SOCIAL HIERARCHY IN FLOCKS OF THE CANARY

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INTRODUCTION

THE attention of biologists was focussed by Darwin upon the question of animal fighting and competition. It was not until many years later that biologists began to realize that group integration and cooperation was an equally important force in the living world. Colonies of ants and termites, herds of mammals, and flocks of birds demonstrate types of social organization familiar to all. Allee (1931) has shown that the roots of this social life extend far lower than these in the animal kingdom, even so far as to include all of the phyla of animals. Many social groups as of ants and termites have utilized the potentialities of cooperation to such an extent that fighting within the social unit does not exist. With vertebrates, however, this high degree of harmony within the group never exists and some fighting usually occurs between members of the group and may even occur between male and female of a monogamous pair and between them and their offspring. The survival value of such grouping is shown in many ways: (1) greater defensive strength in numbers; (2) more eyes in more directions to detect predators; (3) heat conservation in severe weather; (4) ease of finding food to be shared by the group; (5) proximity of sexes insuring greater fertility; and finally, (6) group breeding may result in lessened mortality of the young.

The fact that societies of vertebrates often are organized so that the individuals exhibit a certain order of precedence is probably not familiar to many except in human institutions where it may frequently be seen, as for example in a university community, an industrial organization, or an army. While students of the social insects have pointed out that this method of organization is much inferior to that found among the termites and Hymenoptera, it is recognized to be superior to no organization at all and appears to be basic, at least for vertebrates. Human society has gone a great distance in substituting intelligence for force in inter-individual relations but only a glance at a daily newspaper should be sufficient to show that man is still upon the lower level in dealing with international relations. The present study of canaries is not meant directly to solve our human problems but it does form one small chapter in the field of general sociology of which the sociologies of men and canaries form parts.

In studying a flock of domestic fowl, Schjelderup-Ebbe (1922a) found that the individuals usually arranged themselves in a definite linear order of dominance as determined by pecking. This he called the 'peck order.'

In such an order A pecked B, C, D, E, and F. B pecked C, D, E, and F, etc., down to F who pecked no bird. This order of position was established upon the first meeting between two individuals and remained constant until a revolt occurred after which a new constant order persisted providing that the revolting bird was winner of the fight. When strange birds were introduced into a pen with resident birds, the latter usually took the dominant position. While this last phenomenon is not strictly comparable to 'territory' as used below, it is probably basically similar.

The social organization was frequently complicated by a triangle situation in which A pecked B, B pecked C, and C in turn pecked A. Since an order is based on a series of first combats and, once established, tends to remain constant, it is easily seen how such a triangle could become fixed. Schjelderup-Ebbe studied birds of more than fifty species, including the common canary, and in all of them this fixed hierarchy was supposed to have existed. It should be noted, however, that detailed description was given for the domestic fowl only.

Katz and Toll (1922) attempted to correlate the position of fowls in the social hierarchy with the ability to learn certain simple problems. While the chicken which was highest in the social hierarchy gave the best performance in most of the problems, the others failed to show any obvious correlation.

Masure and Allee (1934a) repeated Schjelderup-Ebbe's observations on fowls and extended them to include the pigeon. Their findings with the former supported remarkably well the findings of Schjelderup-Ebbe. The findings with the pigeons demonstrated a kind of social organization previously undescribed. Here it was " . . . the rule for inferiors to peck superiors and for the latter to retreat at times before the attack of an individual which is more usually subservient in its contact-pair relations with that particular bird." They found also an effect of spatial relations on dominance. For example one bird stood higher in the social order when near the food pan and the other when at the entrance to the roost. This effect of territory is of interest because, as will be seen, territory has a strong influence on the social reactions of the canary.

Later Masure and Allee (1934b) described the flock organization of the Shell Parakeet. This species proved to have a social organization of the type described for pigeons which is characterized as a 'peck-dominance' rather than a 'peck-right' as found in fowls. In breeding flocks the males were dominant over the females while in non-breeding ones the females were dominant. They found no significant correlation between the peck-dominance order and scores made in learning to run a simple maze. This species differed from the pigeon in that the peck-dominance, once established, tended to remain fairly constant.

Murchison (1935 a, b, c, d), studying fowls found a positive correlation between peck order and distance moved toward another bird in a runway. The former he called 'social reflex No. 1' and the latter 'social reflex No. 2.' He also found that these were correlated with the amount of treading which he called 'social reflex No. 3.' Like the other investigators with fowls he found roosters to be dominant over hens. Murchison, Pomerat, and Zarrow (1935) found no positive correlation between peck order and the size of the bird or the size of any of its organs.

Evans (1936) described a social hierarchy in the lizard *Anolis* particularly during the breeding season when sexual fighting was at its height. Winter mating and fighting were induced by injections of sheep pituitary or by antuitrin S. Normal males, castrate males, or castrate females fought and defended territory while normal females did not. A female with atrophied ovaries in January, when injected with testis material, fought males but an uninjected female failed to fight. Evans (1938) also made a field study of the territorial behavior of *Anolis*.

