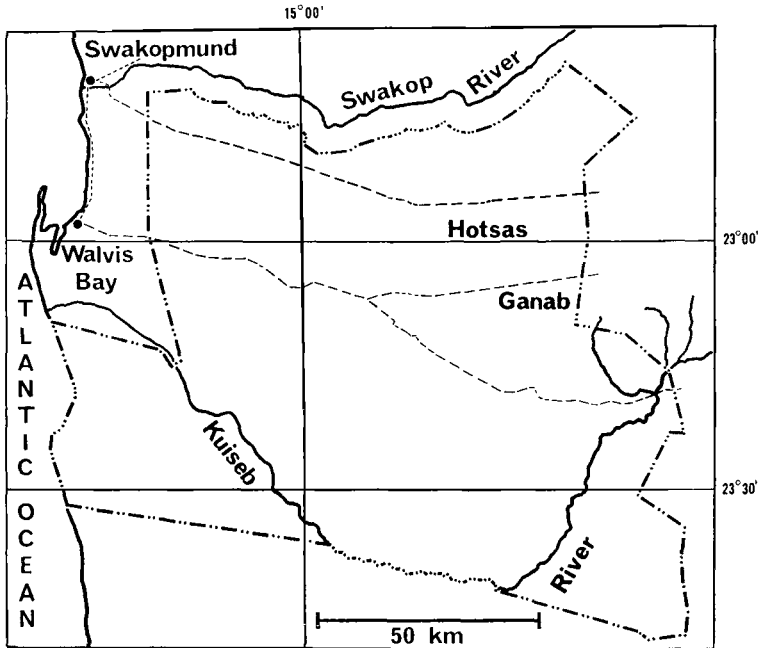


Figure 1. Namib Game Reserve, South West Africa. boundary of the reserve, ---- access roads.

Granitic outliers of the Great Escarpment border the plains in the east. Mountain ranges, dominated by the Langer Heinrich, form a sizeable barrier along the deep and broad Swakop River in the north. An excellent report on the geography, geomorphology, and climate of this region was published by Logan (1960).

The exceptional rains in March and April 1969 yielded an unusually lush vegetation compared to the region's usual windswept barren condition. The rich cover of grasses, predominantly nutritional *Aristida* species, spread even over the commonly barren rocky basalt hills ("kopjes" in Afrikaans) and ridges that border Tinkas Flats in the region of Blutkuppe and Langer Heinrich. Even in December of 1969 grazing was still excellent and attracted large numbers of herbivores, including hundreds of mountain zebras (*Equus zebra hartmannae*).

In our 1964 studies we judged the South African Ostrich as a highly flexible and successful opportunist breeder whose reproduction was controlled by the quantity and quality of food available over a certain period of time. Now these birds seemed to bear out our characterization. The excellent nutritional conditions caused a major peak of reproduction

approximately 4 months earlier than usual, and the birds continued to propagate in nearly undiminished fashion until they reached a new reproductive high in December.

Under the influence of the strong sexual motivation that affected most of the adult birds, they abandoned the chicks and juveniles and drove them off much earlier than usual. In the former years of our study (1957, 1958, and 1964) we found immatures commonly associated with their adult guards until they were 1 year old. Even then the yearlings were only driven off when the adults initiated a new reproductive cycle (Sauer and Sauer, 1966a). The exceptions to this rule were a few off-season fledglings that the flocks and herds rejected in the communal pastures and at the water. Now in 1969 I found adults commonly abandoned chicks only 2 and 3 weeks old. For a while the chicks and small juveniles maintained a strong following response and finally tried to establish contact with any adult bird that came in sight, although they were driven off quite regularly. Only a very few found a tolerant adolescent or adult bird for a guard; most of them finally drifted off leaderless and formed flocks and herds of up to more than 700 birds at a time. Under these conditions 2- and 3-week-old chicks actually survived without parental care.

The lastingly favorable food supplies and the buildup of reproductive pressure led to a number of uncommon events. For example hens aborted more eggs than usual. As a result of continuous intra-specific mutual agitation, hens laid scatter eggs even in the communal area and at the water site. In the mixed flocks of adults they interrupted their continuous "hiss-snort-and-kick" displays momentarily to abort an egg in the middle of the milling crowd. Some of the cocks turned homosexual or performed sexually into a vacuum.

The social turmoil between adults and offspring and among the adults reached its peak in December 1969 with a new and profound outburst of courtship at a time when hatching was widespread and literally a daily event. As the result of the social and reproductive pressures Ostriches spread far from their normal centers of reproduction in the inner Namib and sought nest sites far out in the coastal range. Chicks were hatched successfully barely 16 miles from the barren coast. As one might suspect, the population density and particularly the ratios of the sex and age groups were, in part, responsible for the aberrant behavior.

Late in September I made my first count of the Ostriches in 1969. Adults numbered above 500, while chicks and small juveniles in excess

of 750 roamed the flats around Hotsas. By December the young generation had exceeded 1,000, and hatching still increased day by day.

