SOCIAL NESTING HABITS OF THE SMOOTH-BILLED ANI[1]

BY DAVID EDWARD DAVIS

INTRODUCTION

THE study of the social nesting habits of the Smooth-billed Ani, *Crotophaga ani,* a species which builds communal nests, was undertaken in order to increase the information about the subject of social parasitism and in order to help clarify the concept of territory. In this paper these two problems are considered in relation to the behavior of this bird.

The field work for this study was done at the Atkins Institution of the Arnold Arboretum of Harvard University at Centrál Soledad, Cienfuegos, Cuba. This Centrál is a large sugar estate, and the arboretum is an oasis in a desert of cane, since the only other places suitable for birds to live are roadsides, pastures, and a few spots unfit for cultivation. In addition to the field work at the arboretum, short excursions were made to the nearby Trinidad Mountains and also to Bahia Honda, in Havana Province.

The species studied, *C. ani,* belongs to a distinct subfamily, the Crotophaginae, of the Cuculidae, and occurs in the West Indies and South America. Included in this subfamily are *C. major,* inhabiting northern South America, *C. sulcirostris,* ranging throughout Central America, and *Guira,* a monotypic genus found in Brazil and Argentina (Peters, 1939). The habits of the members of the subfamily are discussed in innumerable collector's notes, which usually repeat the observations of the natives. *Guira,* the most primitive in generic characters, is poorly known but seems to be the least specialized in its behavior; these birds are reported to build their own nests, sometimes in colonies, and also to lay eggs in the nests of other birds. The life history of *C. sulcirostris* has been studied by Skutch (1935; 1937), and resembles that of *C. ani.* The habits of *C. major,* also social in its nesting behavior, have been observed by Young (1929). The behavior of *C. ani* is described by Gundlach (1874; 1895) who made very accurate but brief observations on the species in Cuba and by Young (1929) who briefly discussed the bird's habits in British Guiana. More recently Dr. Frank M. Chapman (1938), describing the history of the colony at Barro Colorado Island, has given the only

[1] Thesis submitted in partial fulfilment of the requirements for the degree of Doctor of Philosophy in the Division of Biology of Harvard University, June, 1939.

accurate account of the species. In addition, a mass of data concerning the genus, some of which is correct, was collected from travellers by Leverkuhn (1894).

I am indebted to many persons for assistance in this work. Mr. David Sturrock and Mr. F. G. Walsingham, of the Atkins Institution, made the complete facilities of the laboratory available, and Mr. William Leonard of Centrál Soledad granted innumerable favors. I am indebted to my friends there for making my stay most pleasant. This study was made during the tenure of an Atkins Traveling Fellowship and with the aid of a grant from the American Association for the Advancement of Science. I wish to acknowledge the painstaking criticism of Dr. Glover M. Allen. Without the encouragement of Dr. Thomas Barbour, this study never would have been made.

METHODS

A study of bird behavior in the wild is dependent upon the methods of field observation. To observe the bird's behavior I carried on studies from May 8 to September 13, 1937, and from April 8 to October 16, 1938. During these two breeding seasons I spent approximately 1300 hours in the field. The fact that the birds of a group sleep in the same tree made it possible to keep account of the different groups by coming to the garden at dawn. In trying to follow several groups intensively there are innumerable practical difficulties, and deficiencies in the records inevitably result. The identification of individual birds was made possible by the use of colored leg-bands. During the two years, thirty-three adults and fifteen young were trapped and banded. In addition, the fact that the yearlings are distinguishable by the bill for nine months after hatching aided greatly in identification. In order to study the nests at close range a blind twenty-four feet high was built and placed at several different nests.

The best method of presenting to the reader a picture of the bird's behavior is to use descriptive words, such as 'complaint,' 'perplexed,' 'mad,' and descriptive phrases. In this connection I wish to emphasize the fact that these terms are used merely for description, and that no knowledge of the state of the bird's mental processes nor of purpose is implied. Throughout this paper direct quotations from my field notes are preceded by the date and enclosed in quotation marks. The vernacular names 'ani' and 'judio' are used, and the terms 'colony,' 'flock,' and 'group' are used synonymously. For convenience each colony was named.

PART 1. SOCIAL HABITS

FLOCK BEHAVIOR

Crotophaga ani is a social species, living throughout the year in groups. Although occasionally a pair may live alone, usually the number in a flock is about seven; the largest group recorded by the writer contained twenty-four, and groups of fifteen are not uncommon. Since the number in the colony is continually changing, it is meaningless to derive an average size. In most flocks there is a surplus of males, although colonies composed of an equal number of each sex or having an excess of females are not uncommon. These flocks retain their individuality for a year or more. Although the yearlings remain with the flock throughout the year and may breed with the parent flock, in general there is a sharp decrease in the number composing a group (Table 1) just before the building of the first nest. In one case (Cypress) this decrease corresponded to the number of yearlings that were in the group.

The membership of each flock gradually changes, especially in the period just previous to nesting. Individuals of both sexes may leave the colony for no apparent reason and wander about searching for a colony to join. Table 1 shows the changes in number in the groups studied intensively during 1938 although the addition of new individuals is masked by the decrease due to mortality, and by departures.

TABLE 1

POPULATION CHANGE (1938)

Date / *Colony*	*4–16*	*5–8*	*6–5*	*7–3*	*7–31*	*8–28*	*9–25* (*adults only*)	*Dates nest started*	
Pond	20	18	15	14	14	13	13	6–10;	8–10
Gnhs	11	9	8	6	6	6	6	5–20;	7–10
Ceiba	11	11	9	5	4	3	3	7–20	
Cypress	10	10	7	6	5	5	4	6–10;	9–16
Haemat	8	9	6–8	7	6	6	4	6–18	
Phoenix	11	13	5±	7	6	6	6	6–25;	8–19

Some evidence suggests that a colony may divide into two parts. Certainly during the summer and probably during the entire year, new groups form. A typical history of a colony that developed but did not breed is as follows:

July 7. Four birds have taken up territory.
July 10. Still fighting for part of their area.
July 25. Five birds in the group.
July 26. Started to build a nest.
August 4. Still working on the nest; abortive type.
August 10. Fighting in the territory.
August 20. Group gone.

Less commonly these new groups may complete the nest and raise young. A colony may disintegrate if most of the individuals are removed. Although one nest held six incubated eggs, it was deserted when three out of four of the colony were shot. The remaining bird did not get a new mate.

The members of a flock pass the day together. Each colony sleeps as a group in a densely foliaged tree or in a bamboo clump. Sometimes the group may sleep in two parts and the sleeping tree may be changed occasionally, depending upon the number of suitable trees in the territory. In the tree the birds crowd as close together as possible in rows on a limb, pull the head down on the shoulders and fluff out the feathers. Shortly after dawn the birds come out and sit in a group on a branch, sunning themselves and trying to keep warm. Throughout the daytime the flock spreads out over the feeding area, using the 'judio' call to keep together. At evening before going to the sleeping spot the birds collect in a nearby tree and then fly in together.

The individuals of the flock respond to the actions of their fellow members in several ways. First, the birds are very solicitous for other individuals of the flock, crowding around with great excitement when one member is hurt. This behavior was observed when a dove fluttered off its nest and performed 'injury-feigning.' Second, the birds spend much time preening themselves and one another. When two birds are sitting adjacent to each other, one may suddenly stretch out its neck and raise its neck feathers in a movement resembling a reflex, which is stimulated by the touch of the bill of the other bird or arises spontaneously. The other bird then carefully preens its head and neck feathers, pulling out and swallowing all the loose ones. Then the situation may be reversed; or two birds may work on one simultaneously. Third, among the individuals it is probable that there is a flexible order of social dominance, although no criterion was found suitable for judging the rank of a bird. Sometimes two birds scuffle over an insect.

Albino birds occur and are reported by the 'guajiros' to live normally with their respective groups.