Uhrich (1938) investigating the social hierarchy of white mice found fighting to be very common among the males but rare among the females. The commonest type of social hierarchy in mice was exclusive dominance by one male with no fighting or resistance on the part of any of the subordinates. Little or no correlation was found between the fighting order and such factors as weight, age, and copulation order. Castration diminished the fighting of males. A male was more likely to win a fight in his home cage than in a strange one.

Blatz, Millichamp, and Charles (1937) made an extensive study of the social relations of the Dionne quintuplets, when they were between the ages of two and three years. The social ranking was determined by the number of pushing contacts and other criteria noted in a daily observation period of ten minutes. The number of social contacts was not correlated with the mental rank since the total contacts ranking was A, C, Y, M, and E, while the mental ranking was Y, A, C, E, and M.

A recent contribution to the study of social hierarchy in birds made by Noble, Wurm, and Schmidt (1938) was primarily a study of Black-crowned Night Herons but incidentally involved some interesting experiments with pigeons. Like Schjelderup-Ebbe (1935) and Masure and Allee (1934a), they showed that birds fight harder in certain space relationships, thus complicating the results of the social hierarchy study. It was an interesting observation that males, though usually dominant over females, assumed a subserviant attitude in order to 'attract' the females into their territories.

The main problem of the present study was to discover the type of social organization existing among canaries and to discover what factors were correlated with social dominance. No clear analysis of all the factors in-

volved in determining dominance is reported in the literature for any species. Age has been found to be correlated with it in fowls. Sex was found to be a factor with some species in which the male is dominant and in others the female. No correlation has been shown between weight and dominance in birds. Observations connected with this problem extended from 1934 to July 1938, and are being continued. The specific experiment reported here was made after many preliminary observations which pointed the way for planning it and allow comparisons which greatly strengthen the conclusions. Space forbids reporting more at this time.

MATERIALS AND METHODS

The present study was based on five male canaries (*Serinus canarius*), numbered 39, 55, 58, 97, and 98, and five female canaries, numbered 14, 15, 17, 18, and 19. All of these birds, which were raised by the author, were from a somewhat inbred strain. The males were raised by the same pair of birds and were related on one side to the females. With the exception of male 98, which had a small dark cap, all birds were a pure yellow color. In order to insure quick and certain identification by the observer, the birds were given distinctive markings on the feathers with aniline dyes.

The flight cage containing the birds was forty inches long, twenty-four inches wide, and thirty-six inches high. There were four perches extending the width of the cage, two low near the center and two high near the ends of the cage. Small cages eight inches in each dimension were attached to the large cage. They opened to the flight cage through a door which was just large enough for a bird to pass through easily. A nest, seed cup, and water cup were provided for each small cage. Bathing dishes, hard-boiled egg, lettuce, gravel, cuttle-bone, and seed were placed on the floor of the flight cage. The males were observed in this cage for one day in order to get some indication of the peck order without the influence of the females. Then each was enclosed in one of the small eight-inch cages and the door to the flight cage blocked. To each one was then added at random one of the five females. For a week, except during the period of observation when they were allowed to go freely in and out of the flight cage, the same birds were kept in these same small cages. The week was sufficient time for them to become paired with the mates, which they kept throughout the entire experiment. Seed and water were kept constantly before the birds but fresh egg and lettuce were added daily just before observations were made in order to get a maximum of fighting in a short time.

All fighting behavior was recorded but for the purposes of this description only the decision fights were used. By decision fights is meant fights terminated obviously by the retreat of one of the participants. The term 'peck' as used here refers to a decision fight or to any advance toward an-

other bird which retreats in obvious response to the attack. In other words a 'peck' as used in this paper means any pair-contact reaction in which there is a definite outcome. Other notations made included feeding of mates, feeding of young, egg laying, nest construction, copulation, posturing, defense of territory, and any other unusual behavior or environmental incidents. During observation the author stood or sat not more than six feet from the birds which were apparently not disturbed by this factor. Daily observations were made when possible. It was impracticable to observe for the same length of time each day since on some days, during the moulting period particularly, very few pecks were dealt during the twenty to thirty minutes after the time of feeding which constituted the usual period of observation.

Although observations on the social organization of flocks of canaries extended over more than three and one-half years and are being continued, the experiment here reported began in June 1936 and ended in March 1937. During the winter the temperature, which usually remained between 68° and 74° Fahrenheit, was controlled by a thermostat and steam heat. Natural daylight was used and electric lights were never turned on at night. Some light from a street lamp shone in the window but the room was always dark enough at night to inhibit activity of the birds.

OBSERVATIONS

Type of Social Order.—Table 1 presents the distribution of the total pecks dealt and received during the entire experiment. Consideration of these data reveals that each bird dominated each other bird at least three times during the ten months. This type of social relationship indicates either a lack of complete dominance at any one time or a highly changeable system, or both. Later analysis will show that both factors are operating.