The population density in itself should not have caused the birds' abnormal behavior. In 1964, when about three times as many birds flocked in the area, we never saw any sexually abnormal behavior among them. I think the 1969 events were induced by the suddenly available and plentiful food, and they were released by the resulting motivational state of the birds. The rapid increase of the population in 1969, the excessive numbers of chicks, and especially the sex ratio of the adult birds must be viewed as important factors.

The daily counts from 1-18 December 1969 present reliable figures on the stock of adults and reflect the events of the population buildup in the last quarter of 1969. They yielded a total of 15,365 birds. The approximate size of the population was about 10 percent of the total count and involved one-third adults and two-thirds chicks and small juveniles. The adult sex ratio was determined from the counts of 182 flocks composed of only males (1,064) and females (1,214). Their ratio was 1:1.14. Also the count of 46 flocks in which males (93) and females (104) were associated with juveniles (1,219) yielded the same sex ratio of adults (1:1.12).

This ratio of 1:1 seemed rather unusual in this population with its common and well-established polygyny. On the average three hens were mated to one cock. In 1964 when adult females were three to four times more numerous than males, none of these exhibited aberrant sexual behavior. If the polygynous bond is a specific trend and establishment, the 1:1 ratio of adult males and females would create an exceptional social situation with a relative excess of males. Thus it is conceivable that the aberrant behavior was caused by a number of stimuli among which the excellent nutrition, an excess of males, and the rapid influx of masses of offspring must have played key roles.

HETEROSEXUAL COURTSHIP AND COPULATION

For an understanding of the displays of the homosexual cocks the homologous performance of the male Ostrich in the normal heterosexual courtship is briefly described as we watched it repeatedly in the wild South African Ostrich.

Early phase of courtship.—This period is normally characterized by occasional outbursts of commotions in all-male flocks in which up to 40 and more cocks, radiant in their nuptial plumage, pursue one another in short dashes, holding their wings high and making snorts, hisses, or "broo" calls. This can be interpreted as a ritualized aggressive behavior

displayed significantly in the vicinity of an assembly of adult females. Its effect is particularly striking as it flares up suddenly, lasts only a few minutes, and ends as abruptly as it began. After this group display the cocks may feed or preen quietly. They usually repeat the display intermittently until they are ready to approach the hens.

This they do in a more or less strutting walk and with sweeping wings. Close to the hen the cock comes to a halt and presents the penial display. The hen may accept or reject the cocks' attentions, and this sequence of performances can be repeated a number of times in a single day. Once a hen accepts a cock, it is commonly the practice of a major hen to reject or permit selectively additional, minor hens to associate with her mate. Once a cock and a major hen have paired off, they drive away any immatures that may have been associated with either one of them (Sauer and Sauer, 1966a; Sauer, 1971).

In summary, the most obvious social activities that control the early courtship and association of mature males and females are the males' group displays, their approach to chosen females, and their wing and penial displays. In some cases the females may play a more active role in pair-formation.

Precopulatory courtship and copulation.—This part of the courtship is commonly initiated by the male. He singles out one of the several hens of his polygynous mating group and, while sweeping and flagging his wings conspicuously, he chases her to a remote area. Here the cock and hen are temporarily secluded from the group. The infrequently monogamous pairs behave similarly.

The birds initiate the ceremony when they feel alone and safe from outside interference. Male and female walk about, quietly and slowly, and both begin to feed in a highly synchronized and increasingly superficial fashion. They keep their heads close together near the ground and make every move and turn in unison. Their lowered wings are held free of the body, slightly curved and pointed downward (o-posture), and moved rhythmically outward and inward. This feeding behavior, which can last for 20 minutes, is more or less symbolic. It is done in a very nervous fashion, very rapidly and superficially, which is characteristic of a ritualized act. As the excitement increases, the two birds walk toward and around a chosen, usually sandy area. Up to here the birds easily interrupt their courtship in the event of a disturbance caused by other animals, man, or even a high-flying plane.

The sandy place is chosen for the symbolic nest-site display. The two birds poke about the sand with their beaks, pull grass, or take up some pebbles or grains of sand, and slink the material aside. From one moment to the next, the male throws his wings up (flagging) and

then beats them down and up in an alternating right and left beat (sweeping) that flashes his white wing feathers. As the hen walks aside, the cock drops to the ground, coming to rest on his heels or plunging right on his belly, and begins wheeling his spread wings. Bending right and left he sweeps the ground successively with his right and left wing in such an exaggerated manner that the dust is whirled high. His tail is fluffed; the legs are kept at rest, that is, the cock does not kick sand as he may do when nesting. All the time he twists his neck in a way that resembles a continuous corkscrew action. Resting on his heels, he swings his neck right and left in phase with the rocking movements of the body and frequently jerks it forward in the moment when it is swung back from its low position on the side of the momentarily lowered wing. (This is different from the movement executed during dusting.) During the backstroke of the neck, the head is tilted downward so the beak tip comes near the throat. During this show, which rarely lasts more than 3 minutes, the cock gives his booming courtship song about once a minute and on the average three times. The song is identical with the territorial singing, mostly a four-syllabled booming with a fair amount of individual variation. Thus the same song pattern serves different purposes, as is common in many species of birds.

