

FURTHER ANALYSIS OF THE SOCIAL BEHAVIOR OF THE
BLACK-CROWNED NIGHT HERON¹

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In a previous study of the social behavior of the Black-crowned Night Heron (*Nycticorax nycticorax hoactli*) two males were found to court for long periods in the presence of unmated females without securing mates. Both of these birds had damaged crowns and plumes and it was inferred that the failure of these birds to secure mates was due to either the one or the other of these defects (Noble, Wurm and Schmidt, 1938). Which factor, if either, was responsible for the failure to breed was of considerable theoretical interest because Lorenz (1937) considers the plumes an "organ of a peace-making ceremony without any sexual meaning." In brief, "it is there strictly as an organ developed in the evolution of the species to control the normal repelling reaction by releasing a greeting reaction which supersedes it" (Lorenz, 1938). In this previous study Noble, Wurm and Schmidt (1938) presented evidence why this conclusion could not be accepted, but they did not have adequate material to determine by experimental procedure whether the plumes, crown, or both were indispensable for breeding.

During the past two years we have had a colony of Black-crowned Night Herons breeding both in outdoor cages and in one of the live-bird rooms of the Museum where our previous studies were conducted. For the use of the latter we are indebted to Dr. Frank M. Chapman. We have attempted by experimental procedure to determine the function of the plumes in the social behavior of the species. The Black-crowned Night Heron develops a rosy tinge to its legs during the breeding season. We have tried to determine by artificially coloring the legs if this color is indispensable to its breeding behavior. Lastly, the rôle of 'releasers' in the feeding behavior of the species was not well understood and we have devised experiments to reveal more clearly the factors involved. The present paper, in brief, supplements our previous study by analyzing the function of the plumes and nuptial leg color of the adults as well as determining the behavior patterns controlling the feeding reactions of the young.

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COMPARISON OF BREEDING BEHAVIOR OF AMERICAN AND EUROPEAN RACES

Unfortunately at the time our previous study was published, Lorenz's 1938 paper on the social behavior of the European race of night herons was not available to us. We were therefore unable to compare in detail our observations on the American form with those made on the European race. Jourdain and Tucker in volume 3 of 'The Handbook of British Birds' (1939), commenting on the breeding behavior of these two forms, state: "Allowing for differences of interpretation, conclusion that a real difference exists in behaviour of the two races seems irresistible." The differences in behavior, however, which these authors stress, seem to us to be chiefly a matter of terminology. Thus, Lorenz (1938) describes well the 'snap-hiss ceremony' of the American form: "With head and wings lowered, he executes a queer sort of courting dance on the spot of the future nest, treading from one foot to the other with a peculiar weaving action. From time to time he suddenly lowers his head and neck vertically, while his shoulders lift as if in a hiccup, and he utters his courting cry. This cry is very deep and quite low, sounding like steam escaping through the safety-valve of a boiler."

Further, Lorenz's 'appeasement ceremony' of the European race, we have identified in our American form as an 'overture and display.' This terminology is preferable to that given by Lorenz because the ceremony is merely the dominance-subordination gestures of young birds to which, in the adult, have been added: (1) a change of voice with concomitant modification of the call; (2) an erection of the plumes, crown-, neck- and chest-feathers; (3) a narrowing of the pupil and protrusion of the eyeball, frequently accompanied by a gaping. The modified 'recognition call' is apparently sexually stimulating to the birds when given with the display and the repeated gesturing, which take place throughout courtship and most of incubation, and serves to form a bond which will hold the pair together.

Lorenz (1938) did not state how he was able to determine the sex of his birds, but concludes: "As it is generally the approaching bird who thus 'greet' first, it is the female who at first seems more intent on this ceremonial, the male answering rather perfunctorily, but soon afterwards it is the other way round. . . . It is always the bird approaching the nest which is most anxious to appease the one that is standing in it. . . ."

We find by a direct examination of the gonads of our colony of the American race that it is the resident male that initiates the ceremony during pair formation to which the female may not even answer.

Later, after the male has become sexually dominant, the female may indicate her subservient attitude by overturing first. The question as to which bird overtures first is important in defining the dominance relation. Lorenz made no attempt to describe this dominance relation in the European race but his description of the pair "getting slowly acquainted" suggests that this race also must work out the same dominance relation as the American form before members of a pair can remain together in a nest territory.

Our evidence for considering the adjustment period an attempt of the male to secure sexual dominance has been fully stated in the earlier paper. Our observations of the last two years merely confirm our earlier conclusions. Details of the behavior of courting European Night Herons during this adjustment period, when sexual dominance is secured, have not been published. At the present moment there is no reason for assuming that the social behavior of the two forms of night heron actually differs in any particular.