Birds numbered 14 to 19 are females while those numbered 39 to 98 are males. It is seen at a glance that males do more fighting than do females; two striking exceptions occur in the female combinations 14–19, and 15–18. In these cases most of the pecking was confined to a very few days during which one bird drove the other about the cage almost constantly. In the first case, 14 pecked 19 two hundred and forty-seven times in two intervals of five days in August and three days in October. In the second case, 15 pecked 18 two hundred and five times in an interval of eight days in September. In each case the despot, after the interval of driving, laid a set of eggs within two to ten days. This suggests an inherent mechanism for removing other females from the vicinity of the nesting site. It is also apparent that males usually dominate females but there are two interesting exceptions to this in the combinations of 15–55 and 19–97. In each of these cases the male dominated is the mate of the female involved. It will be pointed out

later that during the height of the breeding activity it is the rule for the female to dominate the mate.

TABLE 1

Total Pecks for Each Combination of Birds for Ten Months[1]

B pecks A	Bird Number		A pecks B	B pecks A	Bird Number		A pecks B
	A	B			A	B	
66	14	15	47	51	18	19	18
65	14	17	37	85	18	39	3
80	14	18	96	44	18	55	14
98	14	19	376	45	18	58	3
96	14	39	11	61	18	97	14
79	14	55	37	99	18	98	45
78	14	58	60	...	...	...	...
78	14	97	28	66	19	39	7
110	14	98	45	57	19	55	12
...	...	...	...	79	19	58	6
32	15	17	36	49	19	97	55
101	15	18	342	81	19	98	8
61	15	19	70	...	...	...	...
75	15	39	13	227	39	55	89
27	15	55	198	169	39	58	157
111	15	58	39	344	39	97	125
86	15	97	19	712	39	98	356
86	15	98	16	...	...	...	...
...	...	...	...	44	55	58	501
10	17	18	33	396	55	97	64
59	17	19	48	394	55	98	185
68	17	39	57	...	...	...	...
41	17	55	25	273	58	97	344
44	17	58	8	620	58	98	172
68	17	97	18	...	...	...	...
154	17	98	4	175	97	98	1,008

[1] To read table use for example the first line: 14 pecks 15 forty-seven times while 15 pecks 14 sixty-six times.

Effect of Sex on Position in the Social Order.—Table 2 reanalyzes information found in Table 1 on the basis of sex. It is seen that the least dominant male pecks more than the most dominant female. The total male pecks are 8,222 as against 2,471 for the females. It is further seen that these birds peck others of the same sex more than they do others of the opposite sex. Females peck females 1,726 times while females peck males 745 times and males peck males 6,355 times while males peck females only 1,867 times.

TABLE 2

Distribution of Pecks According to Sex

Homosexual female pecks			Heterosexual female pecks					
14 pecks all females			556	and pecks all males			181	total 737
15 " " "			514	" " " "			285	" 799
19 " " "			269	" " " "			88	" 357
18 " " "			209	" " " "			79	" 288
17 " " "			178	" " " "			112	" 290
			1,726				745	2,471
Homosexual male pecks			Heterosexual male pecks					
97 pecks all males			2,021	and pecks all females			342	total 2,363
98 " " "			1,901	" " " "			530	" 2,431
55 " " "			977	" " " "			248	" 1,225
58 " " "			729	" " " "			357	" 1,086
39 " " "			727	" " " "			390	" 1,117
			6,355				1,867	8,222
								Grand total 10,693

In Table 3 the birds are ranked in order of dominance. Again, this arrangement shows clearly that males dominate females as a rule. The exceptions due to the female dominating her own mate are shown by the blanks in the lines following all of the males except 39.

