

AGONISTIC AND SEXUAL BEHAVIOR OF THE AFRICAN OSTRICH (*STRUTHIO CAMELUS*)

NIELS BOLWIG

Department of Zoology
University of Ibadan
Nigeria

From early 1967 to the summer of 1969, the author had the opportunity to observe the behavior of a pair of African Ostrich (*Struthio camelus*) and their hand-raised chicks in the Oklahoma City Zoo. Because agonistic behaviors could be observed almost daily throughout the year, and courtship for at least 5 months, and because the author knew of very few accounts of ostrich behavior, it was decided to accumulate as much information from these birds as possible. Sauer and Sauer (In: *The living bird*, Vol. 5, Cornell Univ. Press, Ithaca, 1966, p. 45-76) in their study, mainly from the Namib Desert Game Reserve 3, pointed out that the hens having molted earlier than the males initiate the prenuptial activities. "They will posture and stand very erect, urinate and defecate, and otherwise behave in exaggerated manners in front of potential or familiar mates." They become increasingly aggressive toward birds other than the male they court, and particularly so toward immature birds. The males begin their courtship later, at which time a red coloration of their shins, feet, and faces appears. Their ceremonial rivalries toward one another become increasingly frequent. They may be seen "chasing around in groups, wings held high, and 'dancing' in flocks numbering up to 40 and 50 individuals," or they may "chase females around with their wings held high or waved alternately right and left and the bushy tail held high and bent forward." In his dominant display toward other males, he may stand erect with his tail high and hiss, snort, or utter a boo. If this sign of dominance is respected, the other male holds his tail lower. Sauer and Sauer found that by observing the height at which a cock held its tail they could estimate its social ranking in the flock. At the time that they work up to full sexual display, the cloaca and penis turn bright red. Having reached this level of excitation, the male may urinate and defecate and display its erected penis. On the nesting-ground the males may be heard uttering the "booming" call by which they establish their territories and attract the females. Sauer and Sauer regard this as a "courtship song" which forms "part of the sym-

bolic nest-site display between male and female during their precopulatory courtship."

The courtship is initiated by male and female as they begin to feed, often with heads close together, while pecking in a nervous, highly synchronized fashion. As the excitation mounts, "the two birds walk towards and around an area chosen for the symbolic nest-site display by the male. He throws his wings up in an alternating rhythm of right-left, flashing his white wing feathers. Then suddenly he drops to the ground and begins nesting symbolically in a very exaggerated manner, whirling dust when his wings sweep the ground. At the same time he twists his neck in a way that resembles a continuous 'corkscrew action'." The female responds by walking with lowered head, curved downward pointing wings, and drooping tail. When finally she squats on the ground, the cock gets up and rushes toward her with flapping wings and mounts her.

AIM, SUBJECTS, AND METHOD OF STUDY

In the present study a more detailed analysis of agonistic and courtship displays was attempted than those known to the author. The principal subjects were a couple of birds belonging to, and housed in, the Oklahoma City Zoo. They were housed in an approximately 3-acre pen, together with a herd of giraffe, and were accustomed to be fed by the public. Thus they had no fear of man. Because it was difficult to observe and make notes of all elements of events, a great number of sequences of threat and courtship, successful as well as unsuccessful copulations, and other behaviors were filmed and later on studied in detail. Many of the behaviors described by the Sauers were not observed, undoubtedly because of the unnatural environment in which the birds were kept. Thus, herd behavior could not be studied, although some of the behaviors directed toward adolescent birds in a neighboring pen were strongly reminiscent of their descriptions of the wild birds. Unfortunately, these birds were not permitted to incubate their eggs because their nest site was regularly flooded during torrential rains. The eggs were removed and artificially incubated. A few observations were made on the chicks from the day they were hatched.

RESULTS

AGGRESSION

In April, the hen showed signs of becoming more aggressive. She was often seen wander-

