PAIRING BEHAVIOR OF PIGEONS RELATED TO AGGRESSIVENESS AND TERRITORY[1]

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EXPERIMENTATION with pigeons and doves in the field of social behavior is complicated by the fact that the social organization is based on peck-dominance (Masure and Allee, 1934; Bennett, 1939) or bidirectional pecking, whereas peck-right occurs in many other birds (Allee, 1952). The peck-right pattern permits a more stable social organization, as the order of ranking individuals under bidirectional pecking is fluid. Experimentaton with Ring Doves, *Streptopelia risoria* (Bennett, 1940), presented difficulties in analysis since some control individuals shifted ranks in the social hierarchy.

Ritchey (1951) noted definite territories among Common Pigeons (*Columba livia*), and suggested a positive correlation between the percentage of encounters won and the amount of territory defended. She concluded that territorialism blocked a rigid dominance hierarchy such as is found among Domestic Chickens (*Gallus gallus*). Bennett (1940), Diebschlag (1941) and others previously suggested that territoriality plays an important role in the establishment of a dominance order. In unisexual groups of the Common Pigeon, each individual defended a portion of the perch upon which it was usually found. Under such conditions territoriality was reduced to what may be called a perch-right. The exchange of pecks between any two individuals showed a balance in favor of the one nearest the center of its territory.

The object of this experiment was to determine if there was any relationship between relative aggressiveness in pigeons and sexual behavior. Among chickens, high ranking cocks sired the most chicks and had precedence in mating (Guhl and Warren, 1946; Guhl, Collias and Allee, 1945), and receptivity in females showed a negative correlation with social rank (Guhl, 1950). To determine whether social dominance or levels of aggressiveness influence sexual behavior, particularly pairing behavior, in pigeons it was necessary to devise a method of evaluating the aggressiveness of the individuals without the influence of perch rights.

The courtship display, pre-mating display and other behavior patterns in pigeons have been discussed in the classic work of Whitman (1919), and also by Craig (1918) and Gifford (1941). Courtship display is usually performed by the male, and shown by the fluffing of the breast feathers, dragging of the tail, cooing, and treading of the feet on the floor. If the female is receptive she will nod her head, after which billing follows. The male presents an open beak into which the female inserts hers. There is evidence that the male regurgitates into the beak of the female. Subsequently the female will crouch, elevate her wings and receive the male, and the pair-bond is formed.

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Experimental Methods and Procedure

The pigeons used in this study were obtained from a farm house near Manhattan, Kansas. Of the 45 birds trapped, 11 males and 13 females were selected on the basis of equality of size and the appearance of good health. These were treated with five per cent chlordane powder to eliminate any ectoparasites.

To determine the sex of the individuals, a method similar to that described by Lee (1915) was used. The male is usually larger and heavier than the female and his pelvic bones are closer together and more rigid than those of the female. Mr. Herman Smith of the Department of Poultry Husbandry tried to obtain semen by methods used for artificial insemination in poultry, but this did not identify all of the males. As a further test for sex the birds were all placed into a small cage for two days, and observed for sexual behavior. As the sex of each bird became evident, it was removed and placed into a cage with others of the same sex.

For identification of individuals each bird received a numbered and colored legband, red for males and green for females.

Several types of cages were used and are described below. During certain tests the birds were kept as unisexual groups in cages designated as the "home cage." Tests for aggressiveness were made in a "combat cage" and those for pairing behavior in a "pairing cage." Finally the sexes were brought together in a "flight cage."

The Home Cages.—The males and the females were in separate cages of similar construction, measuring 6 x 4 x 2 feet. In these cages the birds could move about quite freely but could not fly. There were many interactions among the males and they tended to space themselves and to remain within a certain area. The females showed little aggressive activity and scattered indiscriminately. The pigeons were in these cages for 40 days, during which time they ceased to recognize former mates. According to Carpenter (1933) pigeons will forget their mates after about 24 days. Although there was a tendency, especially among the males, to defend certain areas, it was doubtful whether these relationships carried over into the test situations as the combat cage provided a strange area, the rights over which had to be won.