While the cock is engaged in his ground display, the hen maintains her symbolic feeding posture and walks slowly in circles either around or close to him, or else in semicircles in front of him. As the speed of her movements decreases to a very slow and measured gait, she suddenly signals her readiness by assuming the typical precopulatory posture: She holds her head low, the neck forming a flat arc, curves the wings out and forward, feathers pointing down, and lets her tail droop.

Upon the hen's intention to squat, the cock terminates his ground display at once. He jumps up and runs toward her while flagging his wings, i.e. holding them very high and still. The hen drops flat to the ground and moves her stretched neck slightly right and left, still pecking and scattering grains of sand. The cock mounts, usually somewhat from the side, and copulation takes place for approximately 35 to 40 seconds. The cock rests his feet in the sand right and left of the hen and maintains his balance by beating his spread wings high.

Dismounting the hen, the cock walks back to his symbolic nest-site; the hen gets up, grabs and drops sand repeatedly with her beak, and assumes again her courtship stance, head low and wings opened to the vertically downward o-posture. It may be indicative of an incomplete copulation or the action of a dominant hen when the cock is thrown

off instead of dismounting the hen. After the uninterrupted performance the cock views the hen from his place in the symbolic nest, then sweeps his wings alternately right and left as he walks forward, and assumes a normal posture with the wings held downward close to the body. Shortly thereafter, about 3 minutes after he dismounts, the female assumes the same posture and both birds slowly walk away. For a short time they graze once more in unison, then one bird falls behind or strays aside and reestablishes the usual social distance maintained during communal feeding. The postcopulatory display is over, and eventually the birds rejoin the other hens as they come in sight. Apart from this pattern one finds individual variations in the courtship that may be due to the birds' varying individual temperament, age, and experience. For example, the ground display can be performed without the rocking movements of the body.

A MEASURE OF THE SEXUAL TENSION IN THE MALE POPULATION

As indicated, unusual activities of both males and females pointed to an uncommonly strong sexual tension that affected the adult Ostrich population. Males participated with great endurance in hiss-snort-and-kick displays and group dances; booming songs were heard day and night; certain cocks showed the aberrant sexual behavior.

The singing, plotted in September 1969 during a watch round the clock, provided a measure of the males' sexual motivation. By comparison the comparable singing of three times as many males in the same district at the onset of the successful reproduction in 1964 was less than one-tenth of what it was when cocks were seen acting homosexually in September 1969. Together with another outburst of reproductive activity in December 1969, the singing went then still beyond the level reached 3 months earlier.

The pattern of the Ostrich song is a distinct, usually four-syllabled phrase, often repeated several times at short intervals. Males can be recognized individually when they adhere to individually distinct variations in the length of the phrases, rhythms, and repetitions. The songs serve at least three different purposes. As a means of territorial defense they alert and repel rival males. In courtship they attract and stimulate the females. Provided he is sexually motivated, a male may give his song to secure his individual social distance from other animals, and also when he is disturbed or afraid, particularly at night. Night-prowling hyenas that came too close to a sleeping male easily triggered his booming song. Other males within hearing distance would then wake and start singing, totally unaware of the real reason of the first male's

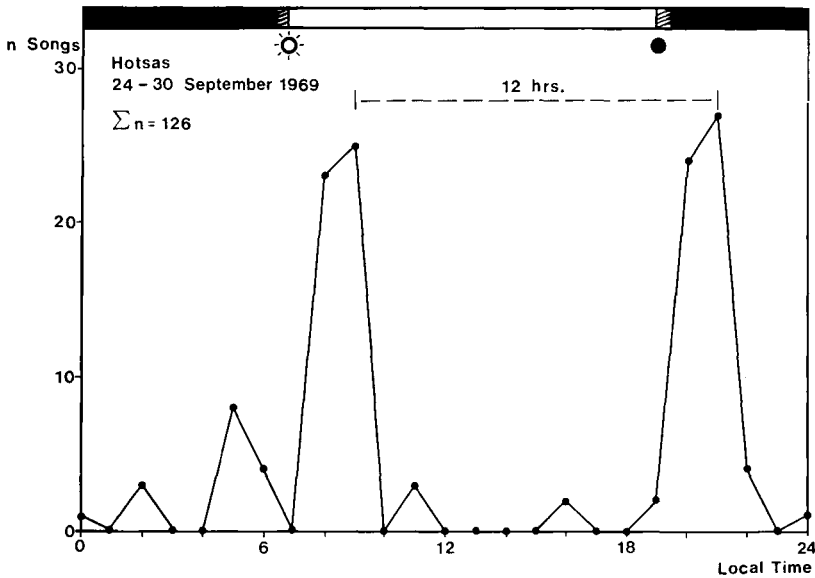


Figure 2. Hourly distribution of the Ostrich songs recorded at Hotsas, 24-30 September 1969. The upper abscissa shows the periods of day, night and twilight, as well as the sunrise and sunset. Further explanations in the text.

outburst. Indeed, the males were more easily roused at night at the onset of reproduction than at other times of the year.

