SOCIAL BEHAVIOR OF THE BLACK-CROWNED NIGHT HERON

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Plates 2–4

THE Black-crowned Night Heron (*Nycticorax nycticorax hoactli*) is a common American bird and its life history has been intensively studied by Gross (1923), Bent (1926) and others. Nevertheless an analytical study of its social behavior has not previously been attempted. Recently Lorenz (1934, 1935) has made such an analysis of the social behavior of the European Black-crowned Night Heron, which is only subspecifically different from the American race. One would naturally assume that the behavior of the two forms would be very similar if not identical, but various details of the behavior of the American race as given by Gross (1923) do not agree with Lorenz's description of the European bird. It has therefore seemed advisable to recheck the life history of the American race, considering not only the social behavior of the adult but also the ontogeny of these behavior patterns in the immature. This investigation was supported by a grant from the Committee for Research in Problems of Sex, National Research Council.

THE PROBLEM

The Black-crowned Night Heron is a species of especial interest because Lorenz considers that the greeting display of this bird illustrates his term 'releaser' in an ideal manner. The 'ornamental plumes' arising from the crown of the adults serve, according to Lorenz, not for purposes of mutual stimulation as Huxley (1921) would assume but to suppress a strong defense response which is supposedly evoked in this heron by the approach of any fellow member of the species. Immature Night Herons lack the dark crown and white plumes of the adults but Lorenz assumes that as they grow older they display the bowing movements toward their parents in order to suppress attacks which their parents might make. The movements appear in ontogeny before the plumes which are destined to have functions never previously attributed to the plumes of any bird. Night Herons have been assumed to exhibit a pecking order (Schjelderup-Ebbe, 1931), that is, a social hierarchy which has been intensively studied in the hen, pigeon and a few other domesticated birds (Allee, 1936). Lorenz has not considered what rôle, if any, these plumes or gestures might have in regulating the pecking order, nor has he considered the courtship of the Night Heron in full, although he denies that the plumes have any function as adornments at this time. In studying the social behavior of the Night Heron we have

paid especial attention to (a) the ontogeny of social behavior, (b) the pecking order and (c) the courtship behavior.

FIELD OBSERVATIONS ON THE IMMATURE

Field observations which we made on immature herons at Orient, Great Neck and Massapequa, Long Island, during 1936 and 1937, showed at once that the social behavior of this race is far more complex than Lorenz has described in the European form. As the young grow older they readily leave the nest and take a position close to the tree trunk a few feet above the nest. If approached at this stage, they usually climb higher in the tree or make their way clumsily to another tree. Most of the young of the Orient colony were in this stage July 8, 1937. Approximately a week later, as the young begin to fly, a profound change takes place in their social behavior. Such a stage was seen in the majority of the young in the Massapequa colony, July 9 and 10, 1937. The young are now widely spaced vertically on the boughs of the nesting trees. Other young birds are making short flights to these trees and there are numerous disputes and vigorous thrusts of bills as a newcomer lands near a resident bird. Gross (1923) has interpreted these disputes as primarily over food. He states: "When the young were hungry, they were also irritable, and the least disturbance by a neighbor would cause them to render a defensive thrust accompanied by a ghastly, sharply accented 'Sque-e-e-e-e-e-ak'." If the birds are in this early flying stage it will be readily observed that the dispute is over territory and not food. Exactly the same behavior is found among the adults when defending nesting areas. When the young are in pairs the resemblance of their behavior to that of paired adults is even closer.

The frequent occurrence of groups of three on mutual good terms defending their immediate vicinity against new arrivals, leads one to suspect that these are young of the same brood which have not left their natal tree. This interpretation leads to the question, Do the young recognize their brothers or sisters when not on their home tree? Do the numerous cases of single birds defending their territories against all comers represent broods where only one survived, or has the family group disintegrated leaving each bird fighting for its own perching site? The fact that one bird can move close to another without resistance while another may be attacked, shows that there is individual recognition. Neither Lorenz nor Gross found evidence of such recognition and neither interpreted the behavior of the young in terms of juvenile territory defense. It was primarily to secure evidence of this territorialism of the young heron that we have reared thirty-eight individuals taken from nesting trees before they could fly and have followed the ontogeny of behavior pattern for over a year. Since fourteen of these young herons bred the following spring we have observed nearly a full

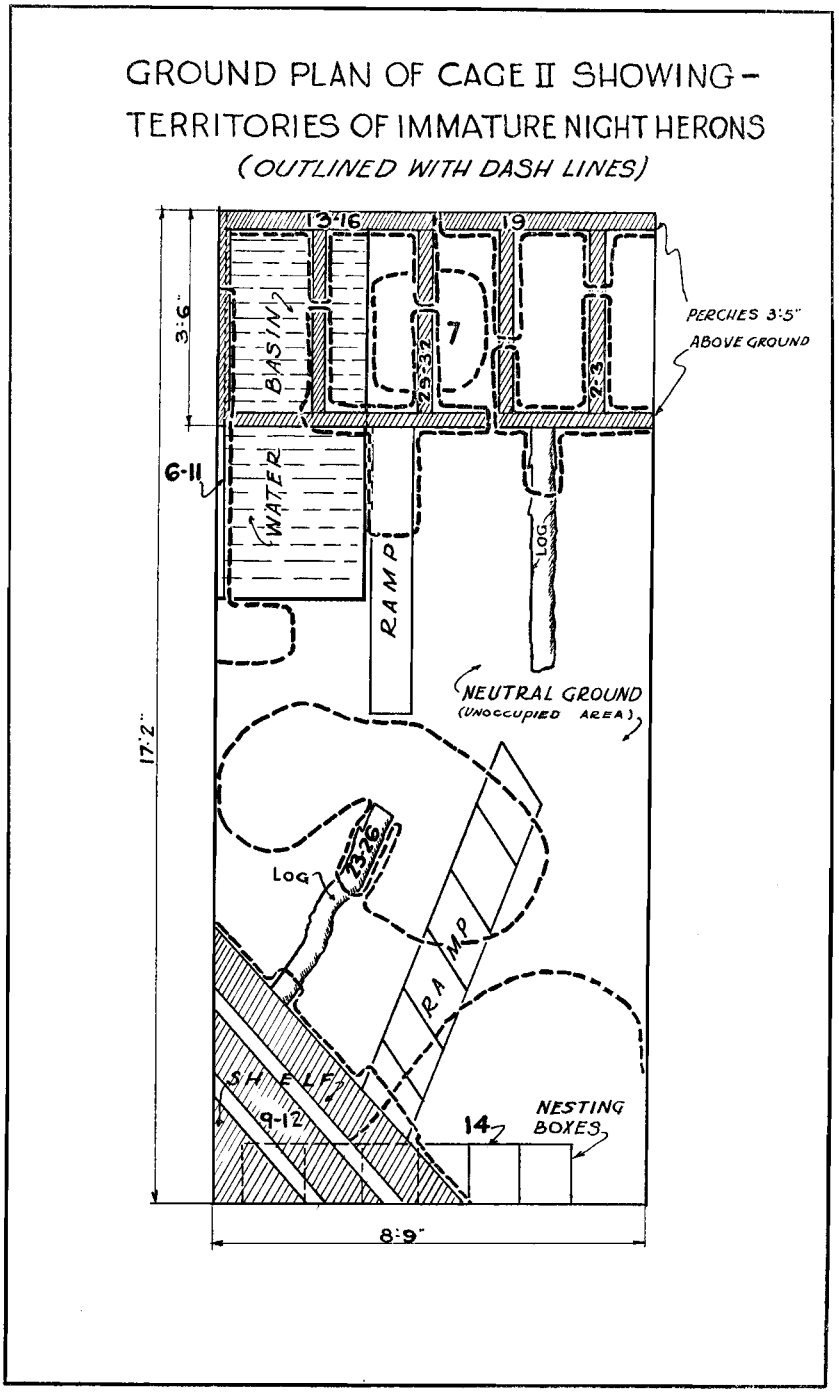
juvenile cycle in these birds. The juvenile birds in the field were not banded and their sex was unknown. We shall therefore base our description of the ontogeny of social behavior on the birds reared in captivity. Many of the details of behavior seen in the laboratory were also witnessed in the field and reference to these details will be made below under various headings.

TERRITORIALISM AMONG YOUNG HERONS

We have studied the development of the type of territorialism described above, in a series of young herons maintained in large cages. Twenty-nine young ranging from five to fifty days of age, to judge from the description of Gross (1923), were divided into two lots, of which one was placed in indoor and the other in outdoor cages. Both groups were given artificial nests and marked with colored bands. Very soon the older birds began to leave the nests and to establish well-defined territories which they defended against the encroachment of other young birds. The four outdoor cages were provided with boxes and irregularly arranged logs, boards and potted shrubs. Cage 1 measured 199 by 85 by 88 inches and was equipped with perches from one to six feet from the floor. Cages 2 and 3 were both 206 by 105 by 75 inches with most of the perches three and a half feet from the ground. The ground plan of Cage 2 is shown in text-fig. 1. All cages were provided with large water baths. Cage 4 was constructed after most of the young birds had left the artificial nests. It measured 218 by 132 by 134 inches and was equipped with perches from one and a half to seven and a half feet from the ground.

The oldest birds (Nos. 17, 18, 19) on later dissection, proved to be males. They were approximately fifty days old at the beginning of the experiment and soon after secured the most isolated and highest perches in Cages 1 to 3. Other birds when approximately seventy days old moved away from the artificial nests and formed the first pairs (Nos. 21–22, 20–14, 9–12, 1–4, 2–3). A younger group, approximately thirty days old (Nos. 6–7–9–10–11–13–16), remained grouped near the nests along the wall while the older birds were securing territories. Each of these groups, either as a large group, a pair, or a lone bird, defended a territory several feet in diameter against the encroachment of any bird of any of the other groups. The oldest and most aggressive birds (Nos. 17, 18, 19 and pairs 1–4, 2–3) guarded the largest areas, often the whole width of the cage. When the observer entered the cage the birds would leave their territories and form a highly agitated group in one corner of the cage. Within a minute after he had left, the birds would return to their respective territories and defend them by vigorous thrusts and squawks against trespassers.