The Combat Cage.—The object of this cage was to induce fighting behavior, the results of which would indicate some measure of relative aggressiveness. The birds were introduced into the cage by twos until each bird had met and settled dominance relations with each of the others of its sex. This procedure is a modification of the initial encounters staged by Collias (1943) for chickens. Individuals were ranked in levels of aggressiveness according to the number of such encounters won. This procedure has proved to be satisfactory (Guhl, 1953) for chickens.

The combat cage was made of chicken wire on a wooden base. It was circular, 13 inches in diameter and 8 inches high. This size and shape allowed the birds to be intimately close at all times with no corners in which to take refuge.

Two pigeons of the same sex were taken from the home cage and introduced simultaneously into the combat cage. The observer then retired behind a screen. After a short interval the males began to fight, but the females had to be stimulated by presentation of food, after being deprived of food for about 24 hours in the home cage.

The Pairing Cage.—This cage was constructed similar to the combat cage but somewhat larger, being 24 inches in diameter and 12 inches high. Each male was introduced into this cage with two females, to determine whether pairing behavior may be related to the relative aggressiveness of the females.

The Flight Cage.—This cage was 6 x 5 x 7 feet. It was built against one wall of the laboratory; two other sides were made of chicken wire netting and the fourth side, or end, was composed of 10 large nest boxes. Perches were constructed near the end opposite the nest boxes. Containers for food and water were placed on the floor.

After the tests for pairing behavior were completed, all the males were placed into the flight cage and permitted to establish territories. The females were then tested singly in the flight cage to determine whether levels of aggressiveness of the males could be related to success in pairing when in competition with other males. As soon as pairing was effected the female was removed and returned to the home cage. Three days elapsed before another female was introduced. After these observations were completed all the females were introduced simultaneously and subsequent pairings were noted.

Observations and Results

Determination of Relative Aggressiveness

The Males.—When two males were placed into the combat cage, one would usually begin to display immediately. A typical display included the fluffing up of feathers of the neck region, dragging of the tail feathers on the floor, treading with the feet, and loud vocalizations. The reactions of the other bird were either positive or negative. In the latter response it would avoid the bird in display, which was then considered the winner of the contest as he established dominance. The length of time required to settle dominance relations varied with the intensity of actions and reactions. Dominance was considered as established when one bird displayed aggressively and the other showed avoidance and maintained such a reaction. A bird assuming the subordinate status would lower his head and tend to carry the long axis of his body in a nearly horizontal position, whereas the dominant one would maintain a stance in which his body would be nearly erect and his head held high. If a subordinate bird raised his head, he invariably would be pecked.

A bird which reacted positively to the one displaying would deliver a series of pecks, and usually a fight ensued. In fighting there was an exchange of pecks and wing slapping with loud vocalizations. During intensive fighting one male grasped the other and tried to shake him. Eventually one of the contestants showed escape or avoidance behavior, which often was intense under such confined conditions. The birds were returned to the home cage as soon as the observer judged that a decision had been reached. Some contests ended in "no decision" even after one hour. In one case the males fought repeatedly without either giving way; in others neither aggressive nor submissive behavior was shown.