An analysis of the song is to be published elsewhere. It is sufficient to stress that the songs on record (Figure 2) are an expression of the sexual motivation of the males at the beginning of their reproductive cycle. The songs were frequently uttered in response to the distant booming of rival males. The record is limited to the birds heard at Hotsas and does not include the songs of other males of the population that might have sung and spent the nights outside hearing distance beyond the flats surrounding Hotsas. Most likely most of the males that sang were unmated or very briefly mated and still uncertain of their status. Also the homosexual cocks belonged possibly to this segment of the male population. Cocks of old-established mating groups were well placed in their family territories and rarely used their voices.

The number of singing cocks was estimated from the number of individually distinct song patterns and the males' preferences for particular sleeping places. This brought to 16, maximally 20, the number of cocks singing within hearing distance of Hotsas. It was an exceptionally large number of males singing within a radius of 3 to 4

km around Hotsas, which comprised mostly communal property rather than nesting territories and individual courtship grounds. This singing expressed the abnormally strong sexual pressure that affected these birds.

The hourly record of the singing shows a bimodal distribution (Figure 2), which we found to be specific. The daily curve of the Ostriches' singing was alike at other times and at other places in South West Africa. The morning peak came when the birds had left their sleeping places and converged from all directions on the Hotsas water hole where they came into social contact with one another. In contrast, the pronounced evening peak began when the birds had broken away from the diurnal herds and settled for the night. The males found little rest, particularly on moonlit nights, until 21:00 hours. The booming then dropped quickly to the usual base level characteristic of this period, showing the birds' slight and nearly continuous excitement during the night. The cocks' stillness at sunrise seemed accidental judged from the active singing at this time later in the year. Typical is the calm, apart from an occasional song, from about 10:00 to sunset when the birds are predominantly occupied with other activities.

THE FORMS OF HOMOSEXUAL BEHAVIOR

HOMOSEXUAL BEHAVIOR INITIATED BY A MALE

The homosexual behavior of an adult cock directed toward another mature male was subdivided into approach, circling (pirouette dance), and ground display. Each of the three phases was composed of a sequence of motor patterns and could be performed alone or in succession with one or both of the other phases. A fast approach was followed regularly by circling, i.e. a swift pirouette dance on the spot. This might be the end of the show or else the prelude of a full ground display. In other instances, males approached their chosen male partners quite slowly and, at close range, immediately began the ground display. Though other forms of approach and rotation on the spot can appear as elements of other displays, the approach and circling displayed by the homosexuals were always of the same type, typical of the early phase of courtship when Ostriches roam in flocks through their communal area. In contrast, the ground display of the homosexual cocks was identical with their heterosexual precopulatory courtship. In fact, the homosexual males followed the normal pattern very accurately. They even went through the motions of singing and inflated their neck according to the rhythms of their booming songs but never produced a single sound.

All of the cocks engaged in homosexual displays were mature males in full nuptial plumage, and most of them were fully red in the face and on the legs. None of the sexually inactive adult cocks, recognizable by the lack of red pigment, was ever involved in a homosexual display.