EXPERIMENTS ON FUNCTIONAL SIGNIFICANCE OF PLUMES AND BLACK CROWN

In 1940, we bred a pair of Black-crowned Night Herons still in the full juvenal dress. These birds, without plumes and with the brown plumage of the immature, laid fertile eggs and hatched young in an outdoor flying cage. A second pair of plumeless herons still in the juvenal dress built a nest together and laid eggs but these did not hatch.

As reported elsewhere (Noble and Wurm, 1940), we were also able to induce chicks only 39 days old to form a pair by injecting them with testosterone propionate. The authors are indebted to Dr. R. MacBrayer of the Ciba Pharmaceutical Products, Inc., for the testosterone propionate (Perandren-Ciba). It is therefore clear that neither plumes nor a black crown are indispensable for pair formation or breeding of this species. Further, an adult female (no. 1241), when exposed to the snap-hiss ceremony of two adult males both of which had the dark crown-feathers cut away, selected the one which also lacked plumes. From such observations and experiments as these it seemed, at first, that the plumes were of no functional significance in the life of the bird. Further observations and experiments revealed, however, an important difference between the behavior of all our birds that lacked plumes and those which had them. A mate of a plumeless heron fails to synchronize its courtship with that of its partner as well as do the controls. When a heron without plumes overtures and displays while stepping toward its mate, the latter will

display nearly as frequently as the controls. But if two mates are standing together and the plumeless bird overtures and displays, this will usually bring little response from its mate. Apparently the plumes emphasize the display, make it more stimulating when given at close range. The result is that pairs containing one plumeless bird are very unstable and tend to break up before egg laying occurs. Detailed observations make it clear that the plumes, instead of being an appeasing organ, as Lorenz assumed, actually form an instrument for enhancing the effect of the display. The repeated display of courtship is not repeated appeasement but a very essential performance for maintaining a bond between the pair.

The plumes appear with considerable irregularity in Black-crowned Night Herons breeding for the first time. In several of our birds they attained a length of from two to three inches at this time. In 1940, we had a flock of 36 herons which we had reared from chicks in the laboratory. When approximately a year old they began to breed in an outdoor flying cage which measured 14 feet by 12 feet by 12 feet. None of these birds had developed plumes. Nevertheless many of them courted and built nests. Male no. 1331 bred with female no. 144 and successfully reared four chicks. Nevertheless the birds stood much more apart than did plumed adults and we did not record a single case of mutual display from the birds when standing together. Female no. 43 was paired first with male no. 1332 and then with an unbanded male, indicating that the bond which held it to the first male was not very strong. It might be argued that this failure to synchronize the display when standing close was merely due to the immaturity of these birds. We therefore devised a series of experiments with adults.

A flock of nineteen night herons in fully adult plumage was maintained in the same indoor flying cage utilized in our 1938 description of normal behavior. This had a floor space of 442 square feet with perches and old nests ranging from three to fifteen feet from the floor. The group consisted of twelve males and seven females which had been sexed by a direct examination of the gonads.

In five males (nos. 203, 241, 1214, 1221 and 1233) the plumes were removed and all the black feathers were plucked from the crown, leaving only a downy covering of short white feathers. In three other males (nos. 1314, 1242, and 242) the plumes were removed but the crown was left intact. In three males (nos. 42, 223, 1313) the plumes were left intact and the crown was plucked. The last male (no. 322) was maintained with the others although plumes and crown were intact. In four females (nos. 1234, 124, 1244 and 1243) both plumes

and black crown were plucked. Another female (no. 1224) had only the plumes removed, while another (no. 1241) had the black crown-feathers, but not the plumes, destroyed. Another female (no. 1321) was maintained with the others although both crown and plumes were left intact.

Our observations on the courtship of these birds have been summarized in tables 1 and 2. We have omitted reference to the twig and snap-hiss ceremonies and have included only the cases of 'overture and display,' for it is only during this ceremony that the plumes are normally erected. The numerical data include only the overtures and displays initiated by the male. For the sake of brevity we designate an overture and display given while the male steps toward his mate as an 'approach courtship,' while a similar overture and display given while both birds are standing near each other and not preceded by any overt movement, we list in the table as a 'close courtship.'

In table 1, we have recorded 223 instances in which plumeless males

TABLE 1
EFFECTIVENESS OF COURTSHIP INITIATED BY PLUMELESS MALES

Bird	Expt'l	Male Courtship				Remarks
		Answered		Not answered		
		cl.	ap.	cl.	ap.	
♂ 241	-p bh	0	5	8	3	The approach courtships answered only after the female became active in initiating courtships.
♂ 1233	-p bh	1	1	4	5	
♂ 203	-p bh	0	9	0	4	
♂ 1214	--p bh	1	5	22	25	Never paired; no data.
♂ 1221	-p bh	1	16	16	38	
♂ 1313	-p bh	1	6	8	25	
♂ 1314	-p n	1	1	5	8	
♂ 1242	-p n	0	0	3	1	
♂ 242	-p n	0	0	0	0	
		5	43	66	109	

Mean per cent 'close' courtship answered 8.3 ± 2.7

Mean per cent 'approach' courtship answered 27.9 ± 2.8

cl. = 'close' courtship.

ap. = 'approach' courtship.