The territories were not secured suddenly but often by slow adjustment to the other birds in the cage. For example, the birds at the time of leaving


GROUND PLAN OF CAGE II SHOWING-
TERRITORIES OF IMMATURE NIGHT HERONS
(OUTLINED WITH DASH LINES)
13-16
19
3-6"
BASIN
7
25-32
PERCHES 3'5"
ABOVE GROUND
6-11
WATER
RAMP
LOG
NEUTRAL GROUND
(UNOCCUPIED AREA)
17'2"
LOG
23-26
RAMP
SHELF
9-12
14
NESTING
BOXES
8'9"

TEXT-FIG. 1.

the nest seemed to form five major divisions: (a) Nos. 9, 12, 14, 17, 18, 20; (b) Nos. 6, 7, 8, 10, 11, 13, 16; (c) Nos. 1, 4, 5, 23, 25, 26, 27; (d) Nos. 2, 3, 19, 21, 22, 24a, 28; and (e) Nos. 24, 29, 31, 33, 34, 35, 36. As stated above, Nos. 18 and 19 early isolated themselves from these groups but No. 17 was first grouped with 14. Other pairs which formed and broke were Nos. 20–14, 20–9, 10–8 and 10–7.

The immediate cause for the splitting up of the large groups into smaller lots was the greed of the young birds. At about fifteen days of age the young herons begin to snatch at food brought them instead of merely shaking their heads and bobbing with widely open mouths in the manner of very young herons. In the latter, discrimination is poor and they will attempt to swallow pieces of wood or the hand of the observer. Often two young birds will attempt to swallow the wings, neck or feet of a third. Undesirable objects which can be swallowed are later regurgitated. The young birds stuff themselves until part of the food is protruding from the mouth. Even then the sight of more food will induce new feeding movements. At approximately forty days of age the birds prefer to pick up food for themselves and are usually reluctant to feed from the hand. With the change of behavior there arises a type of intimidation call which is directed toward driving other young birds away from the food.

The food cry of the young heron at the time it leaves the nest is a persistent cackle which may be written *kak-kak-kak-kak-kak* rapidly repeated and persisting while the observer is present. It is accompanied by a slight waving of the head sideways or vertically. The intimidation call is a continuous chesty gurgle given while the body is held low and the wings are slightly raised and spread. The intimidating bird steps sideways toward the offending neighbor, gently pushing with the spread wings.

This intimidation display is directed only toward one of the bird's own group. When the birds have become further separated a very different response occurs which is a clear indication that one or both birds have separate territories. Again the body is held low but the wings may or may not be spread. The head is drawn back over the body and the mouth is opened wide while the feathers of crown, neck and back are erected. Then, as the head is darted forward in a vicious peck, a high-pitched screech, or frightening call, is emitted and the mouth again is opened wide. In a less extreme attitude the body is held erect and the feathers of head and neck are raised while a shrill but lower-pitched squawk, or fight call, is given.

In any group of young herons there is one bird that is dominant in the sense that during billing it holds its head higher than the others and in any dispute among themselves the others either withdraw or lower their heads in a subservient manner. A second cause for splitting of the original group is that one of the subordinate birds will no longer lower its head with the

result that the usually observed gentle billing gives way to more aggressive thrusts and finally to typical territory-defense movements.

Approximately seventy days after hatching, the herons begin to fly and much preliminary wing flapping is indulged in. Two pairs (Nos. 21–22, 2–3) were formed at this time and two three-membered groups (Nos. 6–7–11, 24–35–36). The intragroup struggle became more intense. In group 24–35–36 birds Nos. 24 and 36 clicked their bills loudly while billing one another and held themselves tense and erect. Previously No. 36 had submitted to 24 by gradually lowering its head when the two billed. The failure of No. 36 to assume the subordinate position of head soon resulted in an exchange of vicious pecks between the two and No. 36 was driven from the territory. Consequently pair 24–35 formed. Similarly one bird was observed to be driven from the territory of Nos. 1–4–5 and 6–7–11 with the result that pairs were produced. All the pairs of immature herons, excepting those resulting from the forced pairing to be discussed below, were derived from the nestling groups to which both birds belonged.

Once a bird had been driven from a group it retained some memory of its early associates because much later when frequent changing of the bird's territory by the experimenters tended to break down territory distinctions, some regrouping occurred. Thus pairs 5–28, 27–25, 6–11 and 7–11, which were well defined for several weeks, later formed the groups 5–27–28 and 6–7–11. The regrouping of the first of these two lots may have been facilitated by the fact that Nos. 27 and 28 were partly spayed.

The pairs of young birds were usually as well defined as that of breeding adults. Introducing a pair into a cage full of strange birds invariably resulted in their keeping together and establishing a common territory in the new cage. Further, these young birds remembered their old territories when returned to the original cages some weeks later. Thus pair 23–26 recognized and secured their old territory in Cage 2 after having spent 17 days in Cage 1. Pair 21–22 secured their old territory in Cage 4 after being retained twenty days in Cage 2. Pair 5–28, after three weeks in Cage 1, attempted to reestablish their old territory in Cage 2. In this they did not succeed because their old territory had been occupied by pair 29–32. Similarly pair 2–3 regained their old territory in Cage 2 after five weeks absence, but No. 19, after five weeks absence from the same cage, was badly beaten by the other birds while attempting to regain its old quarters.

The strong territory defense of young herons in a cage where competition for space is great, will sometimes induce the formation of new pairs. For example, birds 5 and 28 were transferred to Cage 2 and birds 25 and 27 to Cage 3 before they were paired. These birds, driven by the others, were forced into a common area and being frightened by the new situation they adopted a subservient attitude which facilitated the formation of perma-

nent pairing. Similarly, pressure of environment caused birds 29 and 32, resulting from the induced breaking of pairs 29–31 and 15–32, to form a permanent pair.

Pairing off is not accomplished by the mere juxtaposition of two frightened birds. One bird must accept subordination to the other and, further, the bond between them is frequently strengthened by gesturing and billing of the pair. In this behavior the subordinate bird apparently always takes the lead. The head is lowered and weaved back and forth while the bill is directed toward the side or feet of the dominant bird and clicked. We have called this gesture the 'overture.' It is answered by the dominant bird which usually keeps its head high but may occasionally lower it to the same position as that of the subordinate bird. Overtures are made at frequent intervals. During a period of twenty-one days fifteen pairs of immature birds were observed for approximately six hours a day. The subordinate bird was found to initiate the ceremony 1,406 times. In thirty-one cases the dominant bird was recorded as making the first move, but it is highly probable that the observer, with thirty birds under observation, failed to notice a still earlier overture on the part of the subordinate bird. Thus each pair of birds made overtures approximately five times during six hours of daylight, with the subordinate bird usually, if not always, taking the lead. A modification of this overture is the actual grasping of the latter bird by the first bird with its bill. Another modification is the stroking of the breast feathers of the partner with the bill. A third movement we have described as 'billing.' It consists of the birds' opening and closing their bills while they are held in contact. During this movement the dominant bird always holds its head higher than that of the subordinate. These movements, although started by the subordinate bird, induce a similar movement by the partner. Once a pair has formed, neither billing nor overturing is necessary for the maintenence of this condition as we shall point out below.

A variety of calls may be given by either member of a pair and as we shall show, these aid in the retention of a group. The one most frequently employed is the recognition call, which may be written as *krwawrk-krwawrk-krwawrk*. The second is a throaty and prolonged variation of the familiar *quawk* or flight call of the species. This occurs between birds which have recently driven off a stranger or with members of a pair which have come together after a separation. The third call is a combination of food and flight calls and occurs when one bird of a pair moves off and its partner wishes to recall it. A fourth is a combination of the food and intimidation cry. It is usually given when two herons are standing beside each other and is usually followed by a bout of billing.

RELATION OF SEX TO PAIR FORMATION AMONG JUVENILE HERONS

Sex was determined at the close of our studies by a direct examination of the gonads of the paired birds. As shown in Table 1 there were thirteen male-female, six female-female and two male-male pairs. The gonads were rudimentary in all cases. Sections revealed some spermatids but no sperm in the testes. No yolk had yet formed in any of the ova.

As stated above, no pairs of young birds formed without one bird becoming subordinate to the other. Once a bird had taken such a position as shown by (a) the lower position of its head during mutual billing and (b) its initiating overtures to its partner, this position was never lost while the grouping was maintained. In the heterosexual pairs the male was usually the dominant bird. The three cases of reversed dominance find an explanation in the special handling the birds received. That is, male No. 11 was a very tame bird which was frequently petted by visitors to the cage. This would account for his taking a subservient attitude to females Nos. 6 and 7. Pair 29–32 was a forced pairing following the experimental breaking of pairs 15–32 and 29–31. Such a forced pairing of formerly paired birds probably never occurs in Nature. Our observations at three different colonies indicated that when competition for space became very severe the bird losing the fight moved on to new territory. Hence we may conclude that in the sexually immature heron the male has a decided tendency to dominate the female. This dominance has no relation to body weight; it is a characteristic of maleness in the Night Heron.

TABLE 1

Relation of Sex to Pair Formation in Immature Night Herons

Heterosexual Pairs		Homosexual Pairs	
Dominant	Subordinate	Dominant	Subordinate
Male Dominant		*Female Pairs*	
13 ♂	16 ♀	23 ♀	26 ♀
24 ♂	35 ♀	5 ♀	28 ♀
21 ♂	22 ♀	Br_4 ♀	Br_2G ♀
36 ♂	33 ♀	12 ♀	9 ♀
15 ♂	32 ♀	8 ♀	7 ♀
29 ♂	31 ♀	12 ♀	14 ♀
10 ♂	7 ♀		
10 ♂	8 ♀		
27 ♂	28 ♀		
27 ♂	25 ♀		
Female Dominant		*Male Pairs*	
6 ♀	11 ♂	2 ♂	3 ♂
7 ♀	11 ♂	1 ♂	4 ♂
32 ♀	29 ♂		

SENSORY MODALITIES EMPLOYED IN PARTNER RECOGNITION

Young herons remember not only their old territories but their partners for long periods as the following experiments show.

(a) The two herons of pair 5–28 were separated for 72 hours. When the birds were placed with many other herons in their original cage they re-formed within twelve hours.

(b) Birds of the same pair separated 96 hours and then placed together with many other herons in a cage previously unoccupied by them, again re-formed within twelve hours.

(c) The two birds of pair 23–26 isolated for seventeen days and then replaced in their original cage with other herons, re-formed their group within twelve hours.

(d) The two herons of pair 21–22 separated for twenty days and then placed in a cage strange to them re-formed their group within three hours. When returned to the original cage they attempted to retrieve their old territory but after being driven out by the herons occupying it, they marked out a new territory in the old cage and continued to defend it.