APPROACH

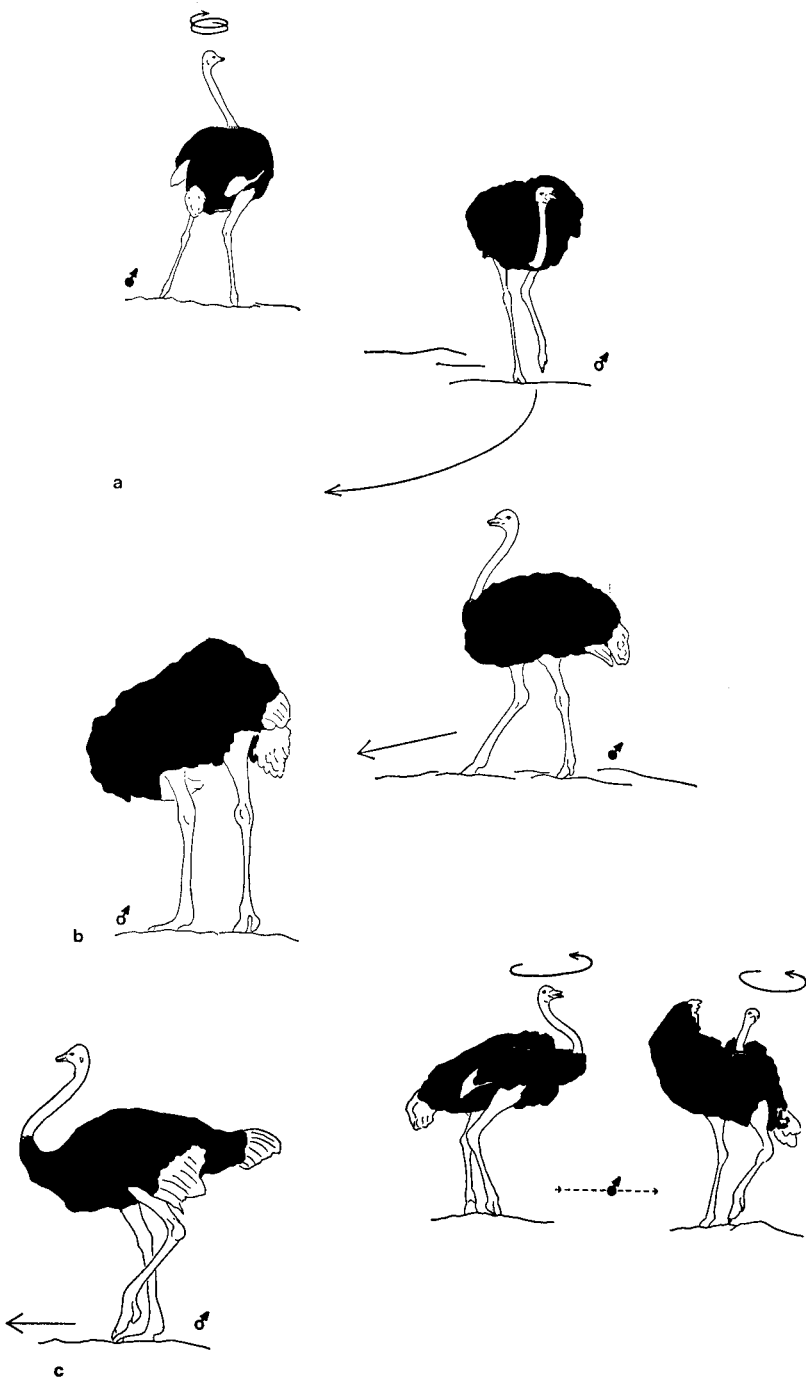
Homosexually inclined males aimed their displays at other mature males and disregarded female Ostriches when these were present. Though a homosexual might single out another adult male even in the center of a mixed flock, his behavior was more commonly directed toward the first and nearest male that came in sight.

Fast approach.—Initiating a fast approach from as far away as 100 m or more, a homosexual male ran toward his chosen partner, quickly increasing his speed to 40 and 50 km/hour. During this dashing and somewhat jerky performance the cock kept his neck a little withdrawn, the head slightly lowered, the wings close to the body, and the tail down (comparable to the posture shown in Figure 3b). Thus, apart from his direct approach, the homosexual male avoided signaling any signs of aggressiveness. Consequently the so-addressed males understood these approaches as being nonaggressive and never responded with fear or hostility. Rather they remained calmly disinterested, inactive, dozing, engaged in preening, or else they stepped aside as if annoyed.

Slow Approach.—When a homosexual male made a slow approach his action was always void of special expressions; therefore it was easily overlooked. The homosexuals came in a relaxed manner typical of the peaceful gatherings of gregarious Ostriches in their communal areas, and only at closest range did they suddenly initiate their display, usually in the form of circling on the spot or rocking on the ground.

CIRCLING

A fast approach was nearly always followed by the high speed circling (pirouette dancing). A homosexual cock approaching at full speed, on an all-out collision course with his unsuspecting or totally surprised partner, would stop his run unbelievably suddenly only a few meters from impact. In the spark of this moment all the energy activated for the powerful and stormy run appeared to be transferred into the energetic and fast whirl of the heavy bird on its long spindly legs. This rotation, not unlike that of a spinning top, might last for one to several minutes without interruption. Then the bird might slow down, even stop for a moment, and gain speed again. Only when the circling slowed down did I become aware of the cocks' driving leg movements and efforts



to balance the motion of the body with the neck, wings, and legs (Figure 3). Through stumbling and improper balance the circling cocks moved sometimes a little right or left, but in general they centered this display on the spot or kept it well within one to two square meters. Circling occurred infrequently after a slow approach.

When a partner seemed annoyed and walked aside, the homosexual stopped his spin as soon as he became aware of the other's departure, approached him anew, and at once continued his pirouette dance (Figure 3c).

Also throughout this stage of the game the birds never acted aggressively. The only visible signs of disturbance revealed by those males that felt bothered by homosexual cocks were their quiet departures. They might briefly assume a subordinate posture (Figure 3a), a momentarily passing gesture, or they showed their annoyance by raising the tail horizontally (Figure 3c). After five to ten leisurely steps, they commonly came to a halt and resumed their previous activity that the homosexual interrupted (Figure 3a, 3b).