TERRITORIAL BEHAVIOR

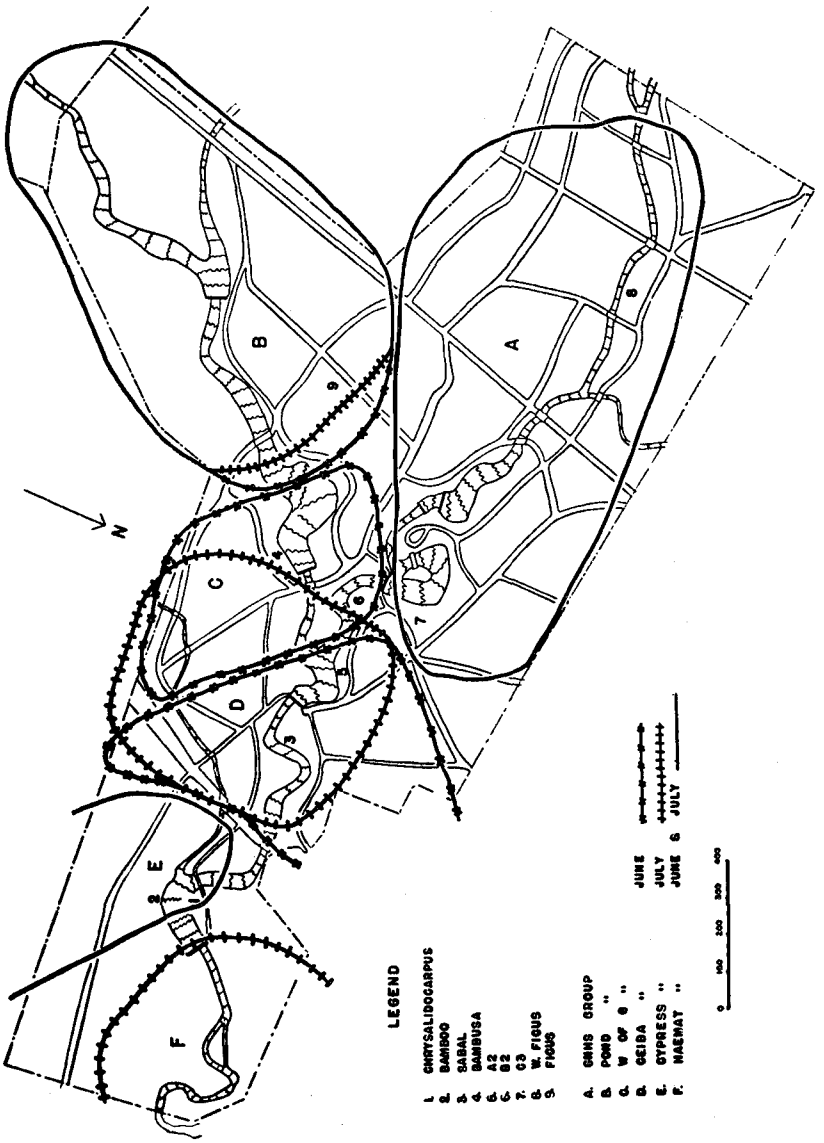
Each flock of *C. ani* possesses a definite territory which it defends against strangers. The boundaries are well known to the members of the colony and are not passed. The individuals cannot be driven from their territory, even when pursued by a man. The size of the territory varies roughly in proportion to the number of birds in the

colony, but is also related to the previous history of the group; a colony reduced in number will nevertheless retain the same territory for a long time. In large colonies (fifteen birds) the territory may occupy ten acres. The territory contains (1) a nesting and sleeping and (2) a feeding division. The size of each division is dependent upon ecological conditions. The nesting section contains several bushy trees for building the nest and sleeping at night, while the feeding area resembles savanna conditions. Except when engaged in nesting activities, the birds spend the day in the feeding division.

Throughout the year there are changes in the boundaries, as shown by the map (Text-fig. 1). A part of the territory not defended may be taken over by a neighboring group in a few days. For example, in July the W. of G. group was not present and the Ceiba group took over part of its territory. A group (Pond) slept about a quarter of a mile out in the cane fields for several nights. Since, for the first few days after the young are out of the nest, the colony sleeps in the feeding area, another colony may attempt to occupy the nesting division and sometimes succeeds in doing so. If in the dry season there are no moist places in which to find insects, the area is deserted, or contracted around the stream courses. The territory is vigorously defended against other individuals. Although any invasion is immediately repelled the colonies are on good terms with their known neighbors and settle boundary disputes quickly by 'agreement.'

Strangers of two distinct types try to invade the territory. One type comes in from a distance, flying high, sits in the top of a tree and calls *whew* several times. This behavior attracts the owners of the territory and the stranger leaves, still flying high, without attempting to join the colony. It seems likely that birds of this type are yearlings, not yet sexually mature. The second type of stranger tries to join the colony. Quietly it enters the territory and when the owners arrive it remains in the vicinity. One or more owners chase it throughout their area, sometimes flying high above the ground but more often circling near the ground. The stranger sleeps in the area but in a different tree and does not know the boundaries of the territory, but may fly into a neighboring territory, only to be chased again. Although strangers sometimes try to join the colony when it has a nest or young, they are less aggressive at this time. As soon as the young are hatched the strangers again aggressively attempt to join the colony.

The behavior used in driving away strangers is referred to as 'chasing' and is described in the following note. June 1, 1937: "Chas-



TEXT-FIG. 1.—Territories for June and July 1938.

ing is an interesting procedure. One bird follows another around and around and back and forth. Sometimes another joins in the pursuit. They fly for about twenty beats and then sail for a long distance. They are able to turn and wheel in the air quite well. . . . It (chasing) starts when two birds are in a tree and one starts 'conking.' The chased then starts to climb and the chaser follows, hopping up the limbs and twigs. Then the chased starts to fly and is followed." This chasing behavior may last for several days, until the stranger is driven out or succeeds in joining the colony, as shown in the following note, July 26, 1938: "Saw a chaser lose a fight with the chased but another bird came to the rescue. The birds chased all morning." Chasing occurs throughout the year but, since just before the breeding season the birds are moving around more, it is more frequent at this time. If the stranger comes while the nest is being built, the nesting may be interrupted and delayed.

Chasing is interpreted as part of the mating behavior by Young (1929). Although in appearance it resembles the mating flight of many birds, especially the ducks, the following facts make it necessary to discard this interpretation. (1) A bird may be on the nest while other birds chase. (2) Chasing may occur at any time of the year, or at any time during the nesting cycle, but does not occur in some colonies. (3) There is a definite mating behavior as described below. (4) There is a definite antagonism between the birds concerned and sometimes fierce fights ensue.

A behavior related to chasing may be called 'rushing.' Uttering a particular call (no. 3), the birds as a group fly from tree to tree. Since this behavior occurs after a period of chasing, it seems to be a method of defining the limits of the territory and searching for any strangers. Other than this 'rushing,' there is no special advertisement of the territory such as there is in passerine birds.

There is no fighting when birds from several different colonies are placed together in a cage distant from the birds' territories. The birds sleep side by side the first night.

The chasing, rushing, and fighting to defend the territory are very fierce. The impulse to defend is so strong that the birds fight a stranger even while a man is at the nest. Stuffed birds placed in the territory are attacked and destroyed, although at times the dummy is ignored, as shown by the following observations. June 24, 1938: "I put the dummy at the nest. After about 45 minutes four birds came in. Two sat on the nest, each for a few minutes. They ignored the

dummy in spite of moving and shoving it at them. They then went away. III came in with a leaf but dropped it and went off." June 25: "The dummy is thoroughly damaged on the back and legs and is upside down. Three birds came back and III sat on the nest and complained a lot. They ignored the dummy although I moved it a lot. III brought in some leaves and sat ignoring the dummy." When attacking a strange bird, the defender spreads its wings and pecks viciously at the invader's head. Fights occur if, during chasing, the chaser overtakes the chased. As the two fall to the ground, screaming and fluttering, the whole colony forms a circle and watches the brief combat. A fight or display performance, described as follows, occurs occasionally. June 13, 1937: "Two birds are on the ground. One started to display in front of the other. It would strut around it and spread its tail and wings. Sometimes it would fall forward as it displayed and raise the tail high in the air. All the time the two were making little noises. At one time there seemed to be a sort of abortive attempt at a fight." The birds then separated and went into different territories. This behavior is probably a territorial dispute.

Possibly birds join a colony without fighting, as suggested by the following observations. July 7, 1938: "Saw AR and A-B sitting peacefully with two other birds in the sabal tree. Later saw two birds chase away a stranger that had 'whewed' from the top of the ceiba tree. AR is on excellent terms with the birds of the Ceiba group. It had its neck scratched and went up to the nest (location). I have watched the birds of this group fairly closely of late and they have been doing a lot of chasing, but I did not see them chase AR, although they could have very easily." AR was formerly a member of the Greenhouse group and was concerned with the nest on June 18. On July 3, the nest was destroyed and it is likely that AR left at that time and joined the Ceiba group.

Birds may leave the colony without being driven out. On July 26, 1938, ARR (female) was on good terms with the rest of the group. She left on July 27 and formed a colony with two males nearby. On July 30, a member of her former group chased her.

There is no difference in behavior among the sexes or immatures in fighting or chasing. Males may chase females and vice versa. When I arrived in April, 1938, birds hatched July 9, 1937, were defending their territory.

The birds will fight a mirror as would be expected, since, although they recognize the other members of the colony, they are not acquainted

with themselves. This behavior occurred on October 4, 1938: "I put the mirror at the nest and two birds came on to the nest at once and started to *conk* and peck at the mirror. It puzzled them greatly especially when they went around behind it. After I took it away they explored the place looking for it and finally went on to the nest."

Fighting is frequently caused by a colony travelling as a group in search for a new territory. In the spring months when the birds are taking advantage of the regions made suitable for nesting by the rains, this travelling is often seen. For example, on April 20, 1938: "Six birds were seen in W. Ficus at 6.30 a. m. They seemed to have a purpose and eventually flew northwest in stages and then to the north out over the cane." In one case a pair which tried for several days to join the Pond group but was repulsed at the nest each time, later built a nest and laid five eggs. The birds arrive in an area and sit about in trees for a while to establish territory. If there is a claim for the particular area brute force decides the issue. The first stage is chasing; the second is rushing and the third is the acceptance of the boundaries or the withdrawal of the unsuccessful group. If there is no claim for the territory, it is at once defended against other groups.

By taking advantage of the fighting behavior, it was found possible to catch the birds, using a live decoy in a trap. A dead or mounted decoy is ineffective, probably because it is not moving and hence is not seen. The owners of a territory enter the trap and in a short time kill the decoy. The decoy does not resist. The birds continue to fight with the decoy until a person is within a few feet.

Several times an interesting conflict between the territorial behavior and the response to the alarm call was observed. Two colonies had nests close together, although their territories extended in opposite directions. When the nest of one colony was disturbed the birds of the other colony responded to the alarm call but never crossed the invisible boundary line of their territory.