It is therefore clear that young herons can recognize their old partners after a separation of at least twenty days. The sensory modalities employed in this recognition could not be determined from observation alone. Some preliminary experiments were directed toward modifying the responses of one bird to its partner by covering the bill of the latter with bitter substances. Neither an extract of aloe nor concentrated solutions of quinine sulphate had an effect on the mutual ceremonies. We were equally unsuccessful in modifying the response by using ill-smelling substances on the feathers. Attention was then directed toward the visual and auditory modalities for these are well known to be of primary importance in the life of most birds. Young herons were found to be much less disturbed by profound changes in the appearance of their partners than has been reported for other birds. Beaks of various individuals were painted brilliant red or blue, the legs were striped with blue, orange and white without bringing any deviation in the reaction of one member of a pair to its partner. When, however, the entire face was covered with either a bright-red or yellow rubber balloon leaving only the eyes and bills exposed, the masked bird induced fright reactions in its partner. But in every case the masked bird had merely to call a few times to reassure its partner before billing and gesturing began again in the normal manner. Merely covering the crown of a young heron with a piece of adhesive tape stained with iodine brought confusion at first to its partner. Since such a modification of appearance was much less conspicuous than the painted bills, it seemed that the young herons paid especial attention to the detailed feathering of the head. However, when most of the head and neck feathers of one member of pair 5–28

were removed and replaced by head feathers from much younger herons, no permanent confusion resulted. In these cases it was obvious that the recognition of the partner's voice, coupled in some cases with the mutual recognition of territory were the bonds which brought them together.

The human observer is unable to distinguish any difference between the voices of the different herons when they were using one type of call, or at least we never succeeded. The birds, however, were able to make this distinction and they require the stimulation of the partner's voice for a synchronization of the mutual ceremonies. Plugging their ears with cotton covered with rubber cement and then bringing the adjacent skin together over the cement with a single stitch proved to be an effective way of eliminating sound without disturbing the birds. Such birds were found not to respond to sounds made by a hidden observer, and their reactions to their partners indicated an obvious deficiency in hearing.

RELATION OF VOICE TO THE BILLING CEREMONY OF YOUNG HERONS

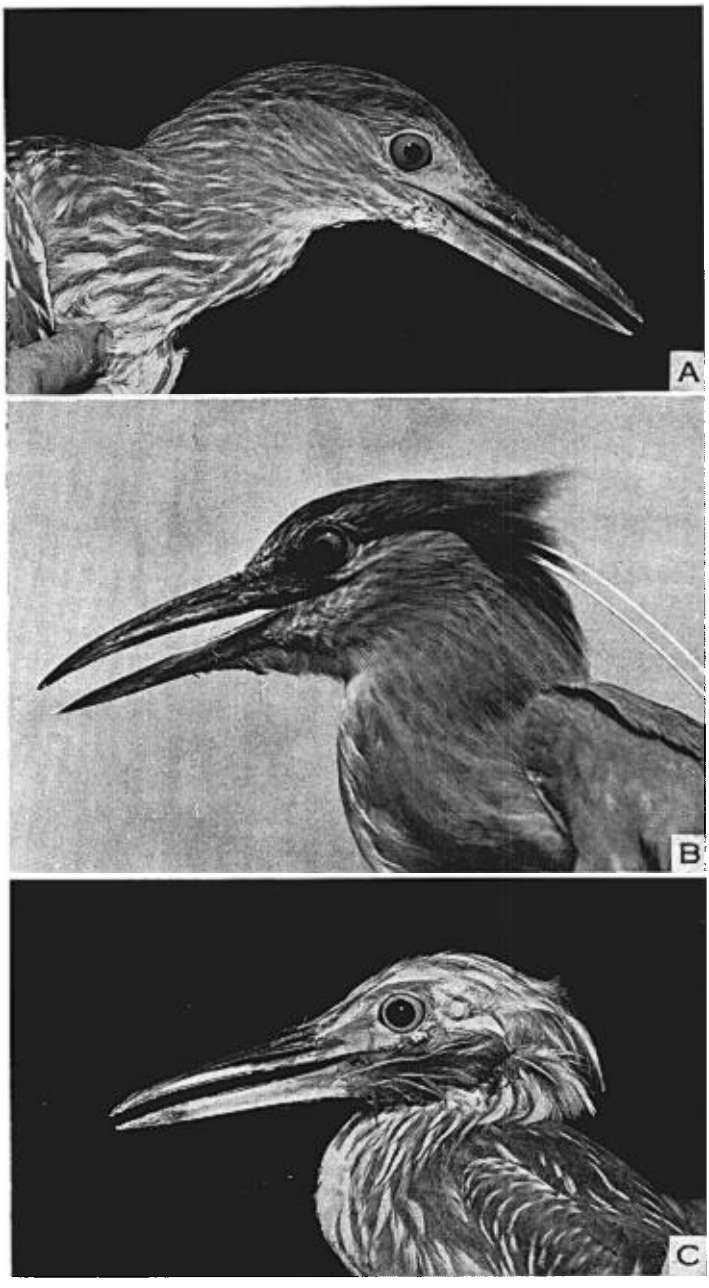
As stated above, it is the subordinate member of each pair which overtures to its mate and this often leads to billing. Although the subordinate bird bows, if its partner has its ears plugged, there is rarely any response from the partner. Birds with plugged ears stand together and defend their territory against trespassers. Further, if introduced into a strange cage, they will mark out a new territory and sometimes defend it together. Hence, overturing and billing are not necessary for partner recognition or mutual territory defense. The response of the dominant partner is to the sound and not movements of the subordinate bird, as the following experiments show.

(a) Pair 23–26 have ears closed with cotton, rubber cement and a stitch. When returned to original territory there is no overturing. When transferred to a strange cage with other herons they occupy a common area and defend it without overturing.

(b) Pair 15–32 have ears closed with cotton and rubber cement only. When transferred to a new cage they take up territory together but do not engage in mutual ceremonies. When ears are opened again the birds begin at once to overture and bill.

(c) Pair 5–28 have ears plugged with cotton and rubber cement only. Head and body of No. 28 sprinkled with blue water color. Pair returned to original territory but No. 5 is frightened by the appearance of No. 28. By the following morning the pair has come together again.

(d) Pair 23–26 have ears plugged in standard way (as in experiment *a*). No. 23 is masked with a yellow balloon and returned to original cage. Both birds are driven by the other birds in the cage. Within twenty-four hours the pair has re-formed.



YOUNG BLACK-CROWNED NIGHT HERONS

(e) Masking reversed in pair 23–26. Plugs removed from ears of No. 23. The latter is now frightened by its masked partner but when No. 26 calls, No. 23 approaches and they bill. No. 26 seemed to recognize No. 23 by its appearance, and was able to attract the latter by calling even though No. 23 was obviously disturbed by the appearance of the mask on No. 26.

(f) Both birds of pair 5–28 have the feathers of their head and neck replaced by their own breast feathers. Ears plugged in standard way and external nares plugged with rubber cement. When both birds are returned to their original cage now emptied of other herons, they stand near together but fail to overture. Normal herons progressively added fail to separate pair.

(g) Both birds of pair 2–3 have head and neck refeathered with own breast feathers. Ears plugged in standard way and pair transferred to a cage in which they previously held territory. Both birds fight other birds for this territory. Pair transferred to two other cages with other herons reform pair both times although slowly (twelve hours).

(h) Both birds of pair 23–26 with ears plugged in standard way have head and neck refeathered with own breast feathers and are transferred to a new cage. Other herons force them apart, but twenty-four hours later they have come together. They fail to overture or bill.

From the above experiments it is clear that plugging the ears greatly reduces or entirely eliminates the overturing and billing of the pairs. While covering a bird's face with a rubber mask tends to disturb the partner, neither this nor the refeathering of the head and neck with the bird's own breast feathers prevents pair formation even in new territory. Young herons with plugged ears can apparently recognize their partners by other features than those found on the head or neck. Whether this is head and body movement or merely coloration of the body plumage, our experiments have not shown.

EFFECT OF TIME LAPSE ON RECOGNITION OF REFEATHERED BIRDS

Refeathering the head and neck of both members of a pair of young herons does not prevent partner recognition after a lapse of a few hours. This was shown in several of the cases reported above and also in pairs 21–22, 29–31, and 15–32 which in a series of tests had their heads and necks refeathered with breast feathers (Plate 2, figs. A and C) but their ears were not plugged. If, however, these refeathered birds are isolated for six or more days, there is complete failure to recognize partners, as the following experiments show.

(a) Birds of pair 29–31 are isolated in separate cages six days. Color pattern of head is modified by the addition of breast feathers. When

birds are placed in Cage 2 where they had previously held territory, the birds remain apart and show no sign of recognition.

(b) Birds of pair 21–22 are separated for eight days and then have feathers on crown and face replaced by breast feathers. When placed in Cage 4 where they had previously held territory, both birds return to this territory and fight each other for it. There is no evidence of partner recognition. When pair is moved to Cage 2 where they also had previously held territory they return to it and fight violently with each other. The subordinate bird No. 22 is forced by No. 21 and the other birds in the cage to a new corner. At no time, in spite of frequent use of voice, is there partner recognition.

(c) Birds of pair 15–32 are separated for eleven days and then have head and neck feathers replaced by breast feathers. The birds are placed with other herons, first in Cage 2 and then in Cage 1, without showing signs of recognition. In Cage 2, when the birds contacted in an attempt to occupy their common territory, they fight each other.

(d) Birds of pair 2–3 are isolated for thirteen days and then have breast feathers added to head and neck. When returned to home cage they fight between themselves for old territory. The subordinate bird, No. 3, is vanquished and is forced by partner to a new position on the ground. There is no gesturing or sign of recognition by features or voice.

(e) Pair 23–26 have their heads refeathered with breast feathers. When placed in a cage with other herons the subordinate, No. 26, is forced into a corner by the other birds. During a month's stay in this cage the group is never re-formed even when the number of birds in the cage is reduced.

Both pairs 23–26 and 21–22 had been previously tested for partner recognition before the refeathering experiments began. As pointed out above, the latter couple had recognized each other after a separation of twenty days and the former after seventeen days. Young herons, therefore, are able to recognize partners much longer if the feathering pattern of the head and neck has not been modified. Evidence has been presented above that young herons recognize their partners also by differences in voice. In the refeathering experiments reported in this section, the hearing capacity remained unaltered and yet the young herons were unable to respond to the auditory cues after an isolation of six days or more.

Further evidence that auditory cues without adequate visual ones are unable to hold pairs together was obtained by placing single birds of various pairs under screened boxes in a new cage. When the other members of these pairs were introduced into the cage, in no case did a free bird take up a territory near its imprisoned partner even though the latter called loudly. Hence while voice seems to play the major rôle in initiating and synchronizing gesturing, pairs are held together primarily by visual cues.