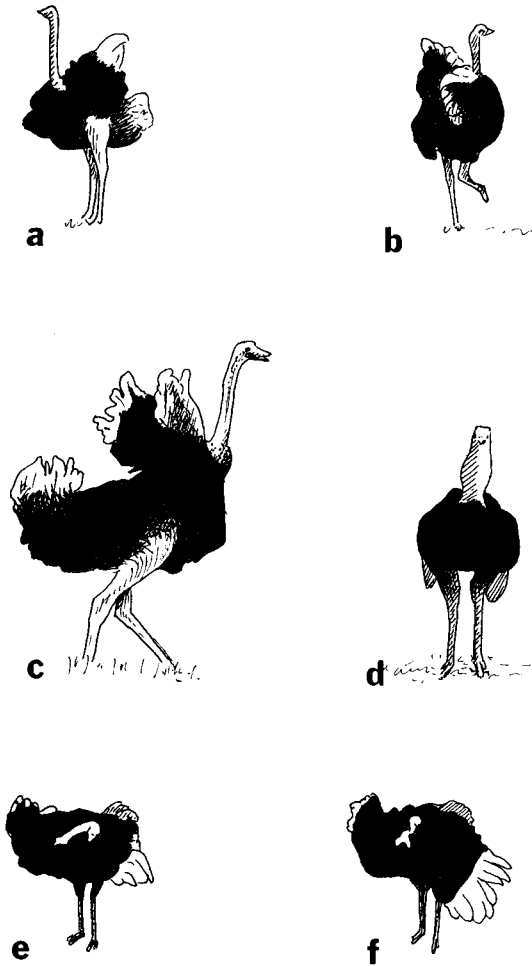


FIGURE 1. The courtship and threat behavior of *Struthio camelus* (male): *a, b* a threatening male waving his wings; *c* an attacking male; *d* a male booming; *e, f* a male in combined threat and courtship display.

ing up and down along the fence behind which the yearlings and adolescent birds were kept. Her head was held high on outstretched neck and her gait tended to be stiff and tense as she approached her adversaries. Close to them, she began to raise alternately her right and left wing. This beating of the wings became stronger as the summer approached. The birds on the other side of the fence seemed to take very little notice of this apparent threat. Either they watched her, and then went on eating, or they walked quietly away.

A similar behavior was displayed somewhat later by the male (figs. 1a, b). It often took on a more violent character and could be directed toward any large animal (including humans), toward the juveniles, and even toward the hen. In the latter case, she might take to her heels, hotly pursued by the wing-flapping cock. Occasionally he would attack

the giraffes, and one instance was observed when a keeper had a narrow escape. When attacking, the cock would storm forward, wings flapping or stretched vertically over his back so that his white plumage formed a spectacular fan over his black-feathered arms and shoulders. His tail was always raised, his neck stretched vertically or even slightly reclined, his chin lifted and his bill open (fig. 1c). After attempting one or two strong forward kicks, he would circle and, if by then his adversary had not retreated, he would repeat the attack.

During the breeding season, the cock became vocal and his booming call was frequently heard. On every occasion observed it was induced by someone suddenly approaching and was directed toward him. If, for example, the observer unexpectedly appeared in the distance and proceeded to walk toward the pen, the cock would approach him, inflate his dark red neck to almost thrice its usual thickness, and utter a series of loud booms (fig. 1d). There has never been any indication that the presence of the female might induce the call and it was never directed toward her. On no occasion did it form part of the courtship as described by Sauer and Sauer. Probably it serves as a warning to competing males or other animals threatening his female or his territorial rights.

RETREAT AND SUBMISSION

Withdrawal was observed among the juveniles as well as among the adults. Usually the threatened bird walked away, head low, neck bent into a U, and tail hanging. Occasionally, when the threat was more vigorous, the inferior bird would flee, hotly pursued by the opponent. On two occasions, when the cock was more than usually aggressive, although not directing his aggression toward any particular individual, the adult female was seen squatting with her neck stretched flat on the ground. This posture was similar to that often adopted by young resting chicks.

COURTSHIP AND MOUNTING

As long as the breeding season lasted, the two birds were usually seen close together, hardly ever losing sight of one another. Frequently, one of the birds, but most often the male, engaged in a stiff prancing walk during which the feet were lifted high off the ground.

Courtship was usually initiated by the two birds standing side by side—the female with wings and tail hanging, while pecking nervously at the ground, probably without swal-



FIGURE 2. Courtship behavior of *Struthio camelus* (male and female): a The ceremonial "feeding" initiating courtship; b,c response of the female to the courting male.

lowing anything (fig. 2a). Urination such as described by Sauer and Sauer was noticed only occasionally.

The next stage was marked by the male going down on his heels while craning his neck backward over his shoulders. Thus squatting, he proceeded to swing his neck from side to side causing a backward jerk of the head each time it reached the extreme right or left position. With each swing, the wing on the side toward which the head moved was lowered to the ground while the other one was raised high (fig. 3a, b). This display could last as long as 5 min or more.