-p bh = plumes plucked and crown plucked.

-p n = plumes plucked and crown normal.

were observed to initiate the courtship ceremony. These consisted of 71 'close' and 152 'approach' courtships. In 92 per cent of the close courtships, it was observed that the female mate did not respond with either overture or display to the courting male. There were, however, five exceptions, or 8 per cent of the cases, in which a courting plumeless male succeeded in evoking a similar reaction from the mate.

As a control, we have observed four birds with intact plumes (Table 2, Part A). Three of these animals also suffered plucking of the entire black area of the crown. Although only fourteen 'close' courtships were observed, twelve of these, or 86 per cent, were cases in which a male could stimulate its mate to court without approaching from a distance. There were, however, two exceptional cases in which the female did not react to the close courtship of the male even though the latter possessed normal plumes.

Another type of control involved repluming males that had previously been observed while deplumed. The difficulty of this procedure is that artificial plumes cannot be erected and any display of these structures is purely accidental, occurring during movements in which the head is lowered. Furthermore, these plumes become distorted or are lost in a few days. The results (Table 2, Part B) of these attempts can therefore be considered as only suggestive.

4 'close' + 9 'approach' answered; 5 'close' + 2 'approach' not answered.

The same birds while deplumed showed (Table 1):

2 'close' + 2 'approach' answered; 12 'close' + 14 'approach' not answered.

Male no. 1313, which was first observed after (a) the black crown was plucked and normal plumes left intact and then (b) when the plumes were also removed, gave the following results:

(a) 4 'close' + 21 'approach' answered; 1 'close' + 0 'approach' not answered.

(b) 1 'close' + 6 'approach' answered; 8 'close' + 25 'approach' not answered.

From Table 1 it may be concluded that the failure of the female to answer the male's courtship is due to the absence of plumes and not the plucked crown. Males nos. 1314 and 1242, from which only the plumes were removed, showed the same type of behavior as the other males in which both plumes and crown were plucked. Similarly, Table 2, Part A, shows that males nos. 223, 42 and 1313 were usually successful in stimulating their mates to courtship even

TABLE 2
EFFECTIVENESS OF COURTSHIP INITIATED BY PLUMED MALES

Bird	Expt'l	Male Courtship				Remarks
		Answered		Not answered		
<i>Part A—Control</i>						
♂ 223	n bh	cl.	ap.	cl.	ap.	
♂ 42	n bh	2	0	1	0	
♂ 1313	n bh	3	1	0	0	
♂ 1313	n bh	4	21	1	0	
♂ 322	n n	3	3	0	1	
		12	25	2	1	
Mean per cent 'close' courtship answered		86.5 ± 7.1				
Mean per cent 'approach' courtship answered		91.6 ± 5.9				
<i>Part B—Replumed</i>						
♂ 1233	+p bh	3	0	0	0	Plumes artificially replaced.
♂ 1314	+p n	1	9	1	2	Plumes artificially replaced.
♂ 1242	+p n	0	0	4	0	Plumes artificially replaced; distorted soon after bird was released.
		4	9	5	2	

cl. = 'close' courtship.

ap. = 'approach' courtship.

n bh = plumes normal and crown plucked.

n n = plumes normal and crown normal.

+p bh = plumes replaced and crown plucked.

+p n = plumes replaced and crown normal.

though the black crowns alone were damaged. Furthermore, the results of damaging the crown are comparable with those of the completely normal male no. 322.

Although removing the plumes seems to affect chiefly the synchronization of display of two mates when standing together, the absence of plumes also cuts down the effect of a display given while a bird is in motion. In a total of 152 'approach' courtships, 72 per cent of the ceremonies initiated by the plumeless male were not answered by the female (Table 1). Data from control observations (Table 2, Part A), in which the males possessed normal plumes, show that only 8 per cent of the 'approach' ceremonies were not answered.

Our quantitative data, although not extensive, seem to demonstrate that the plumes of the male night heron increase the bird's chance of calling forth a display from his mate following his own performance. Similar experiments with the females' plumes were not as

clear-cut because our number of cases of female courting prior to the male is too small to reveal significant differences. Records of the courtship activity of deplumed female no. 1234 showed that after 29 approaches by the female, male no. 241 was stimulated to courtship only three times. The same female when paired with another male also failed on occasion to stimulate the mate, as indicated by the following observation records:

June 16.—Female 1234 joins male 203 which approaches, courting with eyes bulging, breast-feathers fanned, cheeks puffed and overtures. Female 1234 responds with complete overture and display. Birds stand together on U.N.E.N. and bill. Male 203 walks out of nest; female 1234 courts; male 203 walks back into nest without answering and attempts to mount female 1234, which draws to one side and overtures. Male 203 again circles female 1234, mounts, successfully copulates and dismounts; no voice employed.