CALL NOTES

The vocabulary of *C. ani* is varied and distinctive. Each call has definite uses and may serve to distinguish behavior patterns. The first six calls listed below are modifications of no. 1, but the other calls are not founded upon a common pattern. The calls have been given descriptive names which may assist to convey their characteristics. *Mimus polyglottos* mimics some of the calls, especially the 'judio' call and causes confusion not only for the investigator but for the anis themselves.

No. 1. 'Judio' is the flock call, used whenever a bird is flying for a distance or when the group is travelling to the feeding area, to notify the members of the movements of the group. This call resembles the Spanish word, thus giving rise to the Cuban name for the bird.

No. 2. The alarm call is used as a signal of warning or annoyance. When a person approaches the flock one member gives the call and the rest of the birds fly upward to a bush or tree and continue the alarm until the annoyance passes. The note is rapid and not nasal, but begins with an *ñ* sound. At each utterance the tail jerks. The young develop this call first, but require a month to reach perfection.

No. 3. The 'shout,' always repeated very rapidly, is used during the rushing behavior described above.

No. 4. The 'complaint' is a slow, high-pitched wail, similar to the alarm but higher in pitch, and is used only at the nest and mainly during the first few days of building. This call is a certain sign that work is in progress but does not distinguish between an abortive nest and a real one. The note is not given after the nest has been built but is used after pairing occurs. Hence it is a nest, not a pair, call. It should be noted that there is a special call for the nest but not for the territory as there is in many species. It was not possible to determine if this call is given by one sex only.

No. 5. The 'objecting' call is an undeveloped alarm which resembles a 'complaint' in tone, and is used at the nest when the birds are disturbed. First, the alarm call is used and then as the disturbance lessens the 'objecting' call is continued. Sometimes it is heard when a bird wants to exchange the duties of incubation with the bird on the nest.

No. 6. The 'get-up' call, repeated extremely rapidly, is used early in the morning before the birds leave the sleeping tree and sometimes late in the evening before the birds go to sleep. It is also used to attract the young birds out of the nest for the first few times.

No. 7. The 'chuck' resembles the sound *ah* and is used by the bird being chased but not by the chaser. Although the significance of this observation is not understood, several times in April this note was heard under circumstances which normally result in the alarm note.

No. 8. The 'chuckle' is used in the nesting tree when the birds are pairing.

No. 9. The guttural note occurs whenever the birds appear perplexed. This call is induced by a strange object such as the blind or a strange situation such as being caged.

No. 10. The 'whine' is a soft call used in mating. The pair sit in the nesting tree side by side and whine, so softly that the sound cannot be heard more than twenty feet.

No. 11. The 'conk' is used in fighting to defend the territory. After getting below the stranger, the attacker 'conks' a few times before attacking.

No. 12. The danger call is a 'quack,' signifying the approach of a hawk. The judios dive down into a bush or tree at this note. Immature birds give this call on seeing *Cathartes* and *Zenaidura*. Once, when the investigator was placing a decoy near the nest, this note was heard, perhaps indicating the highest pitch of excitement. Other species take advantage of this warning.

No. 13. The 'whew' is used by a stranger of the first type described above.

PAIRING AND NESTING BEHAVIOR

The nesting season begins shortly after the rains permit the vegetation to develop. At this time the diet changes, as shown by a study of stomach contents, from vegetable to animal matter (insects and lizards), and it seems likely that this change of diet is the stimulus for the development of the gonads.

The pre-incubation behavior takes place in several stages. (1) A pair or several birds spend part of the time away from the flock sitting quietly in a tree suitable for the nest. The manner of sitting differs from the type usually observed; the birds sit inside the tree, not on the top or outside. The birds sometimes hop about in pursuit of each other and after the first day or two occasionally break off a twig, but usually drop it. A bird may hold a leaf in its bill for a time or take one from another bird and then drop it. During this period occurs the whining note, which, except for the action of sitting side by side, is the only courtship behavior. The following note records typical behavior. May 21, 1938: "Four birds of the Cypress group were in the bamboo. One (ragged tail) whined for a long time and hopped around the bamboo, finally flattening itself out. The others showed no interest. Another . . . seized a twig but did not break it off and soon lost interest."

(2) Next comes the period of the complaint call, given persistently from a definite location. The observation on May 26, 1938, is typical of the behavior at the beginning of this period: "I went over to the Old Garden at 7.15 a. m., and found three birds sitting in the bamboo. One carried a leaf around after a while but did not know exactly

what to do with it and finally dropped it. Again it carried a leaf around. Moving the tail up and down seems to be characteristic of this time. The birds also complained a bit and whined some. A bird went up into the Ficus and pulled a twig and then was joined by another which also pulled. They sat for a long time and were still there when I left at 8.45." Although by this time the site for the nest has been determined, some birds may examine other locations. June 30, 1938: "At 7.00 a. m. there were two birds near the Sabal and three in it. They sat for a long time and then went over to the Bambusa and sat some more. Two birds left and two . . . more stayed and hopped around a long time. Then they went out and joined the others. Three went over to the Sabal and 'split-tail' went to the nest (location) in the Sabal. The whole group went over to the Bambusa. They cannot decide which to use."

(3) After the location of the nest is determined in the period of the complaint call, the birds begin the period of building. Twigs are broken off from a branch, never picked up from the ground. Usually one bird builds most actively but frequently as many as five carry in twigs at the same time. At this time the birds are so absorbed in nest-building that the approach of the investigator does not disturb them to any extent. The complaint call continues throughout this stage. Sometimes two birds may sit on a nest, side by side, as shown in this field note. June 7, 1938: "One bird in the Chrysalidocarpus complained and another came in from the Litchi. Both sat on the nest for three minutes and then went to the bamboo and sat."

(4) Following this stage for a few days little or no work may be done on the nest.

(5) In the last stage before the eggs are laid, the birds carry in leaves and occasionally a few sticks. An interesting action was observed in a colony which was building a nest after the first nest had been destroyed during incubation. A female sat on the nest and received sticks and leaves from the male, thus continuing perhaps the incubation which she had been performing on her former nest.

Copulation, the climax of pairing behavior, occurs usually in the first hours of the afternoon, but may occur at any time of day. The action shows no special behavior. When the birds are sitting in the nesting tree quietly, the male, without any preparatory performance, mounts the female. Because a stuffed bird is treated as a stranger and attacked, the birds do not copulate with it.

Many irregularities from the general outline above occur. The

nesting behavior may stop at any stage. For example, on June 9, 1938: "One bird interested in the W. Ficus. It hopped around in the tree, sat for a while and complained all the time." No nest was built in this location. In some colonies the birds may break off twigs and then leave the territory, or a nest may be started but not completed. These incomplete nests are termed 'abortive' and, as discussed below, are comparable with the scrapes and trial nests of other species. After an abortion the colony usually starts another nest in another location. That a poor choice of nest site is not the cause of abandonment is shown by the history of the Pond group. This group built an abortive nest in a bamboo and then, after raising a brood elsewhere, came back and built on top of the abortive nest.

A type of irregularity occurring occasionally is desertion. After building a nest and laying eight eggs, one group deserted without obvious reason and built the nest in another place. The birds under observation never deserted the nest because of human interference.

Other aberrations of the breeding cycle occur. A bird was observed carrying sticks alternately to two different trees, indicating that the same bird may work on two nests. Although part of the group may start the nest, others in the colony may take no interest till later; the Bambusa group in 1937 consisted of fifteen birds, yet only nine eggs were laid, indicating that only two females had laid in the nest (evidence presented below shows that females lay between four and seven eggs, usually six). Only exceptionally do all the females of a group lay eggs at the same time. Often one bird, either male or female, is most interested in the nest, is most alarmed by the observer, and is most active in the building and incubation.

At the beginning of the laying period there often is a miscarriage of the building and laying sequence. Sometimes eggs are laid before the nest is completed and are covered in the bottom of the nest or dropped on the ground. One day a colony of fifteen birds dropped six eggs, some as far as twelve feet away from the nest. By placing the unbroken ones in another nest, these eggs were proved to be fertile. Although there is no evidence that the females fight on the nest, occasionally eggs may be knocked out of the nest.

If a nest containing eggs or young is destroyed the birds rebuild at once and with great speed in some cases, telescoping the stages into a few days. Table 2 shows that there is no relation between the stage of incubation or feeding at which the nest was destroyed and the length of time till a new nest is started.

TABLE 2

REBUILDING DATES IN RELATION TO NEST DESTRUCTION

Colony 1937	*Number birds at 2d laying*	*Date destroyed*	*Stage of nest*	*New egg date*	*Days*
Old Garden	12	8–1	3 days incubation	8–12	11
C3 (2)	11	7–5	0 days incubation	7–13	8
C3 (3)	6	8–10	5 days incubation	8–16	6
Cocos (1)	?	6–14	4* days incubation	6–25*	9*
(2)	4	7–1	0 days incubation	7–14*	13*
(3)	7	7–20	12 days incubation	8–3*	14*
Gray's	11	7–5	1 day hatched	7–10*	5*
1938					
Cypress	7	7–5	4 days incubation	7–10*	5*
Gnhs (2)	7	7–3	1 day incubation	7–10	7

*indicates estimate of ±2 days.