Each bird met each of the other males in a systematic manner. Three rounds were made for a total of 330 pair contests. A summary of the results is given in Table 1, which shows the number of individuals that each bird

TABLE 1

RESULTS OF CONTESTS BETWEEN PAIRS OF MALES IN THE COMBAT CAGE
MALES ARE RANKED ACCORDING TO NUMBER OF INDIVIDUALS EACH DEFEATED

Winners	Losers									Number defeated	Rank
6	7	5	2	3	9	13	1	10	11	8	10	1
7		5	2	3	9	13	1	10	11	8	9	2
5			2	3	9	13	1	10	11	8	8	3
2				3	9	13	1	10	11	8	7	4
3					9	13	1		11	8	5	5
9						13	1	10		8	4	6.5
13							1	10	11	8	4	6.5
1								10	11	8	3	8
10				3					11		2	9.5
11					9					8	2	9.5
8								10			1	11

defeated in these contests. The bird listed in the first column gained dominance in two or three contests with each of the birds given on the same horizontal line. The numbers are those of the legbands. The relative aggressiveness of each male is indicated by the number of individuals it dominated, and the last column gives the ranks in aggressiveness. It should be emphasized that these measures of aggressiveness are relative only to others in the same group and can not be used for intergroup compairisons. The ranks were later used to determine the influence of relative aggressiveness on pairing behavior.

The Females.—Encounters by female couples in the combat cage were conducted like those for the males, with one exception. Female pigeons are not as aggressive as the males, and food competition was used to induce aggression. Food was withheld from the females in the home pen for about 24 hours prior to the contests; and a small cup of food was fastened to the floor in the center of the cage. When two hungry females were introduced into the cage, both fed simultaneously until most of the food was gone. Fighting began with the competition for the last few grains. Except for display, the encounters were similar to those of the males. There was slight fluffing of the feathers on the neck and a very mild vocalization. There was no treading of the feet or dragging of tail feathers as observed among the males.

Three rounds of paired encounters gave a total of 468 contests. The results are summarized in Table 2 in a manner similar to that in Table 1. It may be noted that in both sexes there were deviations from a straight-line ranking of aggressiveness; This condition may have resulted from variables during the contests or it may reflect statistical phenomena of minor, unmeasurable differences in aggressiveness.

TABLE 2

RESULTS OF CONTESTS BETWEEN THE PAIRS OF FEMALES IN THE COMBAT CAGE
FEMALES ARE RANKED ACCORDING TO THE NUMBER OF BIRDS EACH DEFEATED

Winners	Losers												Number defeated	Rank
12	14	22	20	18	23	15	21	19	16	17	25	24	12	1
14		22	20	18	23	15	21	19	16	17	25	24	11	2
22			20	18	23	15	21	19	16	17	25	24	10	3
20				18	23	15	21	19	16	17	25	24	9	4
18					23	15	21		16	17	25	24	7	5
23						15		19	16	17	25	24	6	6
15*							21	19		17	25	24	5	8
21*					23			19	16		25	24	5	8
19*				18					16	17	25	24	5	8
16						15				17	25	24	4	10
17							21				25	24	3	11
25												24	1	12
24													0	13

* These birds tied for the same position on the aggressive scale.

MATE SELECTION IN THE ABSENCE OF TERRITORY

Territory plays an important role in pairing and nesting among pigeons. Within the pairing cage there was no established territory. A male and two females were placed simultaneously into this cage and pairing behavior was observed. The relative aggressive ranking of all three birds was used to determine whether levels of aggressiveness exerted any influence on pairing behavior. All three birds were returned to their respective home cages after a pair-bond had been formed.

Only 28 pair-formation tests were made out of a possible combination of 1716 (if each of 11 males were tested with each of the 156 possible female couples). Each male was used at least once and two were used five times. Each female was member of a couple at least two times and one was used 15 times. In four instances the same pair of females was used with two or three males.

The reactions of the three birds usually followed a typical pattern. The male began to display immediately, directing his advances to either of the females, and this continued for about 15 minutes. The dominant female maintained an alerted stance. Subsequently the subordinate began bobbing or nodding her head. This sign of receptiveness was followed by attempts to copulate. At times the dominant female would attack her inferior and thereby prevent copulation. After billing ensued, copulation was successful and the pair-bond was established. Thereafter the mated pair preened or

began to attack the unmated female, apparently in an effort to establish a nesting territory. At this point the test was considered to be concluded and all three birds were removed.