June 27.—Female 1234 approaches male 203 on U.N.E. rung, courting with bulging eyes, breast-feathers fanning and overtures. Male 203 shows no response.

On the other hand, female no. 1234, while initiating the courtship on other occasions, has also been observed to be readily able to induce male no. 203 to court. In every contact between this female and still another male, no. 1214, the latter bird was always observed to react with intense and exaggerated courtship. It appears therefore that, in spite of the absence of plumes in a female, birds of this sex may readily induce a male to respond to their overture and display. Apparently the higher level of androgen in the male sex makes it a more responsive subject to any courtship movements whether or not they are enhanced by plumes. In a previous study (Noble and Wurm, 1940) we found herons treated with male hormone readily display even when confined in small individual cages. Here they were responding merely to some disturbance beyond their cages, sometimes even to the approach of the observer.

Observations of the above plumeless adult birds have revealed additional unique effects of depluming. A frequent observation, typical of every pair, was that the female perched outside of, and at some distance from the nest. A detailed observation of particular pairs revealed that it was the lack of a stimulating performance that prevented their standing together.

June 2.—Male 1221 on nest comes up on rung and courts completely. Female 1241 fails to respond and jumps down to nest. Male 1221 comes down to nest and again courts. Female 1241 again does not answer and walks out of nest on left diagonal bar.

June 5.—Female 1234, mate of male 241, is perched on upper rung above C nest. Female 1234 spends much time away from male 241 and is usually perched on window sill or rung. When disturbance occurs, female 1234 joins mate, issuing loud high-pitched guttural voice, and is always answered by male 241, standing on M.N.W.N. rung.

June 6.—Male 241 lifts leg to back of female 1234 and issues low-pitched, guttural voice, breast-feathers fanned, eyes bulging, while bird overtures. Female 1234 responds with high-pitched guttural voice and immediately flies down to window sill.

June 14.—As male 1214 snap-hisses, female 1234 looks up from floor, flies to window sill. Male 1214 snap-hisses again and again; female 1234 finally flies back to nest rung. Male 1214 courts but female 1234 shows no response.

June 15.—Male 1214 courts female 1234 which shows no response; overtures and displays again, crowding female 1234, who flies down to window sill.

These males, nos. 1221, 1214 and 241, were without plumes during the above observations; female no. 1234 also had none, while female no. 1241 possessed them. The females showed a marked tendency to desert their mates, especially when the latter courted at close range. This behavior stood in contrast to that of females with plumed controls. These tended to retain their positions (Noble, Wurm and Schmidt, 1938, Plate 4).

Normally a pair forms when the female is attracted to a snap-hissing male. During the early stages of courtship this bond is strengthened by 'approach' and later by 'close' courtships. Since depluming weakens the stimulating effect of the display, it would be expected that deplumed pairs would not remain together and the above observations confirm this assumption. Normally only an unmated, sexually active male is observed to produce the snap-hiss. This call ceases soon after a female enters a male's territory and can be made to reappear by removing the female from the cage. We have found that although deplumed herons may actually pair, that is, occupy a common area, show no aggression toward each other, overture and display to one another, the male frequently continues to snap-hiss for a long time after the female arrives. This again is evidence that the lack of plumes has produced some deficiency in the behavior of the female to which the male responds by continuing his snap-hiss ceremony.

The presence of eggs in the nest may be considered a factor which tends to counteract the deficiency and to keep the pair together until

the young have been raised. For example, it was observed that female no. 1234 had successively paired with and had copulated with males nos. 241, 1214, 203 and 1221. All these males had been without plumes and it might be expected that this female would eventually desert male no. 1221 as she had deserted the other males. However, it was found that this pair continued to remain together after the eggs were laid. The presence of eggs in the nest seemed, in brief, the chief factor holding the pair together. This was also shown by the behavior of female no. 1241, male no. 1221 and male no. 1313, which may be given in some detail.

Pair formation first occurred between the female and male no. 1221, although both males had been snap-hissing and evidencing sexual stimulation for some time. It was at once clear that the presence or absence of plumes was not essential for pair formation to take place, because male no. 1221 had neither plumes nor crown, while male no. 1313, the rejected suitor, had at this time normal plumes although a plucked crown. After pair formation, 'close' courtships never resulted in synchronous behavior in the pair, male no. 1221 and female no. 1241. The female perched on the rung above the nest away from the male or completely outside the nesting area. At this time the female began to respond to the snap-hissing of male no. 1313. Copulation and mutual 'close' courtships were then observed in this pair. Male no. 1313 was then deplumed. It was at once observed that the female now failed to respond to 'close' courtships of the male. She soon deserted the area and perched away from the nest. The male now began to snap-hiss even when standing close to the female. The female alternated between the center nest, that of male no. 1313, and the upper southwest nest, that of male no. 1221. Her vacillating between these two males seemed due to the attraction of snap-hissing of one male and the repulsion of the 'close' courtship of the other. Eggs were first laid in the nest of male no. 1313 and the female was now observed to remain usually in this nest area, while the male spent most of the time incubating during the day. However, the female would make occasional excursions to the nest of male no. 1221, loosen twigs from the platform and carry them to the incubating male of the other nest. During these contacts with male no. 1221, there occurred overtures with very little display. After the third egg was deposited in the center nest six days later, the clutch was transferred to the upper southwest nest, that of male no. 1221. During the remainder of that day, the female stood beside male no. 1313 while the latter brooded an empty nest. During the two succeeding days female no. 1241 trans-