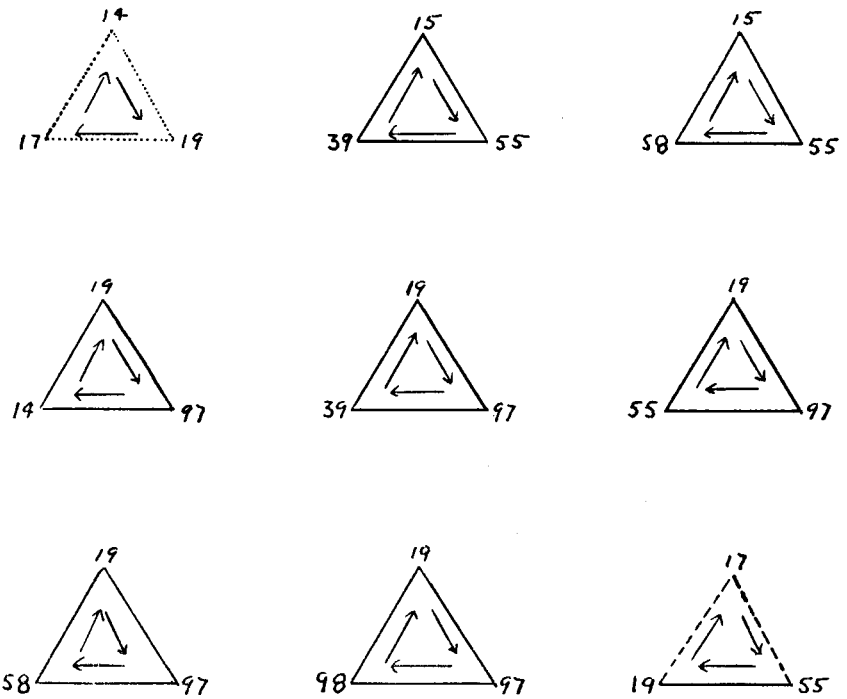
TABLE 3

Dominance during Largest Number of Months

97 dominates eight	14	18	15	17	..	39	55	58	98	..	..
98 dominates seven	14	..	15	17	19	39	55	58	..	..	(ties 18)
55 dominates five	14	18	..	..	19	39	..	58	..	..	..
58 dominates five	..	18	15	17	19	39	..	..	..	..	..
39 dominates five	14	18	15	17	19	..	..	..	..	..	(ties 14)
19 dominates four	..	18	15	17	..	..	..	..	..	97	..
17 dominates four	14	18	15	..	..	..	55	..	..	..	..
15 dominates three	14	18	..	..	..	..	55	..	..	..	..
18 dominates one	14	..	..	..	..	..	..	..	..	..	(ties 98)
14 dominates one	..	..	..	..	19	..	..	..	..	..	(ties 58)

The domination of the males by their mates creates many of the triangle situations among canaries such as have been already described for fowl. These triangles may exist among birds of the same sex as seen by the triangle of females indicated by the dotted lines in Text-figure 1 which is made from data presented in Table 3. One triangle is produced by a female dominating a male which is not its mate, as indicated by broken lines, but

the other seven are produced by females dominating their mates. Attention is called to the fact that 15 and 55 are mates as are 19 and 97. Triangles are always produced when a bird dominates another which in general relations stands higher in the peck order. In the first triangle, for example, 14 dominates 19, 19 dominates 17, and 17, in turn, dominates 14, while from the general reactions the expected order would be: 19 dominates 17 and 14, 17 dominates 14, and 14 dominates none.



TEXT-FIG. 1.—Triangles formed by ranking in order of dominance.

Effect of the Breeding Activity.—When no breeding is going on, so little pecking takes place in the flock that it is not profitable to make observations except for the few minutes after fresh food is given. This is one of the reasons that the birds were not watched for a uniform period of time. It is also pertinent to note that the three highest-ranking males in the flock represent the only pairs to raise any young to maturity. Male 39 and its mate are seen in Table 4 to have raised one young bird to about one-half the age necessary to leave the nest before it died. The pair 58 and 14 had only two sets of eggs, hatched young once, and did not feed these. It is impossible to determine by the information at hand whether these nesting

failures were due to the males, the females, or both. The following observations, however, seem to be significant. An indication that circumstances coincident with breeding affect the order of dominance is brought out by the contacts of 58 and 98. Due to the close proximity of 55's territory, cage

TABLE 4

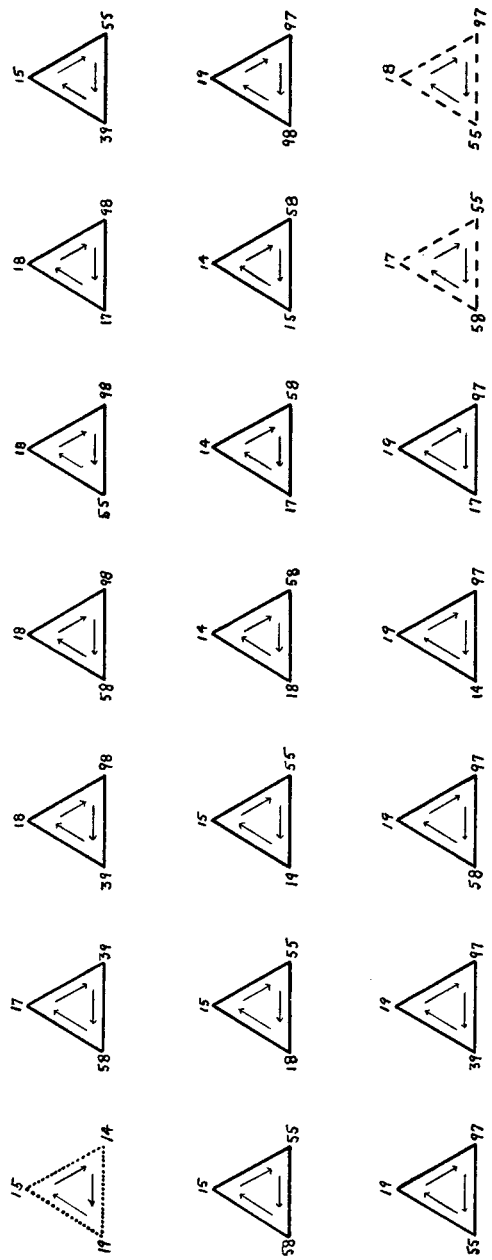
Nesting Activities

Male	Mate	Number of young raised	Sets of eggs laid
98	18	9	5
55	15	6	6
97	19	3	8
39	17	½	7
58	14	0	2