GROUND DISPLAY

The normal male that maintained his place in the face of a homosexual cock and disregarded his approach and circling apparently provided the stimulation for the latter to advance to the next phase of his homosexual exhibition. Stopping his pirouette dance conveniently when facing away from his chosen partner, he dropped on his heels (Figure 4) or flat on his belly. Thus is begun the display rocking, in other circumstances typical of a cock's heterosexual precopulatory courtship. The homosexually displaying males rocked steadily from right to left alternately touching the ground with the spread wings. Hereby the cocks moved and twisted the neck in the typical corkscrew action, swinging it right and left in unison with the rocking movements of the body and frequently jerking it forward in its low position on the side of the momentarily lowered wing (Figure 4c). During the backward stroke of the neck the beak is moved toward the throat (comparable

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Figure 3. Three sequences of a homosexual display following a fast approach. (a) High-speed circling; the normal cock (δ) walks aside and (b) resumes preening while being followed slowly by the homosexual male. (c) The latter performs then an elaborate pirouette dance (shown are two phases), rotating once every 1 to 2 seconds for 3 minutes until the normal male departs. (Figures 3-5 drawn from 35mm color film taken by the author.)

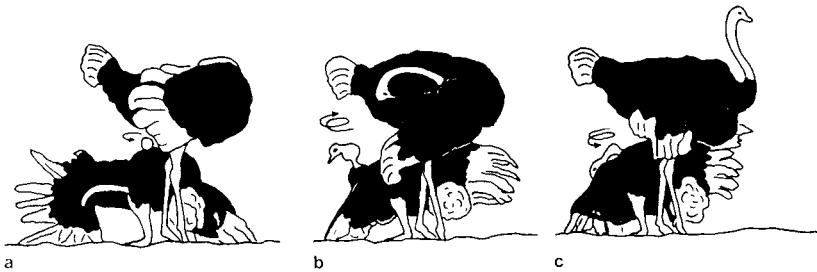


Figure 4. Homosexual male during his rocking display on the ground next to a normal male engaged in preening; (a)–(c) three phases of the same behavior sequence.

with posture shown in Figure 5). The tail is fluffed and oriented slightly downward. During this display the cocks repeatedly, and always silently, went through the motions characteristic of their courtship song by inflating (Figure 4b) and deflating the throat according to the individual rhythm of the specific booming song. None of the homosexual cocks ever uttered a single sound during this performance.

Contrary to the hen's response to her mate's precopulatory rocking on the ground, the male partners of homosexually rocking cocks never gave any relevant reaction but calmly proceeded with their own business, such as preening, or else walked a few steps aside, particularly when this nuisance went on and on (Figures 3, 4).

The homosexual rocking display on the ground lasted up to 10 and 20 minutes in two to three bouts interrupted by a few seconds of rest. Afterwards the homosexual cocks simply got back on their feet and the show was finished. From one moment to the next they turned to preening, feeding, or walked to the waterhole for a drink. Their now calm performance signified that they were relieved of the motivational pressure that caused their exhibition.

Once in a while a sexually aberrant cock arrived so early in the communal area that he was the first and only bird present. After a hurried glance right and left he would then run a few yards with a dashing speed, circle briefly, and drop on the ground for a solitary rocking display (Figure 5). Otherwise a solitary male might slowly approach the communal area and, without any further preliminaries, throw himself onto his heels and begin rocking in a frenzy.

HOMOSEXUAL BEHAVIOR TRIGGERED BY ATTACKING MALES

Agonistic encounters between adult males were sometimes frequent in the communal areas, especially when several hundred sexually motivated



Figure 5. Cock during a solitary rocking display.

birds crowded the water hole. Their exchanges were often restricted to a few mutual threat gestures such as rising into the erect threat posture, advancing a few steps toward another bird, or uttering some hisses, snorts, and boo-calls. At times kicking and short pursuing dashes became more prominent, indicative of the birds' increasing sexual tension. Prolonged chasing was rare.

Normally an attack triggered an escape response by which the confrontation was quickly terminated as the birds were not inclined to foster extended rivalries. Often agonistic behavior was prevented by the birds assuming the subordinate posture. In this efficient appeasement gesture the Ostrich holds its head low, the neck bent in a u-shape, the wings close to the body and lowered, and the tail pointing downward.

When cocks were in full nuptial plumage in 1969, their hostile encounters were occasionally different. A cock being chased by another male might drop to the ground and begin the courtship rocking. This sudden, silent, and lengthy performance of the precopulatory courtship, identical with the behavior described on p. 729, always abruptly halted the attack. The aggressor, towering above the homosexually displaying cock at his feet, seemed frozen on the spot and after a little while, started preening or else walked off. When this male switched to preening, the other bird rocking at his feet waited for a moment when the aggressor's head was hidden behind the wing or body to get up and hurriedly walk away.

FREQUENCY AND TIMING OF THE HOMOSEXUAL DISPLAYS

Male homosexuality as performed in the two functional contexts was a daily event observed in the morning hours during my clock-round watch from 24–30 September 1969. It was not seen at any other time during our studies in 1957, 1958, 1964, 1969, and 1970. The daily rate fluctuated between two to four homosexual cocks that gave displays of

various intensity and duration. The homosexual displays initiated by one male and imposed onto another passive male were usually exhibited in the early morning after 06:00 when the birds arrived in the community center at Hotsas. One exceptionally late display was finished by 10:00. The occasional displays as answers to the attacks by males happened at various times before noon.