ferred her interest to male no. 1221. Another egg was added by the experimenter to the clutch and both male no. 1221 and female no. 1241 began to take turns at incubation.

It should be emphasized that these birds were breeding in the same room that they occupied during our previous (1938) study. At that time there had been no shifts of mates and very few failures to respond to the 'close' courtships of mates. The conclusion seemed obvious that the depluming had seriously interfered with the constancy of the nuptial bonds formed by our experimental birds.

MALE BEHAVIOR BY THE ADULT FEMALE

Although the overture and display of the night heron are mutual, they are not identical in the two sexes, for either one or the other sex holds its head higher at different stages in the ceremony. We have frequently noted that when birds attempt to display with heads at the same level, a maladjustment is indicated, and the birds fence with upraised bills until one gives way or assumes a subservient position of the head. Verwey (1930) saw similar maladjustment of behavior in the European Grey Heron, *Ardea cinerea*, but he interpreted it in terms of one bird fearing the movements of the other and threatening until mutual confidence was established. In the night heron the maladjustment occurs at the time the male, having attracted a female by snap-hissing, overtures and displays, endeavors to become sexually dominant by a series of billing bouts with head in a high position. The Grey Heron also displays with neck elongated vertically but the neck-feathers are not raised in the manner of the night heron. Nevertheless the similarity of movement strongly suggests that its function is primarily to secure sexual dominance as in the night heron.

During the last three years we have frequently bred the night heron under ideal conditions for observation. Although the dominance relations of male and female change during the display, we never saw a female go further and develop any of the other ceremonies characteristic of the male except in one case. This bird, female no. 1224, twice performed the snap-hiss ceremony, on May 22 and again on May 24, 1939. It also showed a typical male twig ceremony twice. In the manner of sexually active males inviting pair formation, it defended its territory weakly against other birds, regardless of sex. Eventually it paired with male no. 1314 in a typical manner and laid three eggs.

We have shown elsewhere (Noble and Wurm, 1940) that the female Black-crowned Night Heron normally produces considerable amounts

of androgen. In fact, her interest in nesting material may be attributed to a male hormone, as also her modified voice and her display. Females which received large amounts of the androgen, testosterone propionate, developed a typical snap-hiss and twig ceremony. We may therefore assume that this bird, female no. 1224, was one in which its own ovary was producing more androgen than that of the typical female.

SIGNIFICANCE OF NUPTIAL LEG COLORING

The Black-crowned Night Heron usually develops pinkish legs in both sexes during the breeding season. Noble, Wurm and Schmidt (1938) remarked "that the tendency for males to attain the full color more often than the female is correlated with the greater use the male makes of his legs during courtship. During the snap-hiss ceremony the limbs are rhythmically lifted and extended as if to catch the eye of a female." We have shown above that while the plumes were stimulating organs they were not indispensable to a successful mating. The question remained if the reddish leg color was an indispensable 'releaser' to female behavior.

In order to test this question we have painted out the red color by covering the legs of breeding birds with a blue-green lacquer. Two mated males, nos. 222 and 303, as well as four unmated but sexually active males, nos. 133, 304, 32 and 341, were treated in this way. In no case could we detect any influence of this change of leg color on the courtship behavior of the birds. The four unpaired males secured mates as rapidly as did the controls.

Further, pinkish legs are not a prerequisite for a female to secure a mate. Occasionally young birds during their first breeding season do not attain the typical color and yet breed successfully. Such a bird was female no. 1321 that paired with male no. 1233. A male when snap-hissing may attract females with either pink or buff-colored legs but, according to our observations, shows no preference for the rosy-legged birds. Thus male no. 1313 was observed in its reactions to females no. 124 and no. 1222, which had buff legs, and females no. 1241 and no. 1224, which had red legs, on several days during May and June. The male snap-hissed to any female that came near him regardless of the color of the visitor's legs. Further, the peck-hiss ceremony, which Noble, Wurm and Schmidt (1938) considered a modification of the snap-hiss, was given by this male to female no. 1241 at the same time that another male, no. 1221, gave a snap-hiss in her direction. This failure of males to discriminate between rosy- and buff-legged females did not, however, seem very

surprising for, as stated above, we had observed males isolated in separate cages give a typical snap-hiss when injected with an androgen.