PECKING ORDER AMONG NIGHT HERONS

In the field we attempted to find evidence for the existence of a pecking order among Night Herons such as Schjelderup-Ebbe (1931) described for "species of herons." When the young herons are beginning to fly they frequently arrange themselves at different heights among the branches of the nesting trees. Since there is an obvious tendency for the young herons to climb upward it seemed that the relative height of any heron in a tree might be an index of its superiority. In the laboratory, however, the earliest maturing young secured the highest perches and defended these against younger birds. The vertical distribution in the field appeared therefore to be an index of age. As many as eleven young herons were found on a single pine at Massapequa, and groups of six and seven were not rare in several other colonies. As soon as the young begin to fly they mark out territories. The owner of a territory has a decided advantage in any dispute with a newcomer. In the field at Massapequa we saw several instances where a young heron successfully defended this territory against an adult. In the laboratory, also, adults fled from the onslaught of a young bird in the latter's territory. It was clear that this infantile territorialism so completely dominated the social behavior of young herons that pecking orders, if they existed, would be very difficult to detect. Certainly in most cases the bird which gave way in any encounter would prove to be the trespasser into the territory of another.

As our experiments with the pairs of young herons continued, some unexpected results were secured. In pairs 29–31 and 15–32, the first-mentioned bird was in each case dominant (Table 1). When these pairs were broken during recognition tests and later crowded with other herons in a strange cage the new pair 29–32 was produced with No. 32 dominant. Since the latter bird was a female and the former a male this reversal was an exception to the rule that males are dominant to females. It therefore seemed possible that there might be present a pecking order in which No. 32 stood higher than No. 29 but below No. 15. Attempts to demonstrate such an order by the usual methods (Masure and Allee, 1934) failed. When food is placed in a cage with the birds they usually fly down to it, one by one, and there is no order of precedence. If the herons are starved for one or more days several birds fly down together and food may be taken by several birds at one moment. The "social reflex runway" described by Murchison (1935) is not suitable for herons because when forced to the ground in a strange environment they do not run toward one another. Similarly the social-discrimination cage employed by Murchison (1935) was found to be useless for herons. We were therefore forced to employ new methods in our study of the pecking order in herons.

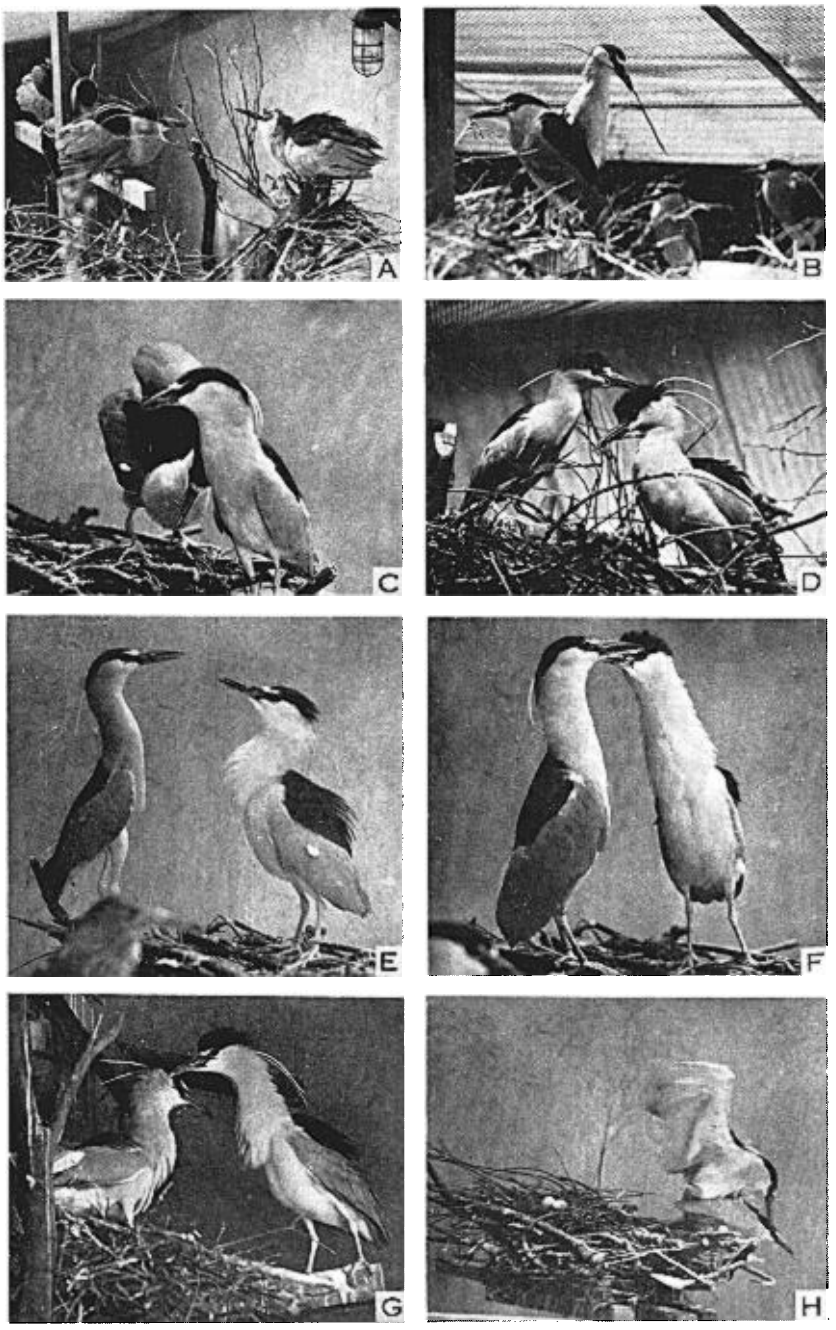
If young herons are driven into one corner of a large cage, the birds that

are strangers in that area tend to flee and those which chance to be resident are the first to revolt against the crowding and successfully force all other birds to yield. In order to eliminate superiority due to territory possession, a series of glass-sided cages was utilized. These had a floor space of either 2.8 square feet or 4.6 square feet, that is, smaller than the territory of any one bird. Three herons at a time were placed in each cage and dominance was determined as in the pairs of unrestricted herons. There was no overturing, except when pairs were introduced, but when two herons billed, the bird which kept its head higher was considered to be dominant. Each group of three herons was tested for a whole day and given at least one day's rest before being tested again. The number of billings in any one day by any two herons varied from 0 to 147. Every combination was tested on at least two different days. Birds which reacted very little were tested for as many as ten days.

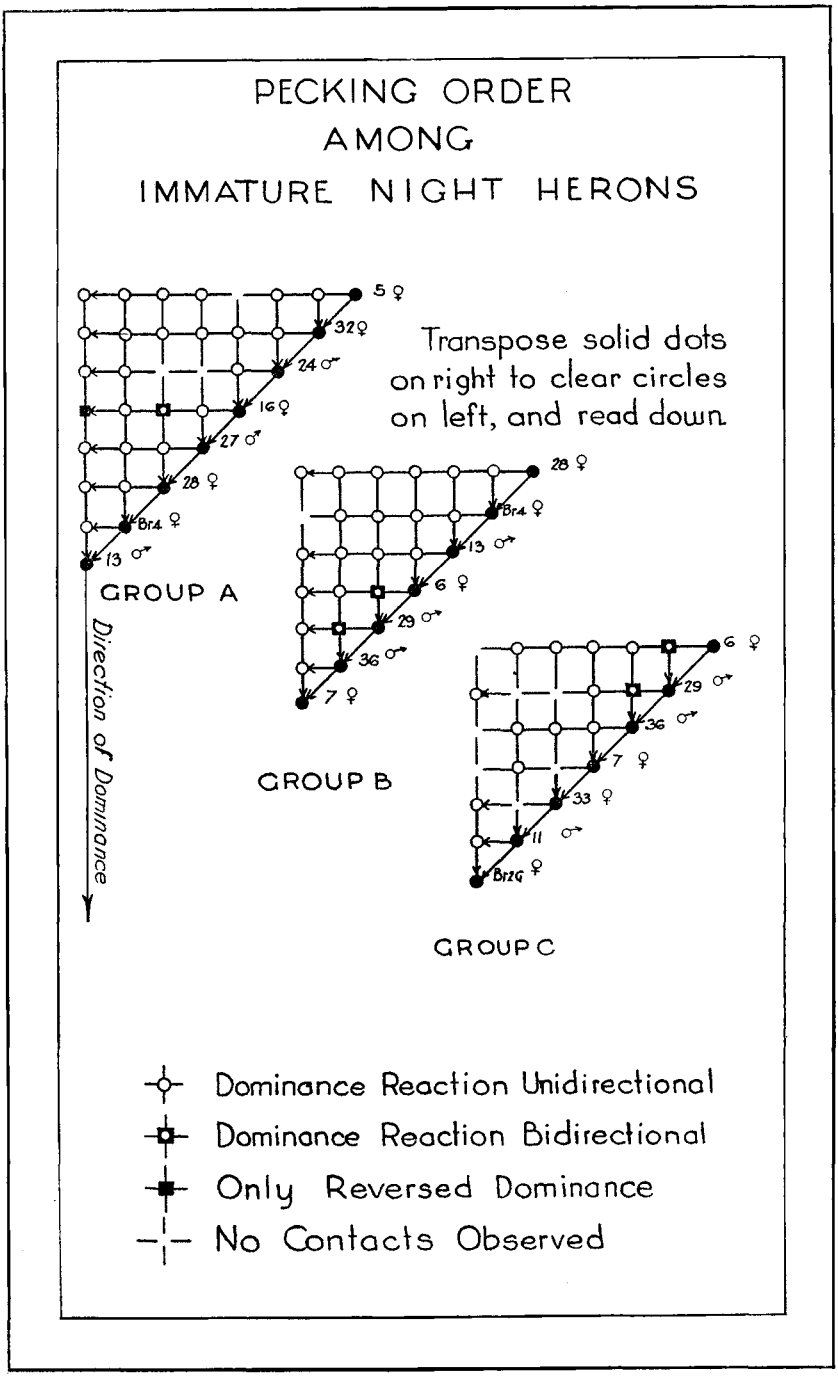
The data secured from introducing fifteen birds, three at a time, in all possible combinations in the small cages are shown diagrammatically in text-fig. 2. In very few cases did a bird which held its head high while billing with one bird, hold its head lower than that same bird when tested again. These cases are shown by the symbol light circle in a black square. In Group A there was only one such pair of birds where the right of holding the head higher in billing had not been decided. Both Group B and Group C (text-fig. 2) included two other such combinations, 6–29 and 29–36. The chief characteristic of Group C was the lack of billing reaction exhibited by the birds. This group was tested on several days and, due to territory-defense reactions and infrequency of billing, dominance relationships were not completely determined. If our criteria of pecking order are correct these birds should be placed near the bottom of the order. Their actual position was determined by the few reactions secured.