RELATIONSHIPS BETWEEN MALE AND FEMALE

Since the birds live in colonies and build communal nests, polygamy may occur. Copulation with more than one individual is the only criterion of polygamy, but since in this species copulation occurs only in very dense foliage, the number of copulations clearly observed is small. Of those copulations seen, none proves a departure from monogamy. In two colonies in which all individuals were identifiable (Ceiba and Cypress), the behavior indicated strict monogamy. Thus, in the Ceiba group all four birds were identifiable and only one pair was concerned with the nest and young while the other pair took no notice of the nest. There were only seven eggs, indicating that only one female had laid. This colony, therefore, consisted of two definite pairs. As another example, at the time the first brood was raised the Cypress group consisted of two definite pairs and two non-breeding birds. At the time of raising the second brood, the group consisted of one female (ABW) and three males (ARW, ARG, and ABB). All relations were harmonious and it was impossible to see any difference in the female's attitude toward the different males.

In many cases, however, polygamy is suggested by the composition of the colonies. In some colonies polygyny is indicated. A colony which consisted of two females and one male was collected and nine eggs were in the nest, indicating that both females had laid. Since the previous history of the group is not known, it is possible that there was another male at the time the eggs were laid. In its second nest, the Phoenix group, which consisted of seven birds, had 23 fertile eggs, and hence, unless some bird laid eight eggs, polygyny must have oc-

curred. But on the other hand, the composition of other colonies suggests polyandry. The Bridge group, which had four eggs, consisted of two males and one female throughout its history. A colony that consisted of four males and one female was collected. In these two colonies there is no proof that more than one male copulated with the females, although at no time were sexually inactive birds collected in any colony. In conclusion, it seems that any of the three possible situations, monogamy, polyandry, or polygyny, may exist.

At the time of pairing there may be antagonism between the pairs. This behavior occurs in the early part of the breeding season, as shown by the following observations. May 23, 1938: "AW followed A into the C_3 (a bamboo) and hopped about it for a long time. It was up in the bamboo and I could not clearly see what went on. There was a lot of whining, often scarcely audible. Then a third bird came in. I could not get a look at its legs and it may have been banded. It joined the others and there was some 'conking.' Presumably AW was mad but I did not see well enough to be sure. Then they went out to the west." June 10, 1938: "Three birds came into the Chrys nest at 5.30 p. m. and then 'ragged-tail' came in. A male attempted to copulate but the female was not very responsive. This occurred on a branch near the nest and they both went over to the nest where 'ragged-tail' was. They hopped around the bamboo and there were a few 'conks' and then they went out to feed." But in contrast, later in the season there is no antagonism. On July 9, 1938, the behavior of the birds ARG and ABW, which were certainly a pair, was recorded: "ARG was actively carrying twigs in to ABW who was sitting on the nest. Two birds came in and shoved ABW off the nest. ABW and ARG went out together, followed by the third bird and the fourth stayed on the nest. ARW came in and stayed on the nest and then copulated with the bird on the nest." July 11, 1938: "Four birds came in to the nest in the Bamboo and ARW and ABW sat on the nest together. Then ARW and a bird went off and ARG began to carry in twigs to ABW on the nest and did so industriously for about 15 minutes." These data indicate that at the time of pairing there is antagonism but that after the mates are determined there is harmony.

Both sexes incubate, although in some cases the male does more than his share. When a bird desires to incubate, it flies into the nest, usually with a leaf or sometimes with a stick. If the incubator does not wish to leave, it must be forced off or the newcomer is unable to incubate. The general behavior is recorded in the following ob-

servations. July 26, 1937: "A bird brought in a leaf and sat on the nest for a minute trying to get the other bird off; but then left. It soon came back and sat with head and breast over the other's back, called and then left. Again the performance was repeated. It came in with a twig but still the other stays on. Two more sticks are brought in in quick succession to no avail. The bird sat on the incubator and called but soon left. Another stick was brought in and the incubating bird took it. Then it (the first bird) brought in another stick. Now it is sitting on the incubating bird and calling. A third bird came in with a stick and both got off. The third bird got on the nest." July 30, 1937: "Several young have their eyes open. Four different birds brought in food at the same time. The incubator left. There are some birds sitting around all the time. Once two birds came in and both seemed to want to incubate. A third did not seem to know what to do with some food. All three stayed on the nest for a while. Finally two went off. Later two brought in food. The young did not eat (the food) offered by one and so the adult ate it." The delay in the departure of one bird is the basis for the belief that more than one bird incubates at one time. According to my experience two or more birds never incubate simultaneously.

RELATIONSHIPS BETWEEN ADULTS AND YOUNG

The young remain with the parent flock for a variable length of time and in some cases nest in the same tree in which they were hatched. For example, the young from two colonies, banded in 1937, were found in 1938 with the parent flock, sleeping in the same tree used in 1937. Nevertheless, in general, most of the young have wandered away by the breeding season. In one case the yearlings sat in the nest tree and seemed interested, but in a few days disappeared; since no chasing or fighting was observed, it is unlikely that they were driven out. The yearling cooperates with the parent flock to defend the territory.

Nearly all the adults in the colony feed the young, although some individuals are much more active than others. For example, in the Bambusa nest there were nine young, indicating that only two females had laid, but at least nine of the fifteen birds in the colony fed these young. In the Cypress group a female did not incubate, although, as shown by sections of the ovary, she had laid eggs. Nevertheless she did feed the young.

The adults call the young out of the nest by the 'get-up' call (no. 6). If the nest is threatened the adults give the alarm note and in addi-

tion click the bill; then the young, although they may be only four days old, climb out of the nest into the tree. The young return to the nest the first two nights after leaving it. One adult sleeps with the young for several days after they have left the nest but are still in the nest tree. After the young are able to fly, the adults take them out to the feeding area and the whole colony sleeps there. The young are fed by the parents for about a month after leaving the nest. If no nests are destroyed a colony in Cuba can raise three broods in one season.

The young are ineffective as a decoy to trap the adults.

RELATIONSHIPS AMONG THE YOUNG

The young of one brood stay with the parent flock while the next brood is incubated and hatched. Observations on the second brood are not satisfactory because the adults become so alarmed. The observer has spent three hours hoping that the birds would quiet down and resume normal behavior. This behavior is in great contrast to the behavior during the development of the first brood.

The young of the first brood may feed the young of the second brood, but they are less active than the adults. In Wares' nest in 1938 the young when 48 days old fed those of the second brood. Analysis of this behavior suggests that the young birds are mimicking the adults, as the individual does in all behavior, or that, as in the case of non-breeding birds, the stimulus of the young in the nest is a releaser which compels the bird to bring in food.

PART 2. LIFE HISTORY

GENERAL CHARACTERISTICS

As individuals, judios show distinctive behavior patterns. The birds sit for interminable periods, preening or doing nothing; an hour is not an unusual length of time to spend in one spot. In the early morning hours when they come out of their sleeping tree, they spend a long time sitting and working over each other's feathers and stretching their wings out in the sun to dry, frequently shaking the tail rapidly from side to side. After a hard rain the birds may sit out on a limb in an extremely bedraggled group. During the rain the birds sit together in a sheltered place and try to keep warm and dry; if it is late in the afternoon they make a dash for the sleeping tree. In the heat of the summer the birds pant much of the time during the warm part of day. In the cool and dry season they spend the cooler morning hours sitting on the ground in a dry place, protected

from the wind. When it is cold, a bird on the outside of the row may hop on to the others and squeeze down between them.

The behavior of the birds indicates a lack of ability to withstand low temperatures. To analyze this situation the weight of the feathers was calculated by obtaining the difference between the weight of the bird before and after stripping it of all its feathers except the remiges and rectrices. For six specimens (three males and three females) of *C. ani* the feathers averaged 3.03% of the body weight. From the data of Kendeigh (1934) the average value for twelve species of temperate-zone birds is 4.26%, suggesting that such birds in general have a greater feather covering than *C. ani*. To get a valid comparison the feather weights of tropical birds should be compared, however. The feathers on one specimen of *Ptiloxena atroviolacea* weighed 3.7% of the body, which suggests that *C. ani* may differ from even tropical birds in the small amount of feather covering.

The birds are awkward in all movements. They walk with a peculiar disjointed gait and sometimes run a few feet; on the ground they seldom hop. In flight the bird flaps and soars alternately and when landing in a tree, the wings and tail are uncontrolled. Although sometimes taking the trouble to arrange the tail and wings, the bird usually leaves them just as they fell.

The birds feed almost entirely on the ground, searching through the grass and pouncing upon the hapless insects or following an ox to snap up the insects it disturbs. In catching an insect the bird makes a dive, the wings flop, and the tail waves in the air. On April 13, 1938, judios were observed catching junebugs on the wing, in the manner of a flycatcher. The birds were usually successful but never graceful. The birds were never observed eating ticks although they are reputed to do so in Cuba and certainly do so in other West Indian islands. The fruit of the royal palm (*Roystonea*) is swallowed, the hull removed in the gizzard, and the seed regurgitated. In the dry season the birds drink water, raising the head to swallow.

Captive birds were unable to learn to eat non-moving food, and therefore starved. Some of the birds lived as long as eight days, presumably without eating anything.

A difference in size, which with practice can easily be recognized in the field, distinguishes the sexes. The mean of the weights of fourteen males is 114.3 ± 2.26 grams and that of ten females is 97.0 ± 1.78 grams. The standard error of the difference between the two means is 2.88 grams and hence the difference is very significant. Since these

weights were generally taken in the morning they are comparable. Baldwin and Kendeigh (1938) consider the difference in weight of males and females to be significant if it is more than 3% of the weight of the male. Since for *C. ani* this difference is 14.9%, it is certainly significant. Females at the time of laying may weigh as much as a male. A female containing an egg ready to lay weighed 123.2 grams and even after the egg, ovary and oviduct were removed, she weighed 112.0 grams. Large amounts of fat were deposited in the abdomen. A female with an egg, collected by Danforth (1937), weighed 115.6 grams. This evidence suggests an increase in fat deposition at the time of laying, although Riddle (1934) has found in pigeons an increase during the incubation only.