If the hen was remotely interested in the male's performance, she would spread her drooping wings forward, holding them as a vertical shield, anterior edge pointing downward. The pecking and snapping continued but, although directed toward the ground, the bill frequently did not achieve contact (fig. 2b, c). The extent to which the wings were brought forward appeared to be an indication of the hen's preparedness to receive the cock. An extreme forward position seemed to be the signal for him to get up and storm toward her with lifted wings as when attacking. There were, however, noticeable differences. The wing-erection was never interrupted by alternating beats as could happen, and usually did happen, during an attack. Both wings were held stiffly over his shoulders and could often be seen quivering, probably as an expression of his exaltation. Moreover, the bill was not raised but pointed downward and engaged in snapping and swallowing movements (fig. 3c). This difference became clear if the author disturbed his approach to the hen, causing him to change from courting to attack. The film shows him lifting his chin as he advances toward the camera with beak open.

The swift approach of the cock was invariably a signal to the hen to sit. Reaching her, he would place a foot on each side of her body, crane his neck slightly backward, and while

still snapping he would press his chin down against his now quivering throat (fig. 3d). Standing thus, he lowered himself chest first and came to rest on top of her. In this position he resumed his former rocking display, swinging his neck from side to side over his shoulders while attempting cloacal contact and intromission. During this performance, the female remained in her former position, head held high, looking unconcerned (fig. 3e).

Intromission was marked by the hen lowering head to the ground while swinging her almost outstretched neck from side to side, virtually in a semicircle. While doing this, she pecked the ground, taking up small amounts of sand and letting them fall again. This resulted in a semicircle of small pits being formed in the dust.

The cock's behavior also changed during intromission. He bent his neck forward, still swinging it from side to side but now with half its former speed and while doing so he poked his bill alternately under the hen's right and left clavicular region. The spread wings which had stopped beating were held horizontally and quivered vigorously in a vertical plane (fig. 3f). The intromission usually lasted for about 40 sec.

After intromission, the hen would rise to her feet, thereby throwing off the cock, and the two birds would part. During the peak of the breeding season, it would be about 50–55 min before the next mounting could take place. Successful mounts with intromission were observed only within two very limited areas where the birds also liked to dig their nests. These areas were low-lying and close to the fence where the excited public easily disturbed them. Exact records of the proportion of successful and unsuccessful intromissions were therefore not kept most of the time. During the time notes were taken, intromission was achieved in only 25–30% of the cases. Unsuccessful intromission did not appear to shorten the courting cycle.