Certain other exceptions indicated in the diagram require explanation. The two failures to react in Group A involved No. 24 which was killed in a fight before these reactions could be recorded. This is not to be confused with failure to respond, found frequently in Group C. Since the birds in the latter group had enjoyed the usual isolation that territory defense gives all Night Herons above a certain age, their failure to react cannot have been due to their previous mistreatment by other herons. It seems that birds at the bottom of the pecking order described here owed their position to physical weakness which prevented them from engaging in billing bouts with other herons when forced into their proximity.

In the entire series of tests there was only one small group of birds which engaged in a 'triangle' formation such as Schjelderup-Ebbe (1931) has described in hens. In Group A, No. 16 is definitely subordinate to No. 13 and yet is clearly dominant over No. 27, No. 28 and Br.$_4$. Nevertheless the



SEXUAL BEHAVIOR OF BLACK-CROWNED NIGHT HERONS


PECKING ORDER
AMONG
IMMATURE NIGHT HERONS
5 ♀
32 ♀
24 ♂
16 ♀
27 ♂
28 ♀
Br4 ♀
13 ♂
GROUP A
Transpose solid dots on right to clear circles on left, and read down
28 ♀
Br4 ♀
13 ♂
6 ♀
29 ♂
36 ♂
7 ♀
GROUP B
6 ♀
29 ♂
36 ♂
7 ♀
33 ♀
11 ♂
Br2G ♀
GROUP C
Direction of Dominance
Dominance Reaction Unidirectional
Dominance Reaction Bidirectional
Only Reversed Dominance
No Contacts Observed

TEXT FIG. 2

last three birds were dominant over No. 13, the 'tyrant' of No. 16. Such a roundabout sequence of dominance if found in hens would be attributed to one of the social factors elucidated by Schjelderup-Ebbe (1931) but in herons with their marked territorialism other explanations must be sought. This group was an extremely active lot which never quieted down entirely in the experimental cages. It is highly probable that distracting factors, such as the activity of other members of each test group, were responsible for this exceptional result.

The work on these herons continued from October 24 to November 24, and several test groups were run at one time. The advent of molt in some of the birds made it inadvisable to continue beyond this point. Although the work was incomplete it at least showed the presence of a pecking order which owed its existence only partly to previous social experience. That is, Group A includes three pairs of birds (5–28, 13–16 and 27–28) which had previously held territory together in the large cages; Group C, three of these pairs (36–33, 6–11 and 7–11). The position of head in billing in the small cages would be merely a repetition of the thoroughly ingrained habit begun in the nesting area before the aggregations of young acquired the territory drive. But this would not account for the equally well-fixed order of dominance exhibited by birds living continuously in well-marked territories and having no social contacts other than territory defense. It seems then that the birds recognize physical differences unapparent to our eyes and that these determine the order of dominance when any two birds engage in mutual billing. There are, however, some birds which through physical weakness or temperament fail to engage in social contacts and are therefore, as stated above, assigned to the bottom of the order.

COMPARISON WITH THE DOMINANCE AND TERRITORIALISM IN PIGEONS

The sequence of dominance in herons, which we have called a pecking order, regulates the formation of pairs but it seems to be of little practical value in the social life of captive herons once the territory drive has isolated various pairs of young birds. The question arose, Might not territorial rights overshadow the operation of dominance reactions in other groups of birds? In pigeons there are well-marked territory claims (Taylor, 1932) although neither adults nor young fight for these rights in the vigorous manner of herons. Masure and Allee (1934), who have investigated the pecking order in pigeons, found some evidence of this territorialism. They state, ". . . BB always seemed to do the pecking when she was at the entrance of the roost: when BY tried to enter she would be pecked and would retreat. On the ground, however, BY was usually dominant." Schjelderup-Ebbe (1924) pointed out that a bird introduced into the territory of a stranger will become subordinate to the latter. Hence it

seemed to us possible that if we studied pigeons in their own territories, the pecking order would be masked in the same manner as in Night Herons under normal conditions.

For this study four pairs of male and female pigeons were introduced into small cages measuring 23 by 11 by 15 inches and 25 by 19 by 16 inches and two additional males were placed in single cages of the same size. Each cage was screened from the other and provided with one or two perches. The pigeons were well fed for two days and then tested by transferring each male bird into one of the other occupied cages. In every case the resident male charged the newcomer and drove him in frantic distress against the screening of the cage. The experiment was repeated with the four adult females with exactly the same result. An adult female introduced into a small cage which has contained an adult female for two days is vigorously attacked by the resident bird. When the attacked female is returned to her own cage and the former tyrant introduced into this strange territory the resident bird is exactly as dominant as the tyrant was in her own territory. When the experiment was repeated with immature male pigeons, six weeks of age, nearly the same results were obtained. That is, in tests with six young pigeons only one bird (R-G) when introduced into the cages occupied for two days by the other young pigeons, was able to dominate the resident birds and he did so in only two cases. Since this bird swelled its throat while driving, its superiority was probably due to an incipient sex drive.

Repeating the experiment with the adults but recording the heterosexual contacts gave many more exceptions. That is, some resident females were successful in driving introduced males but often they retreated and in some cases permitted the introduced males to tread them. The sexual drive of adult pigeons, therefore, prevents the females from exhibiting strong territorial claims while in the presence of males.

MECHANISM OF SEX RECOGNITION

Male pigeons recognize females by their behavior, as Craig (1908) pointed out long ago. What cues male Night Herons might utilize in sex recognition have not been described in spite of the relative abundance of the species. We therefore planned to study the breeding behavior both in the field and in the laboratory with a view to comparing the mechanism of pair formation in immatures with that of adults.

Eighteen wild adults were secured from the National Zoological Park through the kindness of Dr. W. M. Mann. These birds were first tested in the large outdoor cages where we kept the young until it had been demonstrated that each bird defended its immediate surroundings against the encroachments of other herons and that there were no two birds tending

to occupy the same territory. They were then transferred through the kindness of Dr. Frank M. Chapman to one of the live-bird rooms of the Museum, which has a floor space of 442 square feet and a high overhead ceiling, allowing us to arrange perches from three to fifteen feet from the floor. The birds were maintained in this room at an approximate temperature of 70° F. and fed porgies once a day throughout the winter. The first pair courted February 15, and the last egg of their first set was laid April 3. At this time another pair began to breed and their laying ran synchronously with the earliest ovulation we observed in the field, namely, at the Great Neck colony. Four pairs of white adults laid eggs, four in number at intervals of from forty to fifty hours, in nests of their own construction and at least attempted to rear young. The eggs hatched in from twenty-two to twenty-four days and not twenty-four to twenty-six as stated by Gross (1923). This was probably due to our higher temperature in the bird room. One pair laid twice, each time in a different nest. In addition, seven pairs of first-year birds kept in the outdoor cages built nests and laid eggs. These pairs were formed with new partners indicating clearly that pairing off at the breeding season involves other factors than those which regulate pair formation before the breeding season. One group of three first-year birds built a nest and took turns at incubating the eggs. This group consisted of Nos. 5, 28, 27, birds which had formed a three-membered group during the earlier observations. Later, this group of one male and two females was split at different times into various pair combinations. The mechanism of mate selection at breeding time operates to break up juvenile pairs but in this group of three birds in a cage 150 by 300 by 108 inches not only did the pair 5–27 not break but an old partner of both birds was able to join the nesting pair without interference. The exceptional breeding behavior of this group of birds is probably due to partial spaying of Nos. 5 and 28. Further study on this aspect of the problem is in progress.

The behavior of these breeding herons in both the indoor and the outdoor cages was checked against the breeding behavior of adults in the field, especially at Great Neck. The latter birds were not banded and they could not be captured for the verification of sex. Nevertheless their behavior was nearly identical with that of the captive birds. We found it therefore possible to identify sex in the field by the following criteria, first worked out with the captive birds.

(a) *Plume length.*—In any mated pair the male usually has the longer plumes and sometimes one or two more than the female (Plate 3, fig. G and Plate 4, fig. B). This was true for six of the seven pairs of adults in the laboratory. In all of the first-year breeders the male had a short plume and the female none at all. In the one exception, the female had a plume three inches long and the male none. A careful check of fifty-six breeding pairs

at Great Neck, using two or more of the criteria listed below, revealed fifty-two with longer plumes in the male, three with them equally long and one with the female having an advantage in plume length.

(b) *Twig ceremony.*—The male standing over a crude nest platform, or at a distance from it, holds a stick in its bill and loudly snaps its bill on it while its head is moved rhythmically up and down. Frequently the neck is stretched vertically upward to nearly its full extent and the bill brought in close to the neck while the snapping continues. Although the stick may eventually be placed in the crude platform it is more often dropped.

(c) *Snap-hiss ceremony.*—The unmated male while standing alone on a nest platform but more usually while moving alone about a tree, takes two or three steps forward, halts, arches the back, lowers the head until the bill is nearly as low as its feet and then while raising one foot produces a click or snapping sound in its throat, immediately followed by a prolonged hiss. The performance is repeated while either the same or the opposite foot is raised. From eight to ten performances may be given a minute and the series lasts over two minutes, to be followed a minute later by another series. In the laboratory we were present when this call was produced by male RB of pair F, male BH of pair G and by two other males which remained unmated throughout our studies. The call was also given by one of the first-year birds (RB–G) immediately before it secured a mate. In the field the call was heard many times and on four occasions we followed its author for long periods, making sure the bird had no mate. It is therefore assumed to be characteristic of the male before he secures a mate.

As a modification of this call may be listed the *peck-hiss* which represents a combination of the usual peck of territory defense with the snap-hiss ceremony. It is given by the male soon after a female has joined him and before the paired condition is fully established. It was best seen among our birds in pair F but was also heard in the field.

(d) *Overture and display.*—When a female arrives in the vicinity of the breeding male he overtures and displays. The overture is identical with that of the juvenile bird except that the male often turns his head until one cheek is parallel with the ground (Plate 3, fig. C). At the same time the male utters a greeting call more guttural than that of the female or immature and less prolonged. The head is then raised and the feathers on crown, neck and back are raised. At the same time the pupil is contracted and the eyeball actually protruded from its socket, exposing the red iris to its maximum extent. The plumes are erected and may even fall forward over the head as the male bows again to the female and either repeats the greeting or turns his partly open mouth toward her. The female in turn repeats the salutation including the overture, feather raising, plume erection, pupil contraction and eyeball protrusion, but her lower-neck feathers do not

protrude or extend so far laterally as those of the male and her higher, more prolonged salutation distinguishes her at once from the male (Plate 3, figs. D–G). Only when both birds call loudly together do their voices seem alike. The male usually overtures first and he holds his head lower than does the female. When, however, he displays he usually holds his head higher than does the female. If the overturing is followed by billing the male still holds his head higher. At the beginning of courtship the female may not display at all.