In the population at large there is an excess of males. Table 3 shows the data on the sex ratio. Using the Chi-square tests, the museum data are statistically significant. There is no reason to

TABLE 3

SEX RATIO

Source	*Males*	*Females*	*Ratio*
Museum collections	401	328	1.22:1
Cuba, 1937–38	35	24	1.46:1
Embryos, 1937–38	29	16	1.53:1

believe that the collections in the museums are not a representative sample of the population; there are no behavior differences which would influence the collection of either sex and there are no color differences. The data for the embryos (sex was determined by sectioning the gonads) and for the birds at Soledad are consistent but not significant statistically. The factor of longevity may be neglected in the consideration of the sex ratio because the point to be established is that in the breeding population there are more males than females.

NEST

The location of the nest is indicated by the complaint call, first uttered by the bird several days before the actual work is begun. The nest is placed in the fork of a thickly foliaged tree or in a bamboo. The size of the nest is dependent upon the configuration of the site of the nest and the number of birds bringing in material. The usual dimension is about a foot in diameter and, if the nest is placed in a deep fork, it may be six inches deep. To build the nest, sticks are broken off nearby trees and later fresh leaves are pulled from twigs

and carried in. Material for the nest is never picked up from the ground. While working, the individual goes to the same tree repeatedly for twigs. The work is done mainly in the morning. When the nest is robbed, it is covered with leaves and a new nest is started in another place at once.

EGGS

The egg of *C. ani* is blue and measures about 35 by 25 mm., although there is great variation in size. There is a white chalky covering, which may be secreted by special cells in the vagina of the oviduct, as suggested by a preliminary study.

The incubation time, as shown by Table 4, is about thirteen days. Due to the heat of the day and the length of time an egg may be in the nest, some eggs hatched within six days after incubation proper started. By changing the eggs, a colony of three birds was kept incubating for twenty-four days. For the first few days after incubation starts, the eggs are not warmed continuously but only for short intervals as shown in this observation. June 23, 1938: "Watched the Cypress nest for half an hour before a bird came in. Then (no.) I came in, sat around, flew back to the bamboo, was joined by ARW and came back. Another bird (III) came in from the Cypress tree with a twig and incubated but was very restless, often adjusting the twigs. It came off the nest and complained a bit and left. It came back with a stick. I is still sitting around. III came off the nest, complained, and left." After this period the incubator never leaves

TABLE 4

INCUBATION PERIODS

Colony 1938	*Eggs*	*Days incubated*	*Days between start of laying and incubation*
Bridge	4	14	?
Pair	5	12	?
Mango	5	12	?
Phoenix	21	9	9
Pond	22	6	18
Greenhouse	11	13	?
Ceiba	7	15	?
1937			
Old Gard. (1)	6	13	7
Old Gard. (2)	10	15	7
C3	14	13 (estimated)	10

the eggs until another bird comes in to brood. Birds may incubate for a short time immediately after the eggs are taken from the nest.

For example, on July 5, 1938: "Jim climbed over and got the eight eggs. III came back at once and incubated. Then II came in, exchanged and incubated."

The number of eggs laid by each female is difficult to determine. In an attempt to determine the number of eggs laid, serial sections of the ovaries of several females were studied. However, the peculiar development of the corpus atreticum prevents, as explained below, this determination. As a result it is necessary to use indirect means to determine how many eggs are laid by each female. Table 5 shows

TABLE 5

NESTING DATA

Colony 1938		*Date laying*	*No. of birds*	*No. of eggs*	*Laying females*	*Immatures*
Bridge		8–12	3	4	1	0
Pair		8–22	2	5	1	0
Wares	(1)	7–18	7	8	2	6
	(2)	8–30	5	10?x	2	6
Ceiba		7–20	5	7	1	4
Gnhs	(1)	6–18	7	12x	2	–
	(2)	7–10	7	12	2	0
	(3)	8–12	6	11	2	6
	(4)	10–8	6	10x	2	?
Cypress	(1)	6–18	7	8x	2	–
	(2)	7–10	6	12	2	5
	(3)	9–18	4	7x	1	?
Haemat	(1)	6–18	6	6	1	0
	(2)	8–5	6	2	1	0
Pond	(1)	6–10	15	?x	?	0
	(2)	8–10	15	29	5	4
	(3)	9–25	13	12x	2	?
Phoenix	(1)	7–28	7	6	1	0
	(2)	8–19	7	23	4	8
Batey		8–6	3	4	1	0
1937						
Bambusa	(1)	6–10	15	9	2	5?
	(2)	8–2?	15	8	2	0
Old Gard.	(1)	7–6	12	9	2	0
	(2)	8–12	11	10	2	0
C3	(1)	6–16	11	10	2	0
	(2)	7–13	6	7	1	0
	(3)	8–16	6	14x	2–3	?
B2		8–13	7	3x	1	?
Gray	(1)	6–12	11	4	1	0
	(2)	7–10	11	10	2	5?
Wares		6–1	15	19	4	6

x, not used to calculate survival data.

the number of birds in the colony at the time the nest was built and the number of eggs laid; the number of laying females is calculated assuming that the number of eggs per female is between four and seven. This assumption finds difficulty only in the case of the B2 group, but in this instance it is possible that some of the eggs were laid on the ground and not found. Also, the fact that this was the second nest may have affected the number of eggs laid. In the case of the Ceiba group there were certainly two pairs and although one pair was greatly interested in the nest, the other paid little attention to it. In the Cypress group (2) there were three females but shortly after incubation started, one of them left, joined two males to form the Bridge group, and there laid four eggs. Hence, it seems necessary to conclude that two females laid a total of twelve eggs in the Cypress nest. The evidence from the Cypress group (3) proves that one female can lay seven eggs since there was only one female in the group. In summary, these data indicate that each female lays between four and seven eggs.

A female probably lays an egg every other day, but no group in which there was only one female was checked and the data showing the number of eggs laid on each day for a colony did not give a clue as to how often an egg is laid. The eggs may be laid at any hour of the day but are usually laid in the early hours of the afternoon. Eggs were laid before 7.00 a. m. and after 5.30 p. m.

Frequently the eggs appear to be in layers in the nest, each layer separated by leaves. Until the time of hatching the birds usually bring in a twig or leaf to the nest when they come in to incubate; this twig is placed on the nest and in time some of the eggs become covered up. If the nest is deep, most of the eggs can become covered and thus they are not warmed and turned regularly. Another method of forming 'layers' is that some of the females start to lay when the nest is no more than a platform of sticks, and in these cases drop the eggs to the side, where they become covered. These eggs in the lower layers do not hatch, although they are fertile and undergo some development. (No unfertilized eggs were ever found.) Usually the first eggs laid are covered, but it is not uncommon to find that by chance the last eggs laid are covered.

In connection with egg laying, a behavior of unknown significance was observed. The birds placed the fruits of a *Terminalia* (resembling a peach seed) in one abortive nest in which two eggs had been laid but subsequently knocked out.

There is no special behavior before laying. The female goes to the nest without any performance. Sometimes a male is present in the nest tree. At this period the females have an enlarged abdomen for a few hours before laying and the excreta are very fluid.

YOUNG

The young, since they hatch at a late stage of development, are able to leave the nest in as soon as five days if stimulated by danger. At this time the young are excellent climbers, and whenever there is danger, scramble upward by means of the feet and bill. They frequently fall to the ground but, when placed in a tree, hop up at once.

As development proceeds, adult characters are assumed. The alarm call and the characteristic jerking of the tail are soon developed. The crest of the bill remains undeveloped for a long time, which distinguishes the young from the adults for about nine months. The outline of the crest is not as curved or as sharp as that of the adult.

The number of young which reached immaturity, that is, were able to feed and care for themselves, is about 24% (Table 5). In those nests whose history is known, 225 eggs were laid and 55 birds reached immaturity. Since, no matter how many eggs are laid in the nest, no more than eight eggs were ever found to have hatched, a correction is desirable. The total number of eggs above eight in each nest is subtracted from the total laid, giving 153 eggs which had a chance to hatch. Even with this correction the percentage is only 36.0. In comparison with other birds, the data Nice (1937) has tabulated for seven north-temperate passerine species shows that the average per cent fledged is 43.0. Whether the low survival of *C. ani* is normal in the tropics or is related to the abnormal nesting habits cannot be determined until studies are made on other tropical birds.

PLUMAGE

The species has no regular molt, but loses the feathers throughout the year. Birds trapped at the height of the breeding season were found in all stages of loss of the remiges and rectrices. The contour feathers are lost mainly in the spring. Since the old feathers of the head are pulled out when the birds preen each other, the molt of the head is not apparent. The irregular loss of the tail feathers provides a convenient method of distinguishing the individual bird when it is possible to get a good view. Although it is easy to study the molt, since the old feathers are brown and the new ones contrastingly iridescent, the molt of an individual bird was not followed through the season.

Albino individuals are occasionally found; in the famous Gundlach collection in Havana there are four birds of various degrees of albinism.