The spontaneous shows of homosexuality by cocks arriving in the communal area were given when none or up to 100 cocks and equal numbers of hens were present. Chicks and juveniles were always ignored by the homosexual cocks and seemed not to influence their behavior. Out of the total population of approximately 250 adult males, 1–2 percent behaved homosexually. As the birds were not marked, it remained unknown whether the same individuals were involved day after day. However after one full performance the cocks never attempted another display for the time they were present in the communal area, and they frequently stayed for most of the day.

It appeared that the cocks' sexual drive, possibly built up during the night, dissipated with one full courtship performance. Once accomplished, the birds mingled freely and fully relaxed with other birds. They did not link up with particular females or males nor with any flock of juveniles.

The behaviorally aberrant cocks were not traced to their individual pastures, sleeping places, or territories (if they were at all territorial); whether they were mated remained unknown. Judged from the normal behavior of known mated males that arrived also singly in the community area, while their respective partners stayed on or near the nests, the cocks that initiated homosexual behavior spontaneously upon their arrival in the community center were most probably unmated solitary birds.

DISCUSSION

FORMS AND FUNCTIONS OF THE HOMOSEXUAL BEHAVIOR

General pattern.—The fast and slow approaches are part of the oriented appetitive behavior that brings the homosexually inclined Ostrich into the proper stimulus situation close to another male. Though the former may converge on his chosen partner with a frightening speed, he neither signals hostility nor creates fear. Indeed, his manners are suggestive of those of a subordinate bird (lowered or withdrawn neck, slightly lowered head, wings close to the body, tail down, wobbly run). Particularly the slow approach, apart from being directed at a conspecific male, appears void of social information. The slow approach by itself seems to hide

the bird's homosexual intention, and even the conspicuous fast approach is ignored by the bird being approached. Its calm stance indicates a complete lack of apprehension and a surprising disinterest in the behavior of the odd bird. This is astonishing as Ostriches usually become alert when they approach one another.

Thus the Ostrich males that enter the communal area with homosexuality in mind make no social impression. Their slow and fast approaches remain solo performances. Were it not for the subsequent behavior, little could be said about the meaning of these approaches as Ostriches are drawn to one another frequently for a number of different reasons. And yet, the birds being approached by homosexual males must at least be aware of the others' harmlessness. From a comparative point of view the approach of a homosexual male can be understood as homologous to the singling out and chasing of a chosen hen by which a cock initiates the precopulatory behavior in heterosexual contacts (p. 722).

Circling or pirouette dancing appears to be the result of a high degree of tension and thwarted drives. It is neither easily nor quickly exhausted. In contrast to the socially highly inductive wild play-dancing of immature Ostriches and the group dances of sexually activated mature birds in both all-male and mixed flocks, the pirouette of the homosexual male is also a solo performance. It induces no follow-up in other birds. It is tentatively identified as a high-speed dancing derived from the dances of the early courtship phases within the communal center and then outside of it when the polygynous and, less often, monogamous mating bonds have been formed.

In the mating group the cock may perform courtship dances simultaneously with all his mates and after he has singled out one of them. The essential difference in the play of the homosexual cock is the enormous speed and the lack of any show of threat signals. The homosexual male does not assume an erect body posture during circling and does not lift his wings or his tail. The spinning motion can be explained as the resultant movement of two simultaneously and strongly activated forces, namely advance and withdrawal. Circling is begun when the bird moves below a critical social distance and faces a strange bird rather than his familiar mate. Like the approach, the circling in itself cannot rightly be considered a homosexual performance unless it is understood and seen in the context with the subsequent rocking display.

At this point it is necessary to stress the fact that the homosexual males directed their display toward males of strange flocks. This in itself can account for the high tension underlying their behavior. As if attempting to keep their excitement at a minimum, the birds always aimed their dis-

plays at inactive or relaxed males that were commonly engaged in preening and often had the head momentarily hidden in the plumage or behind the body.

Seen as a preliminary to the ground display, circling could also be envisioned as a high-energy intention movement of the initiation of the stationary ground display whose start is blocked and delayed by the enormous tension and the conflicting drives activating the homosexual bird.

The ground display, as mentioned above, is so identical with the precopulatory ground display of the cocks in their heterosexual courtship that the two behavior sequences are clearly homologous. Differences are found in the preceding activities and in the curious phenomenon that the homosexually rocking cock goes through the exact rhythmic motions of the courtship singing without producing a single sound.

The forms and functions of homosexuality.—As stated, the homosexual display was either initiated by a male arriving in the communal area, or it was elicited through a sudden attack from an aggressive cock. Common to the two situations is the allochthonous performance of the precopulatory rocking display on the ground. It is this part of the show that is compared here.

One functional aspect common to the two situations is obvious: Homosexuality prevents aggressiveness. Courtship and aggression do not exist side by side; the courtship rocking in the agonistic situation is an efficient way of stopping aggression at once.