The results of the 28 tests are given in Table 3. The data are grouped according to the degrees of differences in the ranking of the females. In the first group these differences are neither very great nor very small. In the second group all the females have the same rank, that is, they were tied for rank number eight (see Table 2). The next group includes pairs of females with wide differences in rank. Then follow two tests in which both females were ranked high in aggressiveness, and in the last three tests both were relatively low in rank.

The legband numbers for the females with which the male paired are printed in bold face type. In all but two tests the pair-bond was established with the female of lower rank in aggressiveness. In these instances number 17 dominated number 21 and 21 dominated 23 (Table 2), in the combat cage and probably in the home cage. Similarly for the pairs in which both females tied for rank eight, the one selected by the male was the subordinate. It did not seem to make any difference in the results whether the paired females were both of relatively high or low rank, or of wide separation in rank. In those tests in which different males were used with the same pair of females, all the males selected the same female. These results and the observations recorded indicate that sexual behavior was facilitated by the submissive stance of the female, and that synchronization of the sexes was influenced by the submissiveness of the female and the aggressive posturing of the male.

Establishment of Territories by the Males

The 11 males were placed into the flight cage as a group and permitted to establish territories. The nest boxes, at one end, were a stack of five orange crates, with each half suitable for a nest. There was some space beneath the bottom nests and the floor. Straw was provided for nesting material. Two perches, at a height of about five feet, were situated near the opposite end. For about one hour the birds flew about in confusion, and then began to select nest boxes. There appeared to be a shifting of perching sites. Some would leave a box for no apparent cause; others would be attacked and driven out; and still others would defend their holdings. This scene of turmoil lasted for about five days. Several more days passed before the territories became more stable.

Seven of the 11 males established territory in nest boxes; two selected sites on the floor under the nest boxes; one elsewhere on the floor, and male number 8 (rank 11) remained on one of the perches. There was no indication that level of aggressiveness had any relation to the nest box selected, which may mean that the location of a nest box had no obvious advantage under these

TABLE 3

RESULTS OF TESTS ON PAIRING BEHAVIOR

FIGURES IN PARENTHESES ARE THE RANKS IN RELATIVE AGGRESSIVENESS

(Legband numbers in boldface indicate the female selected by the male in pairing.)

Male		Dominant female		Subordinate female	
Number	Rank	Number	Rank	Number	Rank
1	(8)	18	(5)	**16**	(10)
3	(5)	18	(5)	**16**	(10)
2	(4)	15	(8)	**16**	(10)
3	(5)	15	(8)	**16**	(10)
6	(1)	18	(5)	**15**	(8)
6	(1)	18	(5)	**15**	(8)
13	(6.5)	18	(5)	**15**	(8)
10	(9.5)	14	(2)	**19**	(8)
11	(9.5)	20	(4)	**19**	(8)
13	(6.5)	20	(4)	**21**	(8)
9	(6.5)	23	(6)	**24**	(13)
8	(11)	**21**	(8)	17	(11)
9	(6.5)	23	(6)	**15**	(8)
3	(5)	**23**	(6)	21	(8)
13	(6.5)	15	(8)	**19**	(8)
8	(11)	15	(8)	**21**	(8)
11	(9.5)	15	(8)	**21**	(8)
13	(6.5)	21	(8)	**19**	(8)
6	(1)	12	(1)	**25**	(12)
7	(2)	14	(2)	**25**	(12)
9	(6.5)	23	(6)	**24**	(13)
8	(11)	12	(1)	**17**	(11)
9	(6.5)	14	(2)	**17**	(11)
3	(5)	14	(2)	**22**	(3)
5	(3)	22	(3)	**18**	(5)
3	(5)	16	(10)	**25**	(12)
6	(1)	15	(8)	**25**	(12)
9	(6.5)	15	(8)	**24**	(13)

conditions, or that trial and error and chance determined the site finally accepted.