ECOLOGICAL RELATIONS

In the locality where this study was made, the division of the year into a dry season from November to the middle of May, and a wet season for the rest of the year permits great differences in the behavior of the species. Since the dry season nearly eliminates the insect food and reduces the number of lizards, the judios are forced to subsist on vegetable matter. Individuals collected in April had fed upon the fruits of a palm (*Roystonea*) and the small seeds of several legumes. Little vegetable food is taken after the rainy season starts. As a result of the seasonal change, during the dry season the birds concentrate along the streams in an attempt to find insect food, but shortly after the rains begin the birds occupy the new areas as these become suitable for living.

The climate with its seasonal change is typically subtropical in its characteristics. The mean annual rainfall (1902–34) is 52.42 ± 1.8 inches, most of which falls from June to November. The mean temperature for 1936 was 25.1 ± 1.1 C. The temperature is also subtropical. For July 1936, it averaged 27.2 ± 2 C., and for December it averaged 22.7 ± 2 C. The temperature seldom is lower than 15 C. or above 35 C.

There is a relation between ecologic factors and the breeding season. Since there is so little variation in the number of hours of daylight during the year it seems probable that a change of food is the factor which initiates breeding. The evidence for the two years covered in this study suggests a correlation between rainfall in May and the beginning of nesting. The rainfall for May 1937, was 8.78 inches and the fields were green by June 1. Breeding behavior was first noted on May 16, but may have occurred earlier and not been recognized due to the inexperience of the observer at that time. The first eggs were laid on June 1, and several other nests had eggs on the 15th. Contrastingly, in 1938, the rainfall for May was 4.05 inches and the fields were brown on June 1, although excellent rains came the first week of June and the grass was soon green. The first indication of breeding occurred on May 20, the first eggs were laid on June 10 and other nests had eggs on the 18th. Although observations over a period of years are necessary for conclusions, these data suggest a tentative hypothesis that there is an internal rhythm which is modified within limits by the change of diet. Experiments designed to test

this hypothesis were a failure due to the fact that the birds could not be taught to eat in captivity.

The breeding season ends before the diet returns to dry-season foods. A bird collected on November 15 possessed a regressed ovary and oviduct and the Cypress group (4) hatched its last young on November 5.

The ecologic conditions of the birds' habitat are quite definite. The birds require an open, savanna-like habitat, interspersed with a few trees to which they may rush at the approach of danger. In addition there must be a few thick, bushy trees in which to sleep. Since the number of suitable trees is reduced by the loss of foliage in the dry season, sometimes the birds have difficulty in finding a place to sleep. There is always a feeding area of open land, although groups may possess a territory containing woods and nest there.

In their relations to other animals, the adult birds have almost no enemies. Their wariness and their habit of going in groups does not permit any of the hawks to surprise them. Although the small boy with a sling shot is a constant source of danger, the birds seem to know the exact range and remain beyond it. The young birds are subjected to the vicissitudes of a nest life. For example, the nest of one group, situated in a heronry, was continually robbed, probably by the herons. Another nest was destroyed, probably by a rat. Accidents and disease result in the death of some birds. An individual which had probably flown into a sharp stick, and two diseased birds, were found. A bird with a broken leg disappeared in three days.

Although constant preening keeps the birds scrupulously clean, a few Mallophaga were found. Dr. F. H. Wilson of Tulane University identified them as *Esthiopterum macgregori* (Kellogg) and *E. crotophagae* (McGregor).

Crotophaga ani has almost no relations with other avian species. They fight with *Ptiloxena atroviolacea* (Icteridae) and, since the 'conk' is used in these cases, it is possible that the blackbird is mistaken for a strange judio. Although the only other species molested was *Corvus nasicus, Falco sparverius* is viewed with suspicion. Other species take alarm at the danger call and alarm note.

The ecological suitability of a habitat is roughly measured by the carrying capacity. The carrying capacity represents the number of individuals which can survive in a given area, and is dependent for most species on the amount of food and cover. The habit of living in colonies and possessing definite territories permits some significant

observations on the concept of carrying capacity. In this species, although there is a great change in the number of birds in the colony, the same colony may own the same territory for a period of several years. Table 6 shows the changes in population from 1937 to 1938 and demonstrates that although the number of birds in the colony may change, there is not necessarily a change in the size of the territory. Consequently the territory habit is a fundamental factor in limiting the population and determining the carrying capacity.

TABLE 6

CARRYING CAPACITY

Colony	*Number of birds in colony*		*Change in area*
	1937	*1938*	
Bambusa-Pond	15–24	20–13	–.05
Old G.-Cypress	10–13	7–5	none
C3-Gnhs	11–8	8–6	none
Cocos-Haemat	8–7	6	–.1
B2-Ceiba	7–8	9–3	–.1
Wares	10–9	6	none

PSYCHOLOGICAL CHARACTERISTICS

The learning ability of *C. ani* is an outstanding characteristic. The birds soon learn that a man with a hoe or a scythe is a source of insect food and, although they fly up in alarm when a man walks along, the birds feed within two feet of a man at work or follow the gasoline mowing-machine. I was convinced that the birds recognized me as an individual but experiments to test this hypothesis were inconclusive. The birds were able to see me in the blind through the slits in the burlap used for observation holes, and one colony would not become quiet while I was in the blind.

Although the birds were excellent learners, they did not learn to eat non-moving food in captivity. A *Ptiloxena atroviolacea* was put in the cage and ate regularly, but the judios never learned.

In addition to the learning ability, the species demonstrates several releasers, as characterized by Lorenz (1937). Both the danger call and the alarm note are good examples. Each note is invariably followed by a definite behavior pattern. For the first call the birds fly downward and at the second they fly upward. One of the characteristics of a releaser is its improbability, such that the behavior pattern will not be set off by 'false alarms.' But the mockingbird has mimicked the alarm note, adding it to its territory song, with the result that the judios respond to the 'releaser' when there is no cause for alarm.

On one occasion the danger call was given when a decoy was put in the trap near the nest. The most likely interpretation of this event is that this was a time of extreme excitement and, since the danger call is at the apex of emotional excitement, it was given.

DISCUSSION

Territory.—The concept of territory, as developed by Howard (1920) and others (Friedmann, 1933; Nice, 1933; Mayr, 1935; Tinbergen, 1936; Evans, 1938), has become a most fruitful generalization for the study of bird behavior. According to Friedmann (1935): "The theory of the function of territory is that it so spaces the breeding pairs of birds as to insure enough food for the young close enough to the nest so that, in their search for food, the parents do not have to desert the young long enough for any harm to come to the latter. In the spring the male leaves the flock with which it has spent the winter, isolates itself on an exclusive breeding territory to which area it confines its activities, makes itself conspicuous by display and song, thereby attracting a mate and at the same time warning other males not to trespass." Each species studied in detail demonstrates a large or small difference from the general behavior pattern.

The characteristics of the territory behavior of *C. ani* show clearly that the defence of the piece of land is the important feature. Sex is not a factor: the whole colony defends the territory against a strange bird no matter of which sex it may be. It is possible that there could be a colony composed entirely of one sex and this possibility should be tested experimentally. Food is not a factor: the territory is not defended in order to maintain the food supply in this species, because the same territory may be owned by a colony no matter how many are in the group; for example, the number in a colony changed from eleven to six, but the same territory was defended. Since *Crotophaga* has no song in connection with territory it may be concluded that song is not a necessary attribute of territory but is, in passerine species, a secondary acquisition. *C. ani* has definite behavior patterns for the defence and establishment of the territory and resembles the wren-tits (Erickson, 1938) and the mockingbird (Michener and Michener, 1935) in maintaining a territory throughout the year. The characteristics, cited here, show that the behavior is related only to a piece of land.

The defence of a piece of land, it is reasonable to assume, developed from the defence of the nest. Although Friedmann (1929) considers that the defence of the area originated first, Tinbergen (1936, p. 7)

implies that the defence of the nest is primal. The nest is a tangible object which is always in the same place and can become the headquarters. For success in reproduction at least one member of the pair must defend the nest; other activities can take place almost anywhere. In various species the defence of the nest location is extended to other activities and in some species this enlargement is developed to such an extent that the same or a different territory may subserve any or all of the four main uses of territory, namely, mating, nesting, feeding of young, and winter habitat. This viewpoint on the development of the defence of the piece of land renders unnecessary the teleological implications of Howard, so decisively attacked by Lack and Lack (1933). This extension of the utility of the territory roughly parallels the development of the altricial nesting habit. Since this development is continuous there are intergrades between all variations of territory and there can be no rigid categories.

The defence of territory in *Crotophaga* has no teleologic motivation (i. e., the birds are not consciously *fighting for* any thing) but is merely an extension of the defence of the nest site. (The analogy of this extension to the development of an anatomical character, the crest on the bird's bill, is striking. This large crest has no function but is merely an hypertrophy of the bill.) It is true that territory has many functions (food, nesting site, etc.) but the teleologic interpretation of the behavior must be separated from the functional value of the territory.

The defence of the sex partner is a separate element, termed sexual fighting, and should not be confused with the defence of the nest and surrounding territory. Mayr (1935) emphasizes the factor of sexual jealousy and states that "territory was originally developed only in connection with mating. . . ." But the behavior of *C. ani* shows that sexual jealousy is not a factor in this species since many individuals live together harmoniously, and a stranger may join a group.