RELATION OF PARENTS TO YOUNG

Although we have reared night herons for three years in both outdoor and indoor cages and have watched both groups from blinds, it is surprising how difficult it has been to see the beginning of feeding behavior. This is probably because the parents treat the young at first very much in the manner of eggs. Both feet and beak are frequently pressed against the eggs as the parent with rapid lateral movements of the body settles down to incubate them, and the same movements of feet, bill and body occur when settling on the young to brood. These contacts cause the young to give their food cry or cackle, which may be written as *kak-kak-kak*. This monotonous and persistent cry is given with an irregular waving of the head. Both sound and movement are apparently stimulating to the parent for the latter eventually draws in its bill, rests the point on the bottom of the nest and regurgitates some partly digested food. This is then held in place between the mandibles while the young birds peck at it, often for a minute or more, before the parent swallows the food again.

The resemblance of the movements used in stimulating the young to those of egg rolling raised the question if there was any real break in the pattern of parental behavior at the time of hatching other than the newly acquired feeding reaction. We tested this question by giving three pairs of adults, which had been incubating their own eggs for approximately a week, sterile eggs in place of their own. Although the normal incubation period in our laboratory cages is 22 to 24 days, these birds continued the incubation approximately twice as long. One pair incubated 51 days, the second 40 days and the third 49 days. It seemed that in the absence of the young's food cry the parent would continue its care of the eggs in the usual way for at least twice the normal period of incubation.

The voice of the young changes with age. During the first two weeks it has a shrill, metallic quality and then gradually becomes harsher. By the third week the aimless swinging of the head from side to side of the young chick is replaced by a sharp, upward angulation of the head while giving the food cry. The chick learns to distinguish its parents from its brothers and sisters and directs its food begging toward the former, as illustrated in the following case. A chick standing outside the nest was stimulated to call for food at the time another young in the nest was doing likewise. The former

then proceeded in the direction of the parent, also standing just outside the nest, and grasped the adult's beak, soliciting food. It is at this stage that the parent returning to the nest gives an overture and recognition call, not at its mate but directly at the young. Some adults have not at this stage lost the guttural quality to their voice and it would seem that they were courting their young. Lorenz (1938) describes the European race as having less knowledge of parents than our birds displayed. He states: "The young birds do not seem to recognize their parents, or else their begging reactions are released on seeing any adult, so that they will most obtrusively molest every old bird they meet, crowding against him and trying to seize his bill. Such impudent youngsters are not only absolutely immune from attack, but the old birds actually seem afraid of them and will retreat whenever they see one coming."

Our young night herons showed very little tendency to wander from the nest during the first month. When three weeks old they would defend their nests against adults not their parents. This is considerably earlier than Noble, Wurm and Schmidt (1938) reported, and there is doubtless considerable variation in this regard. One group of approximately this age attacked a mounted pheasant placed two feet from the edge of the nest. The overturing with recognition cry of the adult approaching the nest apparently helps the young to recognize their parent, although the vigor with which they seize the bill simulates an attack. Although we have witnessed the feeding many times, we have never seen a young night heron solicit food by seizing the beak of any adult other than its own parent.

Gross (1923) describes the feeding of the young under natural conditions very briefly: "In delivering food to the downy young the adult seemed to insert the tip of her beak into the wide open mouth. . . ." We have never seen such behavior in any of our birds and doubt if it occurs in nature. Herrick (1935), in classifying the methods of feeding young birds, states that regurgitation is "characteristic of albatrosses, herons, egrets, and flamingoes, which enlists active coöperation of both adult and nestling; but the transfer of regurgitated food is effected indirectly by a crossing or juxtaposition of bills, rather than by insertion of the parent's bill in a young one's mouth or *vice versa*." We have often seen the young night heron seize the parent's bill nearly at right angles and assume this is the typical method of receiving regurgitated food from the parent.

It is remarkable that although chicks are eager for food held between the mandibles of the parents, they pay not the slightest attention to it when thrown into the nest by the experimenter. We exper-

imented with seven different nests and sixteen times attempted to feed chicks over a week old by placing food in the nest. In no case did we succeed. If chicks the same age are taken from their parents and force-fed for several days, they may be taught to take food from the hand. Some older chicks will take it spontaneously from the hand. But normally only food delivered by the parent appears to be identified as food. Occasionally the food regurgitated by the parent falls into the nest. Under these circumstances it is eagerly picked up and devoured by the young. Hence, it is not the location of the food but the way it is presented that stimulates its acceptance.

Chicks at leaving the nest soon take food from the common feeding area. Our youngest chick observed to take food independently of the parent was 37 days old. Other chicks in the same cage were taking food from the parents at 90 days of age. Under laboratory conditions there is a considerable range of variation in the age at which freedom from parental care takes place.