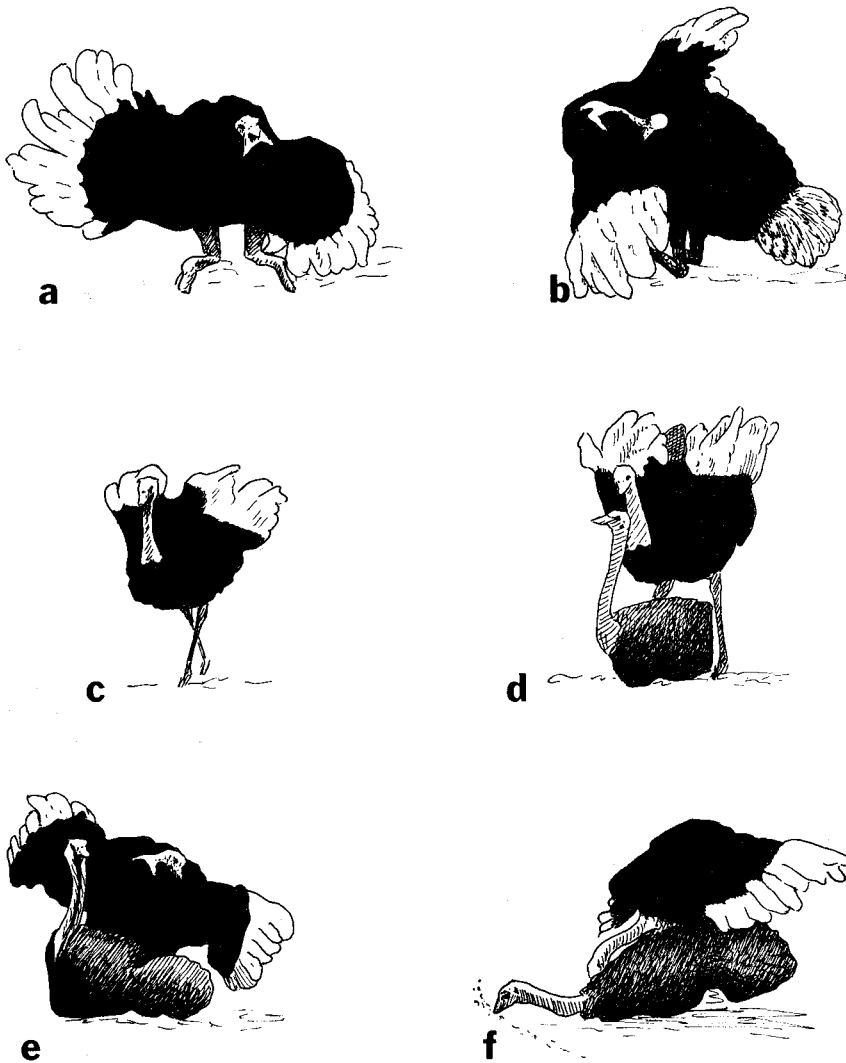


FIGURE 3. Copulation in *Struthio camelus*: *a, b* a male in courtship display; *c* the approach of the male to the female prior to mounting; *d* the male mounting the female; *e* the rocking male seeks cloacal contact; *f* achievement of intromission by the male.

NEST-BUILDING

Nest-building was observed a couple of times and was distinctly different from sand-bathing. During the latter activity, the bird was merely sitting rubbing its body and neck into the sand, while beating the dust with its wings. On both occasions it was the cock who dug the nest bowl. He did this by resting his chest on the ground and kicking the sand backward with his feet (fig. 4a, b). He then proceeded to peck sand up with his bill and to throw it away from him. While doing so, he moved his head from side to side, describing a semicircle. The action was reminiscent of that performed by the copulating hen, but differed by virtue of its greater vigor and was performed with a fully outstretched neck (fig. 4c, d). As during copulation, the result was a

semicircular row of small pits in the sand. After a couple of minutes, he got to his feet and walked away.

Most eggs were laid in the nest bowls, but a considerable number were also dropped at other places. All eggs were collected and artificially incubated.

THE CHICKS

The chicks were tested for the following response the day they were hatched. Although too weak to take more than a few steps at a time, they made clear attempts to be close to and to follow any object, such as a towel, that was dangled overhead. Later on they followed one another and could usually be seen as a small flock that rarely strayed far away from their keeper. When resting, they were often

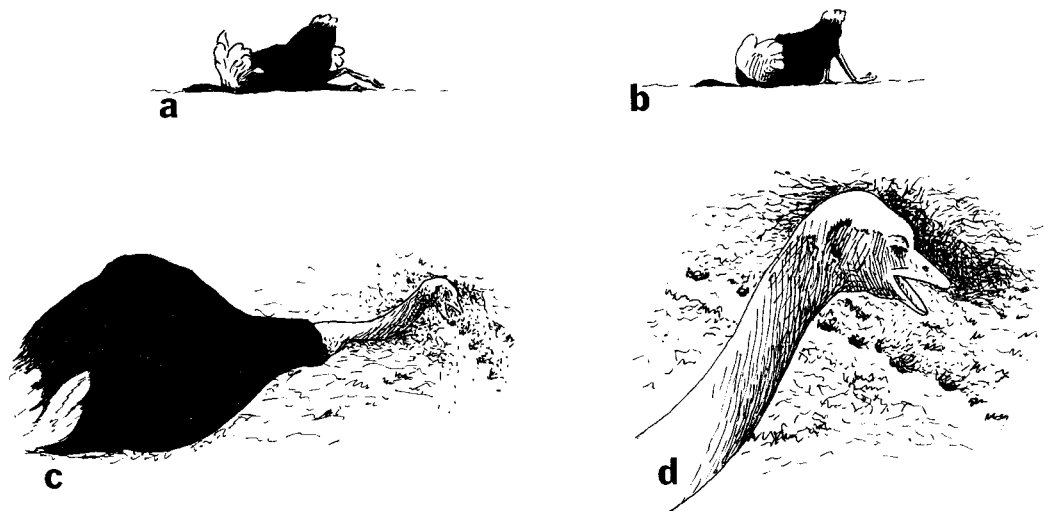


FIGURE 4. Nest building of *Struthio camelus* (male): a,b digging with the feet; c,d pecking the ground.

seen lying with their necks stretched flat in the sand.

DISCUSSION

These observations on the aggressive behavior of the ostrich in the Oklahoma City Zoo largely support those made on wild birds in the Namib Reserve by Sauer and Sauer (1966). The alternating flapping of the wings is a frequently displayed form for threat and it increases in strength with the motivation to attack. What is puzzling, however, is the frequency with which, during the breeding season, the cock displayed the squatting, neck-swinging, wing-beating behavior toward visitors in the Zoo—the same ceremony as he displayed when courting his female. At one stage the author regarded it as a threat rather than courtship. This assumption was supported by observations of intermediate stages of behavior ranging from wing-flapping alone, through a behavior where the standing cock added neck-swinging to the wing-lashing, and finally to the full squatting ceremony. It seems therefore reasonable to assume that the activity of the lashing wings, even when it occurs in the squatting display, is an expression of aggression. The neck-swinging, however, was never observed except during the breeding season. When performing this ceremony, the male always gave the impression of being in a state of ecstasy, becoming more or less oblivious to the presence of humans or other animals. Moreover, it always preceded mating. The whole performance should therefore be regarded rather as an imposing display which naturally includes elements of aggression. Undoubtedly it serves to warn off other males

while at the same time it impresses the receptive females. The reason for the cock's display toward humans could be, and probably is, that these birds have grown up in close contact with humans and do not distinguish clearly between humans and members of their own species.