Definitions of territory have been attempted (Mayr, 1935; Tinbergen, 1936). Although a definition is difficult, the nature of the concept may be clarified by a short characterization of its main features. Territory is a stage in an evolutionary process and is a characteristic of a species. Dobzhansky (1937) points out the difficulties in trying to define a stage in an evolutionary process, in his case, a species. Despite these difficulties, territorialism may be described as the defence of an object (territory) which serves in reproduction. Several salient points in this description should be noted. The concept is con-

cerned with a behavior pattern in respect to a physical object. There is no mention of purpose nor of individual nor of sex. The word 'serves' is intended to eliminate those cases in which the fighting is in relation to sex partner. The concept is very inclusive and can include other vertebrates as well and is functional, not teleologic in its interpretation.

Breeding cycles.—Cycles, analogous to the estrous cycle of mammals, have been postulated by Howard (1929), Huxley (1932), and others. In addition Whitman (1919) refers to the 'synchronization' of the male and female. The study of *C. ani* has obtained data of the type which led to the development of these hypotheses. These data as outlined below are behavioristic and extremely difficult to control and to test experimentally.

One striking phenomenon is that a colony sometimes does not lay eggs until a new member joins. Thus, Wares group in 1938 consisted of seven birds (both sexes) until June 26 and did not show any indication of nesting, although other groups had already laid eggs by this date. On June 26, a new bird (sex unknown) was present (eight in the group), nesting behavior was first seen, and there were eggs probably by July 10. There were eight eggs in the nest, indicating that two females had laid. As another example of this phenomenon, the Ceiba group originally consisted of about eight birds and showed interest in several locations for a nest, but laid no eggs, although other groups had eggs by this date. On July 7, a male joined the group and incubation started on July 28. The group at that time consisted of two males and two females, only one of which laid in the nest.

A colony sometimes takes up a territory and builds an abortive nest but does not lay eggs and soon leaves the area. This sequence of events occurred in two colonies of five birds in 1938. A somewhat similar case occurred. The Haemat group built a nest and hatched six young which were destroyed by a small boy. During the rest of the season the group built three abortive nests and in one laid an egg which was knocked out of the nest. During this time the group decreased in numbers from seven to four. Since a pair may raise a brood, and since there is no correlation between the size of the colony and the initial date of breeding or its success, it is known that a large number of birds is not necessary for success in nesting.

Another characteristic of this species is that the number of days between the destruction of a nest and the rebuilding varies greatly.

Table 7 shows that the interval between the date on which the nest was destroyed and the day the first egg in the new nest was laid, has no relation to the stage of incubation or feeding of the young and is not constant. In addition Table 7 shows that the time between the day the first brood left the nest and the date on which the first egg of the second brood was laid varies between 20 and 41 days and has

TABLE 7

DAYS BETWEEN BROODS

Colony	*Adults at*	*Brood left*		*Days*	*First egg*	*Days*
1937	*second nest*	*first*	*second*		*second nest*	
Bambusa	15	7–1	7–26	25		
B2	7	7–13	9–7	56	8–13	31
Wares	15	6–24	8–23	54		
1938						
Wares	6	8–14	10–5	52	9–2	20
Pond	13	9–4	10–18	44	9–25	21
Cypress	4	8–8	10–18	71	9–18	41
Gnhs	6	9–5	11–5	31	10–8	33

no relation to the size of the colony. In this connection Nice (1937) has found that for the Song Sparrow (*Melospiza melodia*) the interval between the date a nest was destroyed and the day on which the young left the rebuilt nest was a constant (30 days) but that the interval between the dates the young left the nest in two successive broods varies between 30 and 41 days. The renesting after destruction in *C. ani* must be controlled by psychic as well as by endocrine factors. The destruction of a nest is comparable to an abortion in mammals and in that class it is known that after an abortion a female will come into estrous period in a definite length of time for each species no matter (except for the last few days) at what stage of pregnancy the abortion occurs. The Song Sparrow resembles mammals in that it produces young in a definite period of time. But in *C. ani,* factors other than endocrine seem to control renesting.

Other evidence indicating cycles, is that some variation in egg-laying ability occurs as is shown by the fact that not all females lay in the nest. In the Pond group there were thirteen birds in the colony and 29 eggs in the second nest (the first nest was inaccessible and was somehow destroyed), indicating that at least five females deposited eggs. The third nest had twelve eggs, showing that three birds at the most (probably only two) had laid. The size of the colony was reduced only by the loss of a male just after incubation had started

in the third nest. Since it is known that the same female can lay more than once in a season, it is difficult to understand why some females stopped laying for the third brood. One suggestion is that different females laid in the second and third nests; but this solution does not seem likely from the history of other groups.

In addition to variation in laying ability great variation of interest in the nest is shown among individual birds. Individuals may leave the colony at the time incubation starts. For example, ARR (female) left the Cypress colony in which there was a male apparently paired with her on July 27; incubation had started on July 25. She formed a colony with two males, built a nest, and started to incubate on August 18. As another example a male (A432804) left the Pond group (incubation started August 29) on September 1 and joined with another bird. When this pair was collected on September 25 the female had an egg in the oviduct and the male had functional testes.

Furthermore, individuals vary greatly in their activity at the nest. In the Cypress group one pair did most of the work although two females had laid eggs in the nest and a bird which had laid eggs did not incubate at all but did feed the young. In two other cases eggs were laid but the nest was deserted without cause.

An additional point in support of cyclic breeding is that the strangers are most aggressive in their attempts to join a colony if it is in the nest-building stage, although they try to join a colony at any time.

The data cited above show that in respect to breeding behavior there is a difference of some sort between individuals and also a difference in the same individual at different times. Now let us examine the sparse knowledge of endocrinology of birds for any evidence of cycles within the season of reproduction. In the male the testis is always functional except during the incubation according to Schooley and Riddle (1938) and as soon as the feeding of the young stops the male returns to complete function. In the female the relations between the several hormones are inadequately known. The relations of prolactin to brooding and the possible inhibition of FSH (Bates, Riddle, and Lahr, 1937) occur after the eggs are laid and give no clue to the factors influencing egg laying. LH is present (Leonard, 1937) but its function is unknown. A type of corpus luteum is present but it is a rapidly regressing structure. This summary indicates that there is no positive endocrine evidence of a cycle in breeding.

Several features concerning the endocrinology of *C. ani* may be presented at this point. The history of the ovary is of interest. After

ovulation the granulosa layer proliferates and forms a structure considered by Hett (1923) as a corpus luteum, which decreases in size. In *C. ani* the corpus atreticum shows an interesting development. The granulosa of eggs which have not undergone pre-ovulatory swelling, proliferates and in *C. ani,* bursts, the yolk is apparently extruded from the follicle, and lymphocytes enter and take up the fat globules. After about ten days of atresia, this structure cannot be distinguished from a corpus luteum. The function, if any, of these two structures is unknown.

Another feature in reproductive physiology of *C. ani* is that throughout the season birds with small gonads occur. Birds of both sexes were collected at the height of the breeding season. A testis, which weighed one-sixth the normal, contained sperm, although these were not normally distributed, and had none of the characteristics of degeneracy. The ovaries contained eggs which are larger than in the juvenile, but had not reached the pre-ovulatory swelling stage. One explanation for these birds is that they are young hatched late in the previous season (November) which are still too young to mature sexually. Thus van Oordt (1938) has found that non-breeding Oystercatchers *(Haematopus ostralegus)* may be either yearlings or adults. The testes of the yearlings are somewhat developed and have a few sperm but those of the adults possess sperm and resemble those of breeding adults. The ovaries of yearlings are less developed than those of a non-breeding bird. This description agrees essentially with the histological picture of the gonads of *C. ani.* In addition, Kendeigh and Baldwin (1937) find that about 15% of the young House Wrens did not breed in the first year, and Lorenz (1931) finds that young Jackdaws court and pair in the first autumn but do not breed till the second year. Another explanation of the condition of the gonads of these specimens is that they are "old virgins," as described by Schooley and Riddle (1938). According to these authors, these birds have ovaries which "have developed somewhat beyond the juvenile state, but no ova have entered upon the final phase of growth which is induced by a release of increased amounts of pituitary gonad stimulating hormone." The basophiles of the pituitary are undifferentiated and agranular and are smaller than pre-ovulatory basophiles. The acidophiles are nearly normal and resemble those of nesting birds. Although the pituitary resembles that of a senile animal, it is known that these birds are no more than a year and a half old. This condition is essentially pathologic and would not be expected in a natural population.

In reproductive physiology the problem of the factor which determines the cessation of laying in birds is important. Presumably either visual or tactile stimulation reacts through the pituitary to stop the laying process. But since in *C. ani* more than one bird lays eggs in the nest, there is a varying number of eggs, and hence neither sense can be effective. In this connection it is interesting that incubation starts slowly and is intermittent for a few days although most species start abruptly and sometimes before the eggs are laid or the clutch is completed. The fact that incubation starts simultaneously although the eggs may be laid over a long period of time (16 days in the Pond group) and presumably some of the females have completed their clutch suggests that the psychologic factors may be more important in arresting laying than any endocrine factors which may exist. The great variation (4–7) in the number of eggs laid per female may be related to the lack of a suitable stimulus to stop laying.

The hypothesis of Darling (1938) pertains to some of the apparently cyclic behavior seen in *C. ani*. Darling suggests from his work on the breeding of gulls that the birds must be stimulated by courtship to a high degree of emotional excitement before breeding can begin and that in colonial birds there is a great amount of reciprocal stimulation within the flock and hence a minimum number (threshold) of birds is necessary before the breeding can start. Therefore, in colonies where the number of birds is just above the threshold, the breeding is irregular and the number of unsuccessful nests is high. Darling's observations on which he based the above hypothesis can also be explained by the hypothesis of reproductive cycles. In the large colonies, since there are more birds, there is a greater chance of one bird meeting a bird in exactly the same phase with it and therefore in the large colonies there will be a greater success in breeding. Neither of these hypotheses is supported by experimental data as yet.