4, to 58's territory, cage 5, and the strong dominance of 55 over 58, the latter and its mate were unable to hold cage 5. They were usually found invading the nests of other birds. As is seen from the detailed account of territory given below, 98's cage was the one most frequently invaded. Due to this tendency to invade, most of the contacts between 98 and 58 were fought in or near 98's territory and were thus won by 98 since birds fight harder in their own territories. In order to see whether 58 could hold a territory, in January another cage (No. 6) was added to the experiment. It was placed as far from 55's territory as possible and attached just below 98's territory, cage 1. Soon 58 became able to hold cage 6 and was dominant to 98 from then on. The shift is shown in Text-figure 3. This may mean that 58 is fundamentally the superior one of the two but due to the peculiar circumstances involved, 58 appeared inferior to 98 until conditions were revised. At or near the close of the experiment in March, Text-figure 3 shows that 58 became dominant to all but 97, in neutral territory. Shortly after the close of the experiment, 58's mate laid in cage 6 and 58 defended the nest from all for the first time.

The data given in Table 4 do not necessarily imply whether (1) high reproductive activity raises the bird in the peck order, (2) the higher birds in the peck order have a better chance for reproduction and therefore reproduce more, or (3) both functions are controlled by another factor such as the pituitary gland.

Breeding activity alters the pecking order since it increases the dominance of the females over the mates. In an attempt to analyze and illustrate the importance of this factor a detailed study is presented of the data collected during November as one of the months of greatest breeding activity. Table 5 shows the ranking of dominance for that month determined by the number of birds of the same sex dominated over the largest number of days of



TEXT-FIG. 2.—Triangles formed in rank of dominance for November. ..... homosexual triangles; —— heterosexual triangles caused by the female dominating mate; - - - heterosexual triangles caused by female dominating non-mate male.

TABLE 5

Rank of Dominance based on Despotism for Month of November

	Homo.	Het.										
Males	97	4	3	15	..	14	..	17	58	39	55	98	..
	98	3	3	15	19	..	..	17	58	39	55	..	..
	55	2	2	..	19	..	18	..	58	39	..	..	..
	39	1	4	15	19	14	18	..	58	..	..	..	..
	58	0	4	15	19	..	18	17	..	..	..	..	..
Females	17	4	2	15	19	14	18	..	..	39	55	..	..
	18	3	2	15	19	14	..	..	..	..	..	98	97
	14	1	3	..	19	..	..	..	58	..	55	98	..
	19	1	1	15	..	..	..	..	..	..	..	..	97
	15	1	1	..	..	15	..	..	..	..	55	..	..

the month. As might be expected from the above observations all five females dominated their mates during November and this dominance extended in some cases to males which were not their mates. This increased domination of the mate by the females naturally led to a great increase of triangle situations for November. These are shown in Text-figure 2. During this month there were eighteen heterosexual triangles caused by females dominating their mates, eight heterosexual triangles caused by females dominating males which were not their mates, and one homosexual triangle. It is significant that there was no increase in the number of homosexual triangles.

With increased breeding activity dominance increased in many instances. Attention is called to Text-figure 3 for reference to all cases mentioned in this paragraph. Before the experiment began, and before the five regular females of the experiment were introduced, another female had been present with the five males. 39 paired with this female and was the dominant bird in the flock keeping all the other males at a distance. The dominance lasted for a few days after this female was removed and the females of the experiment were introduced. During this time 39 and this female called to each other almost continuously. 39 then went down in the social ranking and 97 became dominant and held its dominance over all through the rest of the experiment except that from August to October, 58 dominated 97. As is seen in Table 4, 97 is the male whose mate laid the greatest number of sets of eggs.

Examination of Text-figure 4 reveals the changes from day to day, some of which appear to be associated with breeding activity. On November 4, 39's young hatched and on November 5, 39 dominated three males and equaled the fourth. On November 16, 39 and its mate were building a new nest when 39 became dominant over 55 and 97 and raised its ratio of pecks

given to 58 and 98. On November 2, when 55's mate laid, 55 became dominant to all other males and on November 15 and 16, when the young hatched, 55 became dominant to 39 and 98. 97 became dominant to all males and overcame 58, which it had never dominated as 97 and its mate started a new nest on November 7 and 8. When its mate laid on November 20, 97 became very despotic and this caused it to show a high ratio of pecks over the other males. On November 27, as 98's mate was about to lay, 98 revolted against 97 and raised its ratio of dominance over the other males.

NATURE OF DOMINANCE IN CANARIES

Due to the fact that the nature of the dominance existing in flocks of canaries is a disputed question, it deserves careful description. The question at hand is whether the social order is of the rigid 'peck-right' type or the 'peck-dominance' type. The former was described for fowl by Schjelderup-Ebbe (1922) and confirmed by Masure and Allee as a type in which one individual invariably, or almost invariably, had precedence over the other. The latter type, described by Masure and Allee (1934a) for pigeons, has been referred to as a 'win-or-lose' relationship where first one bird retreats and then the other, the one retreating the fewest times being said to show peck-dominance. Schjelderup-Ebbe recognizes only the first type and lists the canary as one of the birds manifesting it. A detailed description of the contacts of the same five male canaries is given below. Since the females showed essentially the same thing and since their contacts are much less frequent, they are not described in this section. The orders of dominance, from month to month, are summarized in Table 6 where the number of