(e) *Copulation.*—This act is not immediately preceded by any display or sound on the part of either bird. The female merely stoops and the male steps forward on her back and with shuffling movements of his feet secures a grip on her humeri or shoulders while bringing his tail sharply down and turned toward the female's cloaca. He always assumes this dorsal position except in the case of homosexual unions to be described below.

The formation of pairs was witnessed both in the field and in the laboratory. In the latter the females came directly to males which were guarding crudely built nest platforms chiefly of their own construction (Pairs C, D, E and F). In the field, although the males may take up positions near old nests, the females seem to be attracted by the snap-hiss ceremony and not by the adjacent nest. The following observation made at Great Neck, April 19, 1937, will illustrate: "A bird, apparently a male, moves from limb to limb of a tree while giving the snap-hiss call. Between calls he would break twigs and fumble them in a modified stick ceremony. A second bird with very pink legs flies to the tree and moves toward the performer. A third bird flies in but is immediately driven off by the second bird which is content to remain near the performer."

In the laboratory most of the males which secured mates engaged in a long twig ceremony over a period of several days before females entered their territories. In the field many single birds were seen engaged in this ceremony but we could not be sure that no females had yet entered their territories. The behavior in the field differed from that in the laboratory chiefly in that birds flew about more to the different trees. There was considerable settling down in other birds' territories and a hasty retreat when the resident birds returned. A resident bird, seeing a stranger on its territory, may fly low and give a rasping call which appears to serve as a warning. This is the only call given by birds in the field which we did not hear in the laboratory.

On the basis of the above criteria for the recognition of sex we may describe the sequence of events which takes place in the courtship of the Black-crowned Night Heron. This represents a composite picture of many observations made at Great Neck during April and May interpreted by means of data secured in the laboratory. When flocks of herons return

from winter quarters early in spring they settle down on or near trees which contain last year's nests. Each bird selects a certain territory in accordance with the territorial requirements found even in immature herons. The males soon make themselves conspicuous by developing two new types of behavior pattern: (a) the twig ceremony which may be considered 'symbolic' of nest building; and (b) the snap-hiss ceremony which borrows no elements from any other behavior. The breeding female is attracted by one or both of these performances and settles down on the tree occupied by the male. Out of the breeding season the male would not tolerate this approach but the sex drive has reduced him to an apparent lower position in the pecking order. Instead of attacking, he adopts the attitude of a subordinate bird and overtures to the newcomer. At the same time his changed physiology has modified his greeting to a guttural call which further reveals his sex. As the female lingers in this unguarded territory the male returns to his state of dominance by an elaborate display. This consists of raising feathers of crown, neck and saddle as well as the long plumes of the head. He bows, his pupils contract, eyes bulge and mouth gapes. The latter behavior patterns are available to the female and the male's gestures stimulate her to respond in kind. Neither her plumes nor neck feathers equal those of the male in extent of spread and the male gradually raises his head with frequent displays until he has regained the same advantage in head posture seen in the dominant bird of immature pairs (Plate 3, figs. C–G).

The method of pair formation, while totally different in adult from that in immature companion pairs, results in the male of heterosexual breeding pairs being always dominant. The display, however, has other functions besides returning the male to his dominant position. Observations in field and laboratory indicate that the act of copulation often fails because of lack of cooperation of the female. It is obvious that the male's display stimulates the female for she replies with higher voice and lesser display. It would seem, therefore, that the second function of the display is to raise both partners to the same emotional level in order that the female should bend her body parallel to the nest and permit the deliberate, shuffling movements of the male.

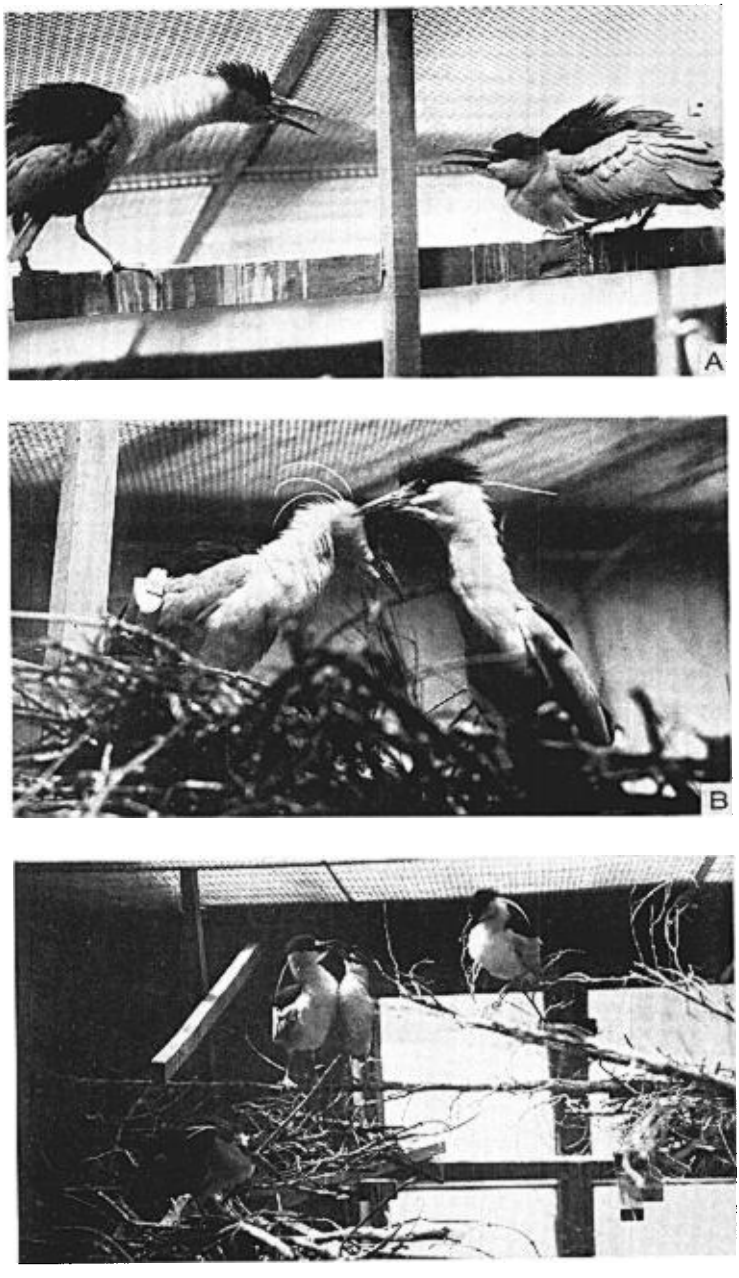
The male's twig ceremony changes gradually to nest-building activity (Plate 3, fig. B). As the nest progresses the male may bring twigs to the female which remains in the nest and actively builds. This stick-passing probably functions as another bond to hold the pair together. The male is greatly stimulated by the sight of an egg in his nest, even one taken from another nest before his mate has laid. He at once begins to brood and in the laboratory cages only males brooded during the daytime of the first few days of incubation. Later the female assumed most of the daytime brooding duties and, in a few cases in the laboratory, would remain on the nest until touched.

HOMOSEXUALITY IN ADULT NIGHT HERON

Since the male heron, in order to attract a female into his territory, adopts the gestures of a subordinate bird, the question remains, May not another male occasionally pair with him in exactly the same way that two immature birds forced into the same territory may form a pair provided one subordinates itself? In the field this probably never would happen because there is a superabundance of possible territories and the snap-hissing male while calling often moves from one to another. In the laboratory cages this is a real danger because of the restriction of space. One of the reasons why only four pairs of our white adults bred was that two other pairs which formed, were male-male groups.

The formation of both of these homosexual pairs was observed in detail. Bird R_4, driven by other adults of the colony, was forced into the territory of B_4. This latter bird had been engaging in the twig ceremony and when R_4, a male, entered his territory he lowered his head and overtured in the manner of a subordinate bird (Plate 3, fig. C). Bird R_4 stood a moment in the territory of B_4 but when the latter displayed in exactly the manner he would to a female, R_4 moved away. Only two other pairs had formed in the bird room at this time and there was still great competition for space. Bird R_4 was forced again and again into the territory of B_4 but he never played with the sticks of that bird's nest or even engaged in twig ceremony. After repeated displays B_4 mounted R_4 but the latter immediately flew away. The next attempt was also unsuccessful. The third attempt was initiated by R_4 which had never displayed. B_4 remained in his territory and permitted himself to be trod. The pair was now formed but B_4 was unsatisfied with his nest and accompanied by his male mate flew a few days later to a new group of branches where he began a new nest. The pair remained together and defended their territory against other birds throughout the breeding season. Bird R_4 was observed to tread B_4 twenty-one times and only once did the latter avoid these advances. On the other hand B_4 trod R_4 eleven times and was avoided by the latter five times. It will be noted that B_4, the original owner of the territory, although displaying, did not succeed in dominating his male mate which mounted him approximately twice as many times as he did the other. Here was a case where two males formed a pair because one was forced into the other's territory. The former male being in a strange territory showed no aggression and the latter male because of its sex drive was forced to adopt a subservient attitude to the newcomer. In time neither succeeded in completely dominating the other, although the newcomer had an advantage over the resident bird.

The second pair of homosexual white males was also formed as a result of crowding. The two birds were holding separate territories until driven to the floor of the bird room by a pair seeking a favorable nesting site. One



ERECTION OF PLUMAGE IN NIGHT HERONS

bird overtured to the other and displayed. This subordination of the overturing bird permitted a further approximation of the couple. A few days later a bond had formed between them and they flew together to a nesting site on the top of our observation blind.

The one pair of homosexual first-year males which formed was not so clearly the result of crowding. Male RB–B was observed to overture and display toward any bird which entered his territory. Almost invariably the newcomer would become frightened and move away. Male RY–Y appeared to be stimulated by this performance and remained to respond with a similar display. Here again there was no territory defense by either bird against the other but strong territory defense against other birds. Soon after the pair had formed they flew to a new territory which they defended against intruders.