A last item concerning the relation of the endocrine system with the behavior is the problem of the incomplete nests, here termed abortive. These have been regarded as 'symbolic nests' (Tinbergen, 1935), the building of which results in sexual stimulation of the mate. But the fact that in *C. ani* many abortive nests may be built after pairing, after copulating, after laying, and even after a nest has been destroyed suggests that these nests are abortive due to a maladjustment of the endocrine and nervous sexual mechanism, and are not stimulative in effect. Tinbergen found that 'symbolic nests' were built after coition and hesitatingly suggested that the function was to keep the pair

together. The 'play nests', built by male wrens which have a mate and eggs, are in a different category.

Parasitism.—C. ani is a member of a family, the Cuculidae, which has developed social parasitism in many species. The genus *Crotophaga* shows one manifestation of the unusual breeding habits developed throughout most of the family. These various abnormalities may be described as a lack of coordination in the sequence of breeding habits, but this description, of course, does not explain anything.

In order to understand the genus *Crotophaga* it is necessary to discuss briefly the types of social parasitism found in birds; Friedmann (1929) and Makatsch (1937) give references to the extensive literature. I suggest that parasitism has developed along two lines: (1) Nest parasitism, where one group of species, probably in relation to a loss of territory instinct (Friedmann, 1928), no longer builds its own nests but lays eggs in the old nests of other species and raises the young in a normal manner. The fact that in most cases the species (Icteridae, Ploceidae) are closely related to the birds whose nests are used, may be explained by the similarity of breeding habits and ecological requirements of the birds. In other cases (*Legatus leucophaius, Tringa solitaria, Zenaidura macroura*) the birds use the nests of non-related species to a greater or less degree. The evolution of parasitism followed from this behavior in various stages. The birds usurped a nest and laid eggs before the owner had used it. The species soon developed the habit of dropping eggs on the ground or laying them in the nest and leaving them, probably often due to competition with the owner. Thus complete parasitism occurs. Some of these species are originally host-specific, but it should be noted that in the Cowbirds the host specificity has decreased to such an extent that in the case of the North American Cowbird, the eggs are laid in nearly any nest. The loss of the nest-building instinct is the cardinal feature in nest-parasitism development.

The other line is (2) egg parasitism. In this development the bird does not usurp the nest, but lays eggs in other nests, more or less haphazardly as is done by pheasants and ducks. Nevertheless in addition it regularly builds its own nest and raises young in a normal manner. In the case of *Heteronetta* this behavior has culminated in complete parasitism. It seems likely that the Cuculidae (for example, as in the North American cuckoos) at first deposited the eggs in nests other than their own while still building nests and raising their young (Herrick, 1910). Then they became more parasitic and eventually

lost the ability to build a nest. It should be noted that in the cuckoos the trend has been from parasitizing many species to parasitizing only one species (host-specific), and that the territory instinct has been retained. The loss of the instinct to raise young is the cardinal feature of egg-parasitism.

A possible explanation of the loss of the instinct to raise young is found in some of the work on the pituitary. Byerly and Burrows (1936) have shown that the pituitaries of non-breeding fowl contain less prolactin than those of broody races. If prolactin produces brooding, as Riddle, Bates, and Lahr (1935) claim, it is possible that birds, non-broody due to a loss of prolactin or a loss of reactivity to prolactin, have been able to survive due to the parasitic habit.

The peculiar breeding habits of Crotophaginae seem to be an offshoot of the egg-parasitism line. This suggestion as to the evolution of behavior is supported by what little is known of the habits of *Guira*. This bird is reported to lay eggs in the nests of *C. ani* and certainly deposits its eggs in the nests of other species (*Phytotoma, Milvago*). The birds drop many eggs on the ground and although laying their eggs in other individuals' nests, do not usurp the nest. It may be considered that *C. ani* has become host-specific on itself, and that the territory instinct has been retained and extended to include other individuals of the species. In contrast to this view Makatsch (1937) believes that *Crotophaga* in not an offshoot but is a step between the habit of laying occasionally in other birds' nests and the full development of parasitism.

The cause of the aberrant breeding behavior is unknown but the following hypothesis is suggested in the hope that it may have heuristic value. There are several examples of one organ assuming the endocrine function of another. I suggest that in those birds in which the behavior is hormonally controlled, it is possible that the pituitary has adopted the control of breeding behavior from the gonads and that the change is either incomplete or partly miscarried, resulting in erratic breeding habits or complete loss of some phases. Parasitism or social nesting has permitted these species to survive.

It is perhaps more than coincidence that in *C. ani* the nesting is so erratic and so often miscarried and the courtship display so simple and infrequent. It has been suggested (see Marshall, 1936) that the function of courtship display is to synchronize the sexual processes of the male and female. That courtship may act on the endocrine system is supported by the fact that Schooley and Riddle (1938) have

shown that the absence of a male pigeon results in changes in the pituitary of the female. This chain of evidence supports the suggestion that aberrant breeding habits are connected to dysfunction of the endocrine system.

Comparison with Social Birds.—True social life in animals has developed coincident with an extension of the familial relations over the greater part of the life span of the individuals. In *C. ani* the young of one brood may feed the young of the second brood but it seems likely that this action is a secondary development. The social habit, permitting the young to remain with the adults for a long time, is found in incipient stages in several birds. Skutch (1935) cites examples of species (*Psilorhinus mexicanus, Psaltriparus melanotis, Heleodytes zonatus*) in which unmated birds help in the raising of the young. In the species *Psilorhinus mexicanus* immature birds brought food to the incubating female. There were presumably no familial relationships among the birds. In *C. ani,* some of the nonbreeding birds are probably immature.

Other species seem to have independently developed the same habits as *C. ani,* although not enough is known of their habits to compare them in detail. In *Corcorax* and *Pomatorhinus* (Friedmann 1935) available information indicates a development of social nesting. In *Balanosphyra* (Ritter, 1938) there is a social nesting behavior which closely resembles that of the judios. These woodpeckers live in groups and probably defend a territory for the whole group, judging from reports of fighting and flights within the territory. Birds whose actions resemble those of the strangers of *C. ani* are described. Seventeen eggs are reported from one nest and the conclusion is that several females laid in this nest. This is most surprising since the woodpeckers as a group are very normal in their breeding habits.

The Jackdaw (Lorenz, 1931) has developed a type of social behavior which has only a superficial similarity to the habits of *C. ani.* The birds live in a group but nest in pairs and observe strict monogamy. Strangers are not permitted to join except in the winter, and the loss of a member of the flock is noticed. In this species there is no abnormality of the breeding sequence. Other species have a social habit to a greater or less degree such as is illustrated by the grackle, *Cassidix* (McIlhenny, 1937). The females are in great excess and the males are polygynous. The male selects an area and drives off all other males in order to collect a group of females, but takes no part in the raising of the young. In these species there is no abnormality of the breeding sequence.

The social habits of the howling monkey have been carefully studied (Carpenter, 1934), showing some interesting similarities to the judios. There is a disparate sex ratio in each group, in favor of the females, however. Single individuals may join a group after fighting, much as strangers join a group of anis.

Social habits may develop readily in a species which has poorly coordinated or irregular breeding habits. The irregular breeding habits permit the presence of non-breeding birds and of an excess of males in the population to result in social nesting habits and in the extension of territorial instinct to include the whole colony. The manner of development of social nesting in *Crotophaga* should be clarified by a thorough study of *Guira*.

In the development of social habits a species acquires many releasers and other behavior patterns of the type described by Lorenz (1937). For *C. ani* the data on this subject are so unrelated that their presentation is reserved for a future time. Nevertheless two social characteristics may be mentioned. In *C. ani* the sense-modality used in sex recognition is probably sight. In some species (Noble, Wurm, and Schmidt, 1938) voice is extremely important while in others sex is recognized by visual cues (Noble and Vogt, 1935). In judios the method of sex recognition is difficult to determine because of the antagonism to strangers. Experiments using dummy birds proved nothing, and the behavior at copulation gave no clue to the sense-modalities used.

The other social characteristic to be mentioned is that probably there is a dominance of the flexible type found in most birds (Allee, 1936). The colonies of *C. ani* live so harmoniously that it was impossible to conclude that there is a strict social rank.

SUMMARY

Crotophaga ani, an aberrant member of the Cuculidae, lives in flocks and builds communal nests. Each colony defends a territory against strangers, which are of two types: one tries to join the group and the other does not. The defence behavior consists of 'chasing' the strange individuals and 'rushing' from tree to tree.

The pairing and nesting behavior occurs in five distinct stages. The behavior sequence is frequently interrupted and is often irregular. The relationships between the adults are in some cases certainly monogamous, but in other cases, the relationships may be either polygynous or polyandrous.

The nest contains the eggs from several females, each female laying between four and seven eggs. The incubation period lasts about thirteen days. The survival of the young is about 35%. The young birds remain with the flock for many months and assist in feeding the subsequent broods.

The climatic change from a dry to a wet season permits great changes in ecological distribution, and regulates the initiation of nesting.

The data concerning *C. ani* indicate that (1) the defence of a piece of land is the crucial factor in territorialism. (2) The breeding behavior is in some manner cyclic or at least variable. (3) The aberrant breeding habits are an offshoot of the egg-parasitism type of social parasitism.

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