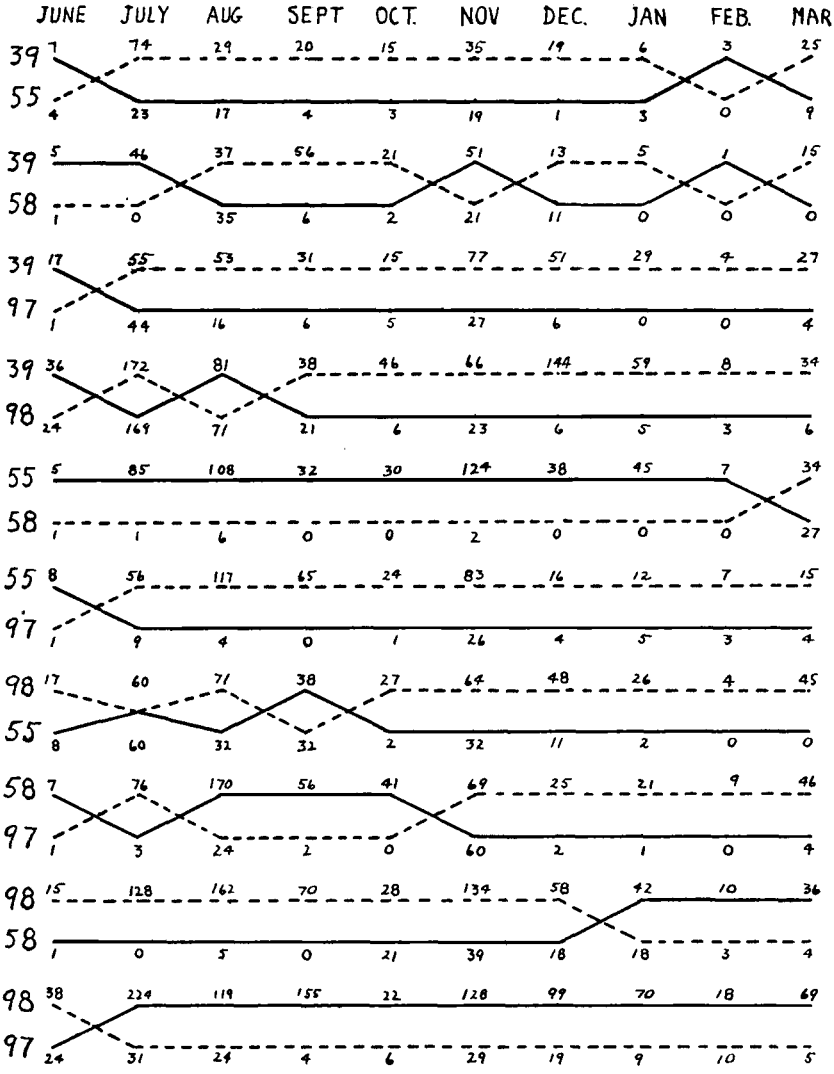
TABLE 6

Ranking of Males on Basis of Number of Males Dominated

June		July		Aug.		Sept.		Oct.		Nov.		Dec.		Jan.		Feb.		Mar.	
Bird	Dom.	Bird	Dom.	Bird	Dom.	Bird	Dom.	Bird	Dom.	Bird	Dom.	Bird	Dom.	Bird	Dom.	Bird	Dom.	Bird	Dom.
39	4	97	4	97	3	97	3	97	3	97	4	97	4	97	4	97	4	97	4
98	3	98	2½	98	2	55	3	98	3	98	3	98	3	98	2	98	2	57	3
55	2	55	2½	55	2	98	2	55	2	55	2	55	2	55	2	39	2	98	2
58	1	39	1	58	2	58	2	58	2	39	1	58	2	58	2	55	1	55	1
97	0	58	0	39	1	39	0	39	0	58	0	39	0	39	0	58	1	39	0

males dominated is listed after the bird dominating. In the case of a tie each of the two birds involved is given one-half. The order of dominance, as a whole, is far from stable but certain individuals tend to remain fixed after the initial period of adjustment. Text-figure 3 gives in addition the birds which are dominated and the scores for each combination for each

month. It reveals for periods of one month, that nineteen of the one hundred pair-combinations (five birds for ten months) have pecks in only one



TEXT-FIG. 3.—Numbers represent pecks for the male at the beginning of the line.

direction. There are all variations from this complete dominance to combinations in which the same number of retreats occurs for each member; sixty to sixty in one case. From Text-figure 3 we are forced to conclude that