INDUCEMENT FOR COPULATION

The three homosexual unions reported above gave further evidence that the male requires no stimulus from the female to attempt copulation. The chief requirement is that the one bird of the pair will for the moment at least take a subservient attitude. We frequently saw normal copulations fail merely because the female lifted her head into the dominant position. Proof that the female is actually subordinate to the male at the time of copulation is shown by the fact that she frequently overtures to him immediately after he dismounts. As shown in the study of the immature bird this is one of the criteria of a subordinate position.

We frequently observed both in the field and in the laboratory, copulations without any preliminary ceremony. In the few cases where there was some introductory behavior this emphasized the fact that the male must regain his dominant position relative to the female before he will mount. In some cases the female may hasten this process by overturing to the male. The following observation made at Great Neck, April 25, will illustrate: "Two birds are standing side by side. The one with three long plumes is attempting to break twigs from a branch. The one with shorter plumes overtures to the other, presumably the male, and attempts to bill. The presumable male at last engages in billing while holding his head higher than does his mate. While billing the apparent female raises her head until it is higher than her mate's. This causes the apparent male to turn away, but his mate gently pushes him with her bill and overtures. A minute later the apparent male mounts mate in typical copulation."

On the other hand if the female is not ready for copulation the act may not be completed even though both partners display. Another observation made at Great Neck the same day as the above will illustrate: "Male bird, to judge from the three long plumes, picks up twigs from incomplete nest

and engages in typical twig ceremony while erecting feathers of lower neck. He displays and apparent female, with two much shorter plumes, responds by erecting feathers of crown and neck. Male continues to build nest and then walks to end of limb to break off a twig. He brings it to her but drops it before reaching her. They stand close together, he mounts but copulation is not effected."

SEXUAL SELECTION IN THE NIGHT HERON

It seemed to us a rather significant fact that the two males of our series of twelve adult males and five adult females that had damaged crowns and broken head plumes, were among the first birds to build nest platforms, and were the most persistent in both twig and snap-hiss ceremonies and yet neither secured mates the entire season. Apparently their unusual appearance caused females to avoid them. This raised the question of the functional significance of plumes. Lorenz was of the opinion that these structures could not be considered ornaments. It may be noted, however, that they are erected primarily during the display. They serve no function in territory defense for they are held flat against the neck at this time. Although these feathers increase in length during the breeding season, their change is not as dramatic as are two other modifications of the breeding adult which have apparently entirely escaped the notice of ornithologists.

In both our first-year herons and in our white adults there was a marked change in the color of the lore and most of the bill at the beginning of the breeding season. In both sexes this turns a dark blue, purplish and finally black (Plate 2, fig. B; Plate 3, fig. F). In our series of first-year birds the females developed blacker lores than the males but in our older birds, while the black was equally intense, the males developed these dark tones earlier and held them longer than did the females. As the lores darken the upper and lower mandibles of the white birds also darken until at the height of the display period the mandibles may be entirely black both inside and out. As the pupils contract and the eyeballs protrude during the display, these dark lores give a sharp color contrast to the red irises. With the onset of incubation they begin to fade until shortly after the eggs hatch they change to a pale greenish or yellowish in first-year breeding birds and to a chalky white in the older adult birds. The second change occurred in the pigmentation of the legs. Hickey (1937), in discussing the variation in leg color of various eastern herons, states that some Long Island Night Herons often have pink legs. Most of our old Night Herons developed pink legs and feet at the height of their courtship. These were distinctly redder in the males of two pairs and equally red in two others. In none of the first-year birds was this color attained although some underwent a slight change in leg color. In the field at Great Neck a check was made of the leg color of

over forty-three adult mated pairs. In thirty-eight both sexes had pink legs, in four the female had yellower legs than the male, in one pair of white birds both sexes had equally yellow legs and one lone male seemed to have yellow legs. Hence, although the laboratory white adults demonstrated a change of leg color during the breeding season, field observations indicated that not all breeding birds attain the full pink color. It may be noted 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 observed in the laboratory that courtship activity was "contagious" in the sense that the movements of one bird started the others to court. Similarly, the courtship movements of the male when repeated by the female serve to stimulate her. When one bird of a pair of immature herons flies to its territory it gives a greeting call which serves to identify it. The partner responds and they bill. We showed that where the partner could not hear there was toleration but few contacts. Similarly in the adult pairs the greeting identifies the arrival and makes possible further contacts. Paired birds, even after the eggs have been laid, when returning to the nest combine a display with the greeting. Since the male's display is greater than that of the female it serves to keep him in a state of dominance in exactly the same way that a superior head posture functions in the immature. Overturing and billing are much rarer in both first-year and white breeding pairs than in juvenile companion pairs. The fact that both sexes of adult pairs display would seem to indicate, however, that both are sexually stimulated. This Huxley (1921) has called 'mutual courtship.' Carpenter (1933) has showed that the courtship of pigeons may be subdivided into acts requiring different thresholds of provocation. These acts in a definite order "serve to synchronize the degrees of sexual excitation in the two animals of a pair." There is, therefore, some evidence, if only indirect, that a mutual selection such as Huxley postulated may have taken place to foster the genesis of epigamic characters in the Black-crowned Night Heron. Those features, common to both sexes during courtship, include (a) black lores and mandibles, (b) red irises which can be expanded by contraction of the pupils, and (c) white plumes set against a black crown.

Future work may show that other herons undergo the seasonal change of lore color which we have found in the Night Heron. Thus the pairs of Louisiana Heron (*Hydranassa tricolor*) which Huxley (1922) found to have different shades of lore color may not have owed these differences to any selection of bright-lored bird by a similar variant. Rather, these differentially colored pairs were in different stages of the breeding cycle. Possibly the bright lores are attractive but all herons of this species would tend to have them at the height of the courtship season.

GENESIS OF DOMINANCE

The earliest feeding response which we observed among the young herons (fourteen days of age) was an attempt at grasping and stroking of the parent's beak. No system of rotation of either parent's supplying food or of feeding young was noted. The oldest and largest bird in the nest secured the greatest quantity of fish. The parent frequently supplied large pieces of fish, when a tug-of-war resulted with the oldest bird the victor. At about three or four weeks it was observed that the older birds vied for the privilege of stroking the parent's beak. In such instances each bird attempted to keep its head higher. Frequently bills were contacted, opened and shut and the opponent's head pushed back. Later these movements became more precise; the smaller and presumably younger birds assumed a subservient position of the head every time they billed with their older brothers or sisters. In this way the billing behavior between young in a nest seemed to be an outgrowth of the feeding responses of the young.

From approximately five days of age, young herons indicate a form of antagonism by a continuous erection of crown feathers during the presence of the observer. At about ten days of age, the oldest bird in the nest initiates an exaggerated form of this reaction, namely, spread wings, erected crown feathers, and a peck followed by the screech call. Parents, when entering the nest, issue a recognition call accompanied by an erection of crown and neck feathers. Immature herons, approximately nine weeks old, overture to their parents, exchange recognition calls and bill with them. The parents may erect the feathers of crown and upper part of the neck but those of the lower neck never stand out in typical courtship manner.

Young herons approximately nine weeks of age recognize their parents and the latter distinguish their own young from other immatures of the same age. This was well shown by transferring four young of the first-year birds to different nests having young of the same age in the same cage. During a single observation period of six hours there were twenty-seven contacts between the foreign young and resident young. The transferred young, whether in the new nest or within a distance of eight feet of it, billed with resident young until one or more young assumed the subordinate position of the head. There was no attempt to secure territory by the transferred birds and only the resident young gave food calls. Twenty-two contacts between adults and young in this experiment were observed. The adults pecked only the foreign young but this attack was not as vicious as it would have been against strange adults. Parents responded to the recognition calls and food calls of their own young only. Adult pairs continued to exchange recognition calls while erecting crown and upper-neck feathers.

Grouping and interchanging the young of a number of nests did not result in territory-defense reactions between young. It would therefore seem that

the feather erection of young birds is a defense mechanism developed before there is any claiming of territory. The first evidence of territory defense begins when the young leave the nest and climb about in the nesting tree. In brief, defense responses begin in the ontogeny of the Night Heron long before there is any territory defense. Contrary to the views of Schjelderup-Ebbe (1924), a pecking order, that is a dominance hierarchy, may appear in nestlings of the heron, but when territorialism later appears it completely obscures this order in all except paired birds or in grouped individuals from the same nest.

DISCUSSION

Throughout our work we have employed the term "territory" in a broader sense than usually found in the ornithological literature. The term has recently been the subject of critical review (Friedmann, 1935; Tinbergen, 1935; Mayr, 1935; Portielje, 1936; Lack and Lack, 1936). The most comprehensive definition is that given by Tinbergen (1936). He states that territory is "an area which is defended by a fighting bird shortly before and during the formation of a sexual bond."

Breeding male herons defend their immediate vicinity against the encroachment of aggressive birds. But if a non-aggressive male or female enters one's territory, the resident male assumes a subservient attitude and in this way invites the newcomer to stay. A courting male does not lose territory entirely. If a bird guarding a neighboring territory should encroach upon his domain he thrusts his head forward in a vigorous defense reaction indicating that territory-defense behavior is still available for use against aggressive trespassers.

There is no doubt that the territory of the adult Black-crowned Night Heron is identical with that of the immature although it may embrace more area. We have shown that two immature herons, strangers to each other, may form a pair if forced into the same territory while too harassed to exhibit typical defense reactions. Similarly, two adult males may form a pair which will remain faithful to each other throughout an entire breeding season provided they are driven into the same territory at the time one of them, because of its reproductive drive, is forced to adopt a subservient attitude. Territory has, therefore, other functions than usually assumed. It aids the formation of bonds between two birds which are forced to occupy a common area. In Nature the female is attracted to the male by his snap-hiss or twig ceremony. Being in a strange territory, she would not adopt any aggressive attitude toward the male. The latter in his turn is forced by his sexual drive to adopt a subservient attitude. The result is exactly the same as if the birds were forced together in a strange locality where neither would develop a defense response.

Once a bond has been formed, the pair may leave the territory together and build a nest in a new locality. We noted both in the laboratory and in the field that such pairs easily drove resident birds from the territories they had been defending. The display of the heron has no rôle in territory defense. In other birds it has been assumed to make the male dominant to the female in order that copulation may proceed (Portielje, 1936). Our detailed observations indicate that it has this important function in the heron as well, even though the response of the female may also serve to stimulate the male. Since males giving the snap-hiss ceremony may have no nest platform in their immediate vicinity, it is obvious that nests do not play as important a rôle in the formation of pairs of Night Herons as they do in some other birds, such as the Grey Heron described by Verwey (1930).