The next step in which the male rushes toward the inviting female with raised wings seems very similar to that of an attack although his chin is held lower, but the snapping movements are very similar. The squatting of the female may, in addition to its primary function as an invitation to mount, also serve to appease his aggression. On two occasions when the cock was particularly aggressive, the female was seen to get down and squat with her stretched neck resting flat on the ground. This is exactly the posture adopted by young resting chicks. In other words, the squatting could be regarded as an infantile appeaser. Whether this suggestion is the right one is difficult to say. Attempts by the author to throw himself flat on the ground outside the fence when the cock tried to attack him gave no clear indication. For obvious reasons, no experiments of this kind were carried out inside the enclosure. Why the female pecks the ground during coitus and why the male does about the same after working on the nest is inexplicable to the author. Nibbling at the ground during the early stages of courtship when tension begins to build up should probably be regarded as ritualized displacement feeding.

Attempts were made to produce an objective graphic illustration of the birds' excitement based on exact recordings. This, however, was

abandoned for lack of clear criteria. There appears to be a steady buildup of tension in the hen until she squats and the cock mounts. At this time she has reached a plateau. A further rise of excitation to a peak is only achieved if intromission is successful. In the male a similar rise in excitation, but with two plateaus, seems to occur. The first plateau is reached when he goes down on his heels and rocks, and there will be no further rise unless the hen indicates she is prepared to receive him. If the signal is given, there seems to be a new sharp rise while he rushes forward to mount her. This brings him to a second plateau, and from now on the behavior of the two birds becomes highly synchronized. As in the case of the hen, his excitation reaches a sudden peak during intromission. After ejaculation, an abrupt drop is noticed. The two birds separate and part, and a new cycle commences. During the peak of the breeding period, each cycle may be 50–55 min.

Urination by the cock as an invitation to courtship was a less constant feature in these ostriches than seemed to be the case among Sauer's and Sauer's wild birds.

Sauer and Sauer mention that at the time the ostrich cock works up to full sexual display his cloaca and penis turn bright red. The whole rump of the Oklahoma cock turned deep red during the breeding season, but his penis became visible only on very rare occasions and was never displayed as an attractant during the courtship. The few times the penis became visible was when he urinated before the courtship, irrespective of the near presence of the hen.

The suggestion made by Sauer and Sauer that the male's booming call was a part of the courtship seems to be ruled out by the present observations. It is, however, understandable that they should arrive at such a conclusion when from a distance they saw a male stalking first in one direction then in another while uttering his warnings toward distant males which might challenge him. The call of the Oklahoma ostrich was always considered as

directed toward an individual approaching his breeding ground and was beyond doubt used as a warning to a potential intruder.

It is unfortunate that the author never succeeded in establishing to which subspecies the Oklahoma birds belong. The few discrepancies noticed between the behavior of these birds and those observed by Sauer and Sauer may be due to genetic factors or as a result of the Oklahoma birds being reared in captivity. The lack of a penis display in the courtship of the latter may suggest a genetic difference.

SUMMARY

Aggressive behavior and courtship are the principal topics discussed in this paper and an attempt is made to explain some of the features. Flapping of the wings is regarded as a threat and seems to be incorporated into the cock's courtship both during its squatting and rocking phase and during the pre-coital phase after mounting. The manner in which the cock storms with raised wings toward the hen when she invites him to mount is almost identical to that seen in an all-out attack. The female's squatting appears to act as an infantile appeaser to the male. Pecking of the ground as seen during the early stages of courtship is regarded as displacement feeding which has become ritualized. No explanation can be offered for the curious pecking of the ground by the female during coitus or by the male after digging the nest bowl. In both cases the pecking is performed while the bird rests on the ground swinging its horizontally extended neck in a semicircle from side to side.

A penis display such as that described by Sauer and Sauer was never seen. The booming call of the male was never observed to be part of the courtship, but it was used for warning off intruders from the breeding ground.

The subspecies to which the Oklahoma birds belonged was not established, but it suggested that they were genetically different from those observed by Sauer and Sauer.

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