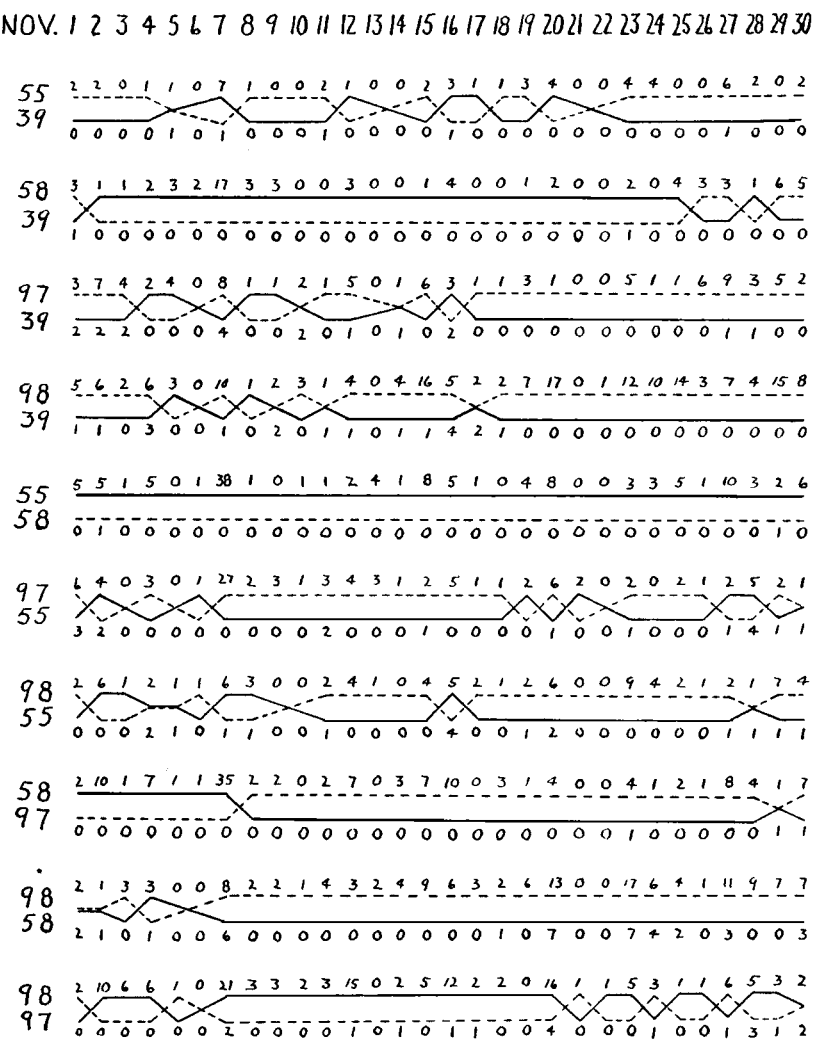
one of three conditions exists: (1) that the nineteen cases represent the 'peck-right' condition and that the other eighty-one represent periods of revolt; (2) that a state of win-or-lose exists between all combinations and that in the nineteen cases the lower bird is not favored sufficiently by circumstances to win any contacts; or (3) that both sorts of peck orders exist at the same time. The last view seems better to fit the facts especially in view of known circumstances which affect the outcome of pair contacts. One of these, the territory in which the contact takes place, is discussed below.

In order to understand better what is taking place from day to day, a daily analysis has been made of contacts during the month of November. Text-figure 4 presents the daily distribution of observed pecks. One interesting combination is 55–58 in which 58 was not dominant a single day of the thirty. On only two days of the thirty did 58 dominate in an observed pair contact and this was seen but once for each day; there were no non-decision fights. From November 3 to 29, the results of this one combination appear to conform to the findings of Schjelderup-Ebbe. The two pecks in the reversed direction are, however, not of the nature of a revolt since there was no non-decision fighting for this combination during November. The case 58–97 presents a reversal of dominance but without an observed struggle. In all there are forty-one complete exceptions to a fixed order of dominance to say nothing of fourteen days in which observed pecks were evenly divided.

A still more detailed analysis was made of the pair contacts of the males for November 7. These contacts are summarized in Text-figure 5, where each dot along either the broken or the unbroken line represents a 'peck' for the bird indicated at the beginning of the line. This figure illustrates that reversals often last no longer than for a single 'peck.' Only four of the ten combinations demonstrate complete dominance for the whole day. The longer lines of dots indicate birds with more contacts and the three longest represent the three birds forming a triangle in which 97 pecks 55, 55 pecks 58, and 58 pecks 97. The facts, that there was an unusually large number of pecks on this day and a complete reversal, placing 97 over 58 before observations were made the following day, may be related. This reversal permanently broke up the only male triangle of long standing and supports Murchison's view that triangles tend to give place to linear dominance if given sufficient time. It is worthy of note that these males had been together for one hundred and thirty-three days before November 7, and their social rank was supposedly on a steady basis. This shift in dominance is normal and in most cases, as can be seen in Text-figure 4, occurs much more frequently.