It seems surprising to find homosexual behavior employed as an efficient appeasement gesture, as it is very rarely available for this purpose, possibly only under exceptional environmental and social conditions. Furthermore these Ostriches can turn off intraspecific aggression either by assuming the subordinate posture or by dashing away from the scene (Sauer and Sauer, 1966a). I therefore conclude that the cock's sexual motivation must be exceptionally strong when he displays homosexually. In fact the drive must have been blocked for some time. Judged from the different durations and compositions of the performances in the two contexts, the lengthy and spontaneous early morning display of the cock trying to initiate a social contact, or else performing into a vacuum when no other bird is present, marks a considerable buildup of sexual tension that presses strongly for a release. In comparison, the relative short response given as a substitute for an escape from an aggressive male may be triggered at a lower level of sexual excitement.

In summary these displays by mature males of the South African Ostrich have two important functions:

(1) Homosexuality relieves the male of high tension when it is strongly motivated sexually.

(2) Homosexuality suppresses or blocks aggressive behavior between males.

Two pieces of information must be added: First, judged from the normal behavior of known mated cocks, the homosexually displaying mature males were most likely unmated birds. Second, at the time of the occurrence of homosexual behavior the sexual tension in the Ostrich population was extremely high. This is interpreted as the result of unusual environmental conditions, and sexuality was at variance with the widely activated incubatory and parental behavior.

The small number of homosexual cocks, out of the total male population, does not mean that homosexuality would be of little significance as a regulatory factor. It does control and stabilize both the individual and gregarious life of these birds under the environmental conditions as indicated. When other rare activities yield a snowball effect in the Ostrich herds, one is quickly inclined to label them important. However, the mere facts that the homosexual displays relieve birds of high motivational pressure and that they thwart aggression make them a socially important phenomenon. They contribute to the maintenance of the social life of the birds in their community centers and, therefore, to the safety of the species.

GENERAL CONSIDERATIONS

The events in the Ostrich population in 1969, in September as well as during December, raised a number of questions. Why was the prevention of a proper release of sexual tension so widespread and lasting? Why did so many sexually active birds, radiant in their full nuptial plumage, perform their various sexual displays consistently in the community center instead of pairing off and leaving to nest? Why did males and females remain engaged in their unceasing hiss-snort-and-kick displays, a kind of "group sex"? Why did hens abort so many eggs in the communal area instead of taking up nesting? Suitable nest sites at proper distances seemed not scarce. Why were so many chicks deserted and driven off at such early stages when they still desired adult guards and showed a strong following response? Was it the sight of the large flocks of chicks and small juveniles that prevented many of the sexually active birds from starting another brood? Were the widespread and mostly communal sexual performances, homosexuality, and vacuum sexuality a natural practice of birth control in the face of a pending overpopulation by a large young generation? Wherever adult birds met young

Ostriches, the latter seemed to stand in the way of the adults and were attacked and driven off. At the same time many birds still incubated and hatched more chicks. When they arrived with their offspring in the communal area, their parental duties were mostly short-lived, and soon they joined the groups of adults and participated in the sexual plays of the group. It is this situation in which the homosexual behavior erupted. The unusual environmental influences that affected the Ostrich population in 1969 are so rare that the phenomenon, most probably, will not be repeated soon and, therefore, will not be available for study again in the near future.

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SUMMARY

Homosexual and other aberrant behavior in males of the wild South African Ostrich is described and compared with the corresponding heterosexual activities. The study was made in 1969 in the Namib desert of South West Africa in the Hotsas water site region. The population of adult Ostriches numbered above 250 males and about equal numbers of females (sex ratio 1:1.14). By the end of the year juveniles populated the flats in excess of 1,000 head.

Exceptional rains in March and April 1969 yielded a rich food supply. This stimulated excessive reproduction, which subsequently led to social stress. Out of the population of some 250 adult males 1-2 percent turned homosexual. These cocks, in full nuptial plumage, displayed male sexual behavior in front of other males. Occasionally they performed into a "vacuum" when no other birds were present. The homosexual cocks were most likely unmated birds.

The homosexual displays, two to four daily from 24-30 September 1969, were enacted within the community center of the population around the water site. They occurred in two functional contexts:

First, cocks displayed spontaneously in the early morning hours when they arrived in the communal area. Their full display was composed of a fast or slow approach, circling (pirouette), and the rocking display on the ground. The chosen male partners never responded sexually but ignored or left the homosexual cocks.

Second, the rocking display was occasionally offered in response to an attack by another cock.

Approach and circling are viewed as borrowed from the early phases of courtship, while the rocking display is homologous with the cock's precopulatory behavior in heterosexual contacts. A full account of the latter is presented.

Homosexuality serves as (1) an outlet of high sexual tension and (2) an efficient way of suppressing aggressive behavior between males. It seems to occur only in unusual circumstances, but may have been caused by a number of stimuli, among which the abundance of food, an excess of males in the face of a specific polygynous mating pattern, and the rapid influx of masses of offspring must have played key roles. An hourly record of the males' booming song shows the sexual tension that affected the Ostrich population.

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