One of the most surprising reactions observed in our young night herons occurred in a group three to four weeks of age. These had been collected in the field when apparently ten to fourteen days old and had been isolated since their arrival from our breeding adults. We changed the voice of one of these young birds by treatment with testosterone propionate and it began to overture and display like a typical breeding adult. When this bird approached one of the untreated young the latter gave a typical food begging with characteristic cry, waving head and slightly raised wings. Because none of these birds had given the infantile food cry since reaching our laboratory, we assumed that the guttural cry of a sexually displaying bird would automatically release food begging in any young bird that was not too inhibited by strange surroundings. We repeated this experiment with many young birds and found that not only the food begging could be elicited but also the 'intimidation call.' That is, the young birds when responding would also spread their wings and give a characteristic note (Noble, Wurm and Schmidt, 1938) as if to protect the imaginary food. This behavior was surprising in that only the voice of the sexually stimulated chick called it forth. Nevertheless, we could not be certain that the reaction was actually innate. We did not know the history of the particular birds which responded. It was possible they had learned to associate the guttural sex voice with that of the parent returning to the nest. The overture and display with guttural voice are characteristic of nest relief and it would be indeed surprising if the chicks had not heard the sound many times while in the parental nest.

The plumes usually are erected when the approaching parent overtures and calls in response to the aggressive behavior of the young. Nevertheless, plumes are not indispensable for normal behavior of the young. Male no. 1331, from which the plumes were absent, was seen to overture to its young with the result that they quieted down at once. He also regularly fed them without difficulty. The young appear to recognize their parent's voice, but this may be due to the fact that only resident adults call when approaching the nest. If they mistake the parent for a stranger, they shift from an attack to food begging when the parent calls.

Our interest in the induced food call was greatly increased when we discovered that at the close of any breeding season fully adult birds, if they lost their nuptial colors of lores and legs before their mates, would frequently give the infantile food cry. In no case did we observe that these adults, which had suddenly developed the childish ways, were ever fed by their mates. Either sex could play the food-begging rôle if it lost its nuptial color first. In pair male no. 303 and female no. 1414, it was the female that begged. In pair male no. 1133 and female no. 1222, the male lost his sexual pigmentation on August 28 while the female continued to show both a black lore and a guttural voice. Subsequent to this date the male, instead of remaining passive to the gestures of his still sexually active partner, responded with infantile food begging whenever the female approached the nest and called. Both adults of pair male no. 431 and female no. 441 had lost their nuptial colors by September 3, but by September 5 the male showed a recrudescence of the dark lore color and the female began to beg food. In only one case where there was a recovery of lore pigmentation did a pigmented female give a food-begging call. She responded to a pigmented female which with an uncolored male had formed a trio. In every case where we could trace the first appearance of a begging call, it was found to be given in response to a guttural sex call by a bird which was out of season or nearly so.

This discovery, that a sex call can release food begging in a fully adult bird that had not called in this way for a year or more, seems of considerable theoretical interest. In many birds it is the female which begs for food from her sex partner. This serves as a bond between the pair and also helps the male to secure sexual dominance (Noble and Wurm, in press). Normally in the night heron, both sexes develop guttural voices during the breeding season and hence neither sex adopts a food-begging ceremony. The night heron has developed a method for securing sexual dominance which is totally

different from those birds that normally practice food begging at the beginning of the breeding cycle.

Although the sexually modified voice seems to awaken the begging response in adult herons and possibly in the juvenile bird as well, young night herons beg for food not at first in response to voice but to tactile stimulations and they continue to beg frequently after the parents have lost their nuptial colors and guttural voice. Thus a chick of male no. 1123 and female no. 1212 did not desert the nest until 115 days old. By this time both parents had lost the breeding colors and sex voice but the chick continued to give the food cry whenever the parents approached and was fed regularly by them. The out-of-season adults that begged from their in-season mates never received food from them in our presence but they nevertheless continued their calling for two or three months after their mates had lost their nuptial colors. Two young herons, which we frequently petted and fed by hand, continued to give the juvenile food call until they were two and a half years old. One had made some attempt to breed, for it paired and built a nest in the meantime, but when an observer approached it would almost invariably sway its head, partially raise its wings and give the characteristic food cry. During adult life these herons were very rarely fed by hand yet nevertheless their response to a human observer remained the same. Presumably these herons had early learned to associate being fed with the presence of a human observer. Since lack of hand-feeding did not decondition them, we may assume that they secured a certain satisfaction from being petted.