COMPETITION FOR A MATE BY TERRITORY-HOLDING MALES

When the male territories were firmly established the females were introduced singly and allowed to remain until a pair-bond had been formed. Under these conditions pairing required two or more days and the high level of activity kept the males from feeding. After the female was removed a lapse of three days occurred before another female was introduced.

The behavior was usually as follows. Several males flew to the female and attempted to display. At first the males were more intent on display than on

areas and nest areas which they defend. It was assumed that two birds, whether acquainted or not, would fight in a strange location to establish area rights. The fact that definite dominance–subordination relations were established suggested that the use of a combat cage permitted the measurement of aggressiveness. If this method is repeated one might isolate the individuals in the home cage with screened partitions, to eliminate the possibility of home-pen effects, if any. Some observations in this experiment suggested that dominance relations in the home pen showed some agreement with the outcome of pair-contests in the combat cage. This may not necessarily reflect seriously on the ratings of aggressiveness as Guhl (1953) obtained high correlations between ranks in a peck-order of chickens and ranks in levels of aggressiveness measured by initial pair contest, i.e., between strangers.

Whitman (1919) defined the mating period as the activities of the reproductive cycle which begin with courting and end with the laying of the first egg. This may be considered as the activities leading to and including the establishment of a pair-bond. With poultry the term mating is usually used for coition since these birds are promiscuous and do not form pair-bonds in the usual sense. According to Whitman the mating period in pigeons embraces courting, copulating, and the hunting, acceptance and construction of the nest. Its duration is six or seven days. Copulation is intermittent throughout the mating period. Both males and females may extend their state of readiness in the sexual cycle for a month or longer if separated. The primary sex impulse may arise relatively automatically. Once a cycle has begun it tends to run its course. Unisexual pairs may stimulate each other to begin the cycle, even to laying by females. As far as could be determined the birds in the home cages were in the state of readiness, for no eggs were laid and pair-bonds were formed in the pairing cage. The relatively crowded conditions and the limited vertical range probably facilitated the maintenance of the state of readiness. In a large flight cage or in freedom, individuals would be expected to vary in the phases of the cycle and certain sex pairs might not synchronize. It may therefore be concluded that the results obtained here, i.e., that the male paired with the subordinate female, was not due to lack of readiness of the dominant one. Furthermore a given dominant female would pair when matched subsequently with one of her superiors in the pairing cage. It should also be noted that the tested birds were removed before the mating period (as defined by Whitman) was fully established; this action therefore maintained a state of readiness.

It was apparent that the male reacted to the display of submissiveness, a crouch-like stance, and not to dominance status. It has been shown in chickens that low-ranking hens crouch more readily for a cock, and that high-ranking hens will show more receptivity when their habit of domination is reduced by removing most of their subordinates (Guhl, 1950). Unisexual

cage containing 11 males with established territories. Female number 12 was not included as she had been in the flight cage two days previously, and it was believed that she might return immediately to the male with which she had paired.

As the females entered the cage, the males immediately started to fly wildly and began to display vigorously. The females were pursued and territorial rights were ignored. The top ranking male, number 6, displayed to a number of females, whereas other males appeared to single out specific females. For two days there was so much activity and calling that the observer could not determine whether a given female was responding to the calls of a particular male. It appeared as though pairings which occurred were largely a matter of chance.