It is highly probable that other species of Ardeidae will be found to have a social system very similar to that of *Nycticorax*. Many features of the behavior of American Ardeidae given by Bent (1926) indicate that the courtships of the different species have much in common. Nevertheless, the life history of no other American species is known in sufficient detail for a close comparison with the behavior of *Nycticorax* as described above. It is necessary to turn to Verwey's description (1930) of the European Grey Heron for these details. Verwey describes both young and old *Ardea cinerea* as directing vicious thrusts toward others of their own kind and his description (p. 15) of this behavior in the field indicates that *A. cinerea* makes the same territory claims as does the Night Heron in freedom. He states that as soon as the young Grey Herons begin to fly they develop a greeting cry which suggests that individuals within the family group recognize one another as in the case of the Night Heron. No attempt was made by Verwey to identify bonds between the young herons but the description of Holstein (1927), as quoted by Verwey, indicates that there is an even more severe competition between the young Grey Herons of the same nest than among nest mates of Night Herons. Nevertheless, Verwey raises the question as to the functional significance of this struggle. It would seem certain from Beetham's (1910) account of the struggle among nestlings of *Ardea purpurea* that age and superior billing ability aid in securing food from the parent. The same struggle was seen by us in young Black-crowned Night Herons and was shown to give rise to the specific dominance reaction which we call billing.

Lorenz (1934) found that young *Nycticorax n. nycticorax* are recognized, fed and protected by their parents outside of the nest. We have observed no feeding of young outside of the nest area in our American race. Nevertheless, parents distinguish their young from other young and the latter can distinguish their parents from other adults. In the Grey Heron adults may feed strange young as well as their own, indicating that there is less recognition of young than in the case of the Night Herons.

The Grey Heron exhibits certain movements not found in the Night Heron but otherwise the courtship behavior of the two species has much in common. The male Grey Heron attracts the female by a modified flight call and not by a snap-hiss ceremony described above. There is no typical twig ceremony in the Grey Heron although the bill clicking practiced by the male only might be considered a twig ceremony without twigs. The neck of the mate is stretched forward and slightly downward, not upward as in the typical twig ceremony of the Night Heron. De Waard (1936) claims that the female may occasionally posture and click the bill in the manner of the male. If this is true, the bill clicking may be merely an overture movement practiced in the Grey Heron primarily by the male.

The stretch movement of the Grey Heron seems to correspond to the overture and display of the Night Heron modified by a vertical posturing of the neck. As in the case of the Night Heron's display, this is at first practiced by the male only but later by both sexes. If our interpretation of this movement is correct, it would serve the double function of securing dominance for the male and stimulating the female to sexual activity. When adult Grey Herons are paired they exchange greeting calls. Verwey found that the young Grey Herons failed to retain this call after the young left the vicinity of the nest. Our captive birds, being kept in close contact throughout the winter, retained their greeting call and we were able to show how this call together with the overture was taken over into the pattern of the adult.

The Grey Heron has one call that has no analogue in the Night Heron. After an unsuccessful copulation the female Grey Heron utters a distinctive cry, according to Verwey. The female Night Heron either remains silent or overtures. The overturing tends to facilitate the second attempt because it places the female in a subservient position to her partner.

No evidence has been found in our studies of the existence of a 'releaser' such as Lorenz (1935) described, that is, of an "organ of a peace-making ceremony without any sexual meaning" (Lorenz, 1937). The plumes are held in an inconspicuous position during the defense response and also during overtures. Steinfatt (1934) describes these plumes as being erected during the attack of the closely related *Nycticorax n. nycticorax.* This occurs in the American race only when an attack closely follows a display. Only during the breeding season when the display is combined with the overtures are the plumes erected at the same time that the heron bows low. In the Yellow-crowned Night Heron (*Nyctanassa violacea*) Nice (1929) describes a case of nest relief with erection of plumes. In the Black-crowned Night Heron such a relief is usually accompanied by recognition calls and the plume display, if it occurs, is part of the courtship. That this display is stimulating, is an inference based on the fact that a heron usually responds

to the display of its mate and also on the fact that early in the season before there has been much display the female Black-crowned Night Heron will not allow the male to mount. Two of our males with damaged crowns and plumes failed to secure mates although they courted for long periods in the presence of unmated females. As we have shown above, the erection of the crown feathers takes place in a wide variety of social situations while the erection of the plumes occurs only as part of the courtship display. Whether the failure of these birds to secure mates was due to their short plumes or the unusual appearance of the crowns cannot be stated. We have shown in the young herons that pairs form before plumes develop but these pairs are not sexually active. The fact that males of sexually mature pairs usually show longer plumes than the females is correlated with the fact that the male must secure dominance over the female before copulation may proceed and, in the process of securing this dominance, the male displays more extensively than the female.

CONCLUSIONS

1. The struggle for food among the nestlings of the Black-crowned Night Heron leads to a hierarchy of dominance which is maintained in older nestlings by billing reactions toward one another.

2. As flight develops young Night Herons claim territories which they defend against other herons. Territorial requirements tend to break up the groups of nestlings and a struggle for dominance in any one territory tends further to disintegrate the group but where dominance relations are well established immature pairs may remain together for months defending common territory even in new cages.

3. The new territorial requirements completely mask the dominance hierarchy among birds maintained in large cages except in the case of pairs or nestling groups. Crowding the birds into a single strange territory causes the reappearance of the dominance hierarchy.

4. Territorialism may similarly prevent the functioning of a pecking order in pigeons.

5. Members of pairs of immature herons may recognize each other after a separation of twenty days. Details of voice and feathering serve as cues in this recognition. Separation of members of a pair for only six days is followed by failure to recognize if the color pattern of the head has been modified by artificial refeathering.

6. Plugging the ears prevents a synchronization of greeting ceremonies, indicating that sound is more important than movement in calling forth these responses.

7. New pairs of immature birds may be formed by crowding two individuals for short periods in a common territory provided one bird accepts a

subservient position to the other. Homosexual male pairs may be formed during the breeding season by the same method. These pairs remain stable in new territory.

8. The normal formation of heterosexual pairs in breeding birds differs from that of the immature. The male attracts the female into his territory by his snap-hiss and twig ceremonies. At the same time the male assumes a subservient attitude toward birds of either sex entering his territory although he still attacks neighboring males which encroach in a belligerent manner upon his territory.

9. Adult pairs practice the greeting ceremony of immature pairs but during the courtship period display while making the gesture. This display differs from the feather erection of other social situations in that in addition to raising the feathers of crown and upper neck those of the lower neck are also spread while the long crown plumes are erected. At the same time the pupils contract, eyes bulge and mouth frequently gapes. The greeting call of the courting male also becomes more guttural than that of the female.

10. The plumes of the crown are only erected during the courtship display and have no function in territory defense or in pacifying approaching individuals as previously reported. Since the display of the male induces the female to gesture in the same manner, the performance is presumably stimulating to the latter.

11. The plumes of the male are usually longer than those of his mate. Two males with damaged plumes failed to secure mates, suggesting that females will not pair with males of unusual appearance.

12. The display and billing ceremonies of the male Night Heron tend to return him to a state of dominance in order that copulation may occur.

13. There is a seasonal change in color of lores, mandibles and legs of the Black-crowned Night Heron. The lores and bill of the courting bird tend to become bluish black, the legs pink. In some breeding birds of the first year the mandibles may not attain this color and the legs very rarely undergo the complete change. Females usually lag behind the males in plume growth and often in leg reddening.

14. The tendency for the males to have pinker legs is correlated with a greater display of their legs during the courtship ceremonies. Greater plume length is correlated with the necessity of males securing dominance over their mates before copulation may proceed. Mutual selection may have aided the genesis of striking color contrasts of plumes, eyes and lores because the ceremonies of overture and display are mutual. Nevertheless, there are sexual differences in this display which eventually lead to the male securing the necessary dominance.

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EXPLANATION OF PLATES

PLATE 2

Young Black-crowned Night Herons

Fig. A. Immature, approximately four months old, showing pale-greenish lore, upper bill black shading to olive and lower bill olive.

Fig. B. Sexually mature Night Heron, approximately thirteen months old, showing dark lore, bright black beak and well-developed plumes. Both the brown and the white adults undergo a seasonal color change of lores and beaks.

Fig. C. Same bird as in Fig. A, same age, showing arrangement of its own breast feathers which were attached with rubber cement to crown and side of face for recognition tests.

PLATE 3

Eight stages in the sexual behavior of Black-crowned Night Herons

Fig. A. Territory defense. The bird on the right with damaged crown and plumes failed to secure a mate the entire breeding season.

Fig. B. Twig ceremony. Although the female will fondle sticks, only the male lifts his head vertically upward and clicks stick loudly. Many sticks employed in this ceremony are dropped but some are built into the nest.

Fig. C. Male overtures. If the female remains in his vicinity the male (left) lowers his head and brings cheek parallel to nest while giving a guttural greeting call not heard outside of the breeding season. At the same time he may fan his lower neck feathers as shown here.

Fig. D. Male displays. Erecting his crown feathers and plumes, raising his saddle feathers and puffing up all the feathers of his neck, the male (right) repeats his guttural greeting while bowing to the female. At the same time his pupils contract exposing the red irises to the maximum and the eyeballs protrude slightly from the head.

Fig. E. Attempt to regain dominance. The male, while continuing to ruffle the feathers of neck and back, raises his head toward the level of the female's head.

Fig. F. Billing for dominance. The male to be dominant must bill with head higher than that of the female. While fencing for this position, the male continues to display.

Fig. G. Display following success at securing dominance. Both sexes display in exactly the same way. The plumes of male (right) are longer and neck feathers are fanned more extensively (compare Figs. F, E, D; Plate 4, fig. B).

Fig. H. Copulation. The male (above) balances himself on the humeri of the female, his bill touches her crown and his tail is brought down and turned sideways.

PLATE 4

The plumes of the Black-crowned Night Heron are erected only during courtship. In other social situations other feathers may be raised.

Fig. A. Plumage in territory defense. The bodies are held low while some of the feathers on crown, neck and saddle are erected. The plumes are laid flat against the back and fail to show while the birds exchange pecks.

Fig. B. Plumage in courtship. Male (left) erects his three plumes, while raising feathers of neck and saddle. The female (right) responds with erected crown feathers and single plume. Her pupils contract and eyes bulge.

Fig. C. Plumage in dominance reaction. Male (left) holds his head in the superior position when billing with the female, his mate. At the same time he puffs slightly the feathers of head and neck but fails to erect the plumes. Male on the right is standing on extreme left of his territory, while bird in foreground with damaged crown and broken plumes maintains the territory he occupied alone throughout the season.

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