DISCUSSION

It has frequently been pointed out that birds and other animals may react innately to particular sounds. When a female night heron, breeding for the first time, comes slowly into the territory of a snap-hissing male, we have every reason to assume that the bird is innately attracted by this particular cry. Similarly, when a parent night heron with its first set of chicks lowers its head and regurgitates in response to their persistent food cry, it would seem that the sound induced a response in the parent. Unfortunately, the stimulative value of the rhythmical leg movements in the case of the snap-hissing male or of the head-waving in the instance of the food-begging chicks is not known. Lorenz (1935) assumes in regard to the plumes, "that the seeing of the form is of far less importance than the seeing of the movements, particularly in mentally inferior birds" (translation). This would seem to apply to the majority of the 'releasers'

discussed by Lorenz. They are merely adornments developed to emphasize movements. Our work with deplumed night herons, discussed above, indicates that the plumes do have a stimulative value during courtship but, since coition can occur without them, they are not indispensable to breeding. The plumes merely enhance movements which are necessary for the continuation of the bond between the pair. A somewhat similar condition was found in the jewel-fish, where both sexes don a red dress during the breeding season, and this was shown by Noble and Curtis (1939) not to be necessary for breeding but it helped in the formation of pairs.

Female night herons are attracted by the snap-hiss ceremony of the males but they do not remain with them unless they are adequately stimulated by the overture and display. The plumes play no rôle in the initial approach, but they seem to have a very definite part in holding the pair together and synchronizing the mating. There is no sexual selection in the sense of initial female choice, but a very definite one of female persistence in her original quest. Marshall (1936) concludes, in regard to the effect of mutual courtship, "it is not the female which selects the male; it is the pair which have the highest capacity for mutual stimulation which are, so to speak, selected by Nature for the perpetuation of the race." He considers mutual selection a special case of natural selection and not one of sexual selection at all. If, however, as in the case of the night heron, we consider the behavior of the female in detail, we find that the female after her original approach to an ornamentless male actually goes in search of a more stimulating mate. The plumes may not attract but they tend to bind, and as such are epigamic characters of an accessory type (Huxley, 1921). We may, therefore, speak of mutual courtship in the night heron at least as a special case of sexual selection with considerable justification.

It might be argued that the night herons in our experiments, being very familiar with the normal appearance of their kind, were merely frightened at the unusual appearance of plumeless birds. To our eyes the crownless birds were even more bizarre than the plumeless ones and yet they seemed as successful as intact birds in holding their mates. It is not the combination of white plumes against a dark background, but the plumes themselves which seem to be stimulating. Unfortunately, it was not possible to eliminate voice in these experiments. But, to judge from the previous work of Noble, Wurm and Schmidt (1938) on the reactions of young birds with plugged ears, voice would seem to play as important a rôle as motion.

Although we secured no deviation from the normal pattern of be-

havior by coloring the legs of night herons before or after pair formation, it does not follow that this nuptial color is not stimulating to the birds. Under the conditions of our laboratory the color, when modified, was not stimulating enough to produce any deviation in behavior. Apparently the red legs, like the plumes, accentuate the movements and these, if visible, are the stimulating devices. It would be interesting to know if coloring the plumes black would have any effect on the retention of mates. To judge from our experiments with the legs, if the light was sufficient, the color would be immaterial. Night herons are often active at dusk and it is possible that light color of the plumes renders them conspicuous under these conditions.

In general it may be said that the nuptial adornment of the night heron serves to emphasize movements of particular types and it is these that are stimulating rather than the adornments *per se*.

CONCLUSIONS

1. The European and American races of Black-crowned Night Heron (*Nycticorax n. nycticorax* and *N. n. hoactli*) have apparently the same courtship pattern, discrepancies in the published accounts being due either to different terminology or to lack of information.

2. The plumes of the male heron serve to emphasize the overture and display ceremony which aids the formation of nuptial bonds. Removal of the plumes weakens the bonds, the pairs tend to disintegrate, the birds stand apart or seek new mates and the male tends to continue his snap-hiss ceremony, unlike a typically paired bird.

3. The difference between the number of responses given by a female to the overture and display ceremony of the male, given when the birds are standing together, is significantly less than the responses given by females under the same conditions to plumed males.

4. The plumes of the female have less functional significance than those of the male apparently because the breeding male is more reactive to, and requires fewer specific, external stimuli.

5. The crown-feathers of either sex may be removed without affecting the synchronization of courtship or weakening the nuptial bonds.

6. The rosy leg color of the breeding night heron serves to emphasize the leg movements of the snap-hiss ceremony. Coloring the legs blue-green has no effect on the speed of pair formation or the duration of the bond.

7. The snap-hiss ceremony is characteristic of the male. A single case was observed of a female which developed this ceremony. It

did not prevent her from mating and eventually showing normal female behavior.

8. The guttural sexual voice of the night heron, even when induced experimentally in chicks with testosterone propionate, may call forth food-begging behavior in untreated chicks. Among pairs of adults, the bird that loses its nuptial color and voice first may respond to the other's sexual voice by food-begging behavior.

9. Night herons, which have been trained as chicks to respond to the observer with food begging, retain the habit for over two years, although rarely fed by hand.

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