TABLE 5

PAIRS FORMED AFTER THE FEMALES WERE INTRODUCED, AS A GROUP, INTO THE FLIGHT CAGE CONTAINING THE MALES

(Figures in parentheses indicate rank in aggressiveness)

Day	Male		Female	
	Number	Rank	Number	Rank
I	8	(11)	17	(11)
	11	(9.5)	15	(8)
	10	(9.5)	16	(10)
II	2	(4)	20	(4)
	1	(8)	25	(12)
III	7	(2)	18	(5)
IV	5	(3)	22	(3)
V	13	(6.5)	19	(8)
	6	(1)	21	(8)
VI	9	(6.5)	23	(6)
	3	(5)	14	(2)

The results given in Table 5 are the pairings as listed by days on which the pair-bonds were established. There was a tendency for low-ranking birds to pair earlier than high-ranking ones, particularly among the males; and no relationships between levels of aggressiveness of mated birds can be considered with confidence. The data in the table tempt one to draw conclusions which would not be warranted by the behavior observed.

DISCUSSION

In testing for relative levels of aggressiveness a method similar to that developed by Collias (1943), for chickens, was used. One major difference was that Collias used birds which were strangers, whereas the pigeons used here were caged in unisexual groups and therefore were not strangers. However, chickens are not territorial and pigeons are, in that they have perching

areas and nest areas which they defend. It was assumed that two birds, whether acquainted or not, would fight in a strange location to establish area rights. The fact that definite dominance–subordination relations were established suggested that the use of a combat cage permitted the measurement of aggressiveness. If this method is repeated one might isolate the individuals in the home cage with screened partitions, to eliminate the possibility of home-pen effects, if any. Some observations in this experiment suggested that dominance relations in the home pen showed some agreement with the outcome of pair-contests in the combat cage. This may not necessarily reflect seriously on the ratings of aggressiveness as Guhl (1953) obtained high correlations between ranks in a peck-order of chickens and ranks in levels of aggressiveness measured by initial pair contest, i.e., between strangers.

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matings were also related to dominance in hens (Guhl, 1948) and cocks (Guhl, 1949; 1953). Unisexual pairing by pigeons was reported by Whitman (1919:28). Mr. Herman Smith (personal communications) has succeeded in establishing unisexual pairs, male and female, by confining two birds of widely-separated ranks in relative aggressiveness. It is the posture and psychological state associated with dominance or subordination which trigger the sexual responses.

Individuals ranking high in a social hierarchy have a precedence in certain activities, such as feeding, and among males, mating rights may be included, as was found in chicken (Guhl, Collias, and Allee, 1945; Guhl and Warren, 1946). When the female pigeons were tested in the flight cage with territorial males, similar results were indicated. However, among the pigeons territoriality increased the opportunities for a relatively unaggressive male to pair if a female tended to remain in his area. Under the highly competitive conditons in this test (a sex ratio of 11 males to one female) the most aggressive males violated territory boundaries most often. This test did show that male pigeons may under certain conditions have pairing rights irrespective of territory.

One advantage of territorialism among pigeons was demonstrated when 12 females were introduced into the flight cage with 11 males. With the sex ratio nearly one to one all the males formed pair-bonds, and highly-aggressive males gave indications of some disadvantages. These males had difficulty in concentrating their attention on a particular female. With the females being distributed about the cage the opportunities for each male to pair were increased. Among free pigeons this competition would be less strenuous since it would be unlikely that many males or females would be in the readiness phase of the reproductive cycle at the same time, and defended areas may have wider distribution. Territory violations might be fewer than in this experiment.

The Common Pigeon is a suitable laboratory animal as it adjusts readily to confinement and handling. Being somewhat ambisexual in behavior, it could serve as an experimental animal in certain studies of the endocrine, social and sexual interrelationships. With refinement of the technique presented here on the measurement of aggressiveness, some of the difficulties experienced in the past (Bennett, 1939, 1940) could be surmounted.

Summary

1. The relative aggressiveness of Common Pigeons was measured by means of paired encounters in a combat cage or neutral area.

2. Pairing behavior was facilitated through submissive behavior by the female.

3. The most aggressive males had precedence in pairing if under extreme competition with other males and when confined in flight cage.

4. Territorialism made it possible for all the males, irrespective of levels of aggressiveness or dominance, to establish pair-bonds, when the number of individuals of each sex was nearly equal.

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