Effect of Territory.—Eighteen (33 per cent) of the fifty-five complete

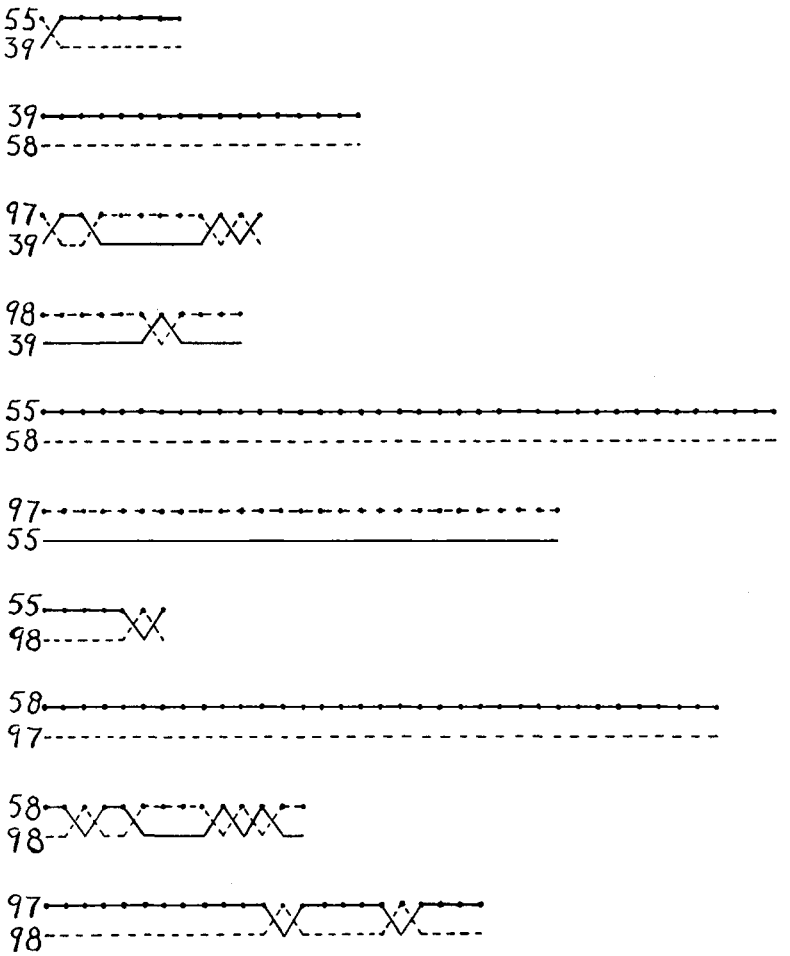
exceptions to the fixed order of dominance and cases of even distribution referred to in Text-figure 4 can be traced definitely to the effect of territory.



TEXT-FIG. 4.—Male contacts for November.

For example, all but one of the deciding contacts which caused 39 to win over 55 for five days, were fought in or near the entrance to the nesting cage of 39. In other words, the circumstance which caused 39 to fight harder in these cases was the proximity of its nest. The areas of the de-

fended territories radiated from the small cages, including the nests, to different distances depending on various factors, such as the dominance ranking of the defender and that of the invading bird. Even for the same combination of birds the area defended differed from day to day and de-



TEXT-FIG. 5.—Male contacts for November 7.

pended, among other known factors, on the time in the egg-laying cycle. At times 39 defended not only its nesting cage from 98 but also the two higher perches. Late in the evening, it was noted on several occasions, that 39 could still hold the nesting cage but not the two perches. This may have been due to a tendency of the weaker bird to become fatigued. On

rare occasions all tendency to defend territory, even of the nesting cage, was lost.

For the convenience of analysis only the pecks won or lost in the nesting cages are included in what is called 'territory' in Table 7. If all contacts in the territory limits between 'resident' and 'intruder' for the month of November are added there are 168 won by 'residents' and twenty-seven won by 'intruders.' Of these twenty-seven, all but two involved the pair 14 and 58 whose territory was not localized to their own cage. They not only defended cage 5 poorly but 'attempted' to defend cages used by other birds. The important influence exerted by territory is shown by the total figures but it becomes still more striking if we rule out the pair 14 and 58. Then we have one hundred and one contacts won by 'owners' and only two lost, or about two per cent of exceptions to complete dominance in territory distributed among twenty-two different combinations of birds. Females drove away females more times than males drove away females and males

TABLE 7

Territory Defense for November

Female

Bird	Times bird defended territory	Times bird lost to invader	Times defended against males	Times defended against females
14	5	1	5	0
15	1	0	1	0
17	2	0	2	0
18	14	0	0	14
19	8	1	8	0
Total	30	2	16	14

Male

Bird	Times bird defended territory	Times bird lost to invader	Times defended against males	Times defended against females
39	39	2	36	3
55	9	0	9	0
58	7	17	7	0
97	32	6	31	1
98	51	0	47	4
Total	138	25	130	8

Total contacts in territory in November—195
Contacts won in territory in November —168
Contacts lost in territory in November — 27

drove away males more times than females drove away males. Though females drove away males slightly more often than they did females, the fact that most of the invasions were made by males made a decidedly greater percentage of the defenses homosexual.

At least one case of territory defense deserves special note.

November 14—Female 18 hatched two young in nest 1.

November 20—When young were six days old and 18 was off nest 1 more frequently 14 was seen to enter nest 1 and proceed with nest building on top of 18's young. Three times 18 was seen to drive 14 out of cage 1, which contained nest 1, and twice to drive her off perch 1, which was near.

November 22—Female 18 drove 14 from cage 1 once.

November 23—Female 18 drove 14 from cage 1 four times.

November 24—18 drove 14 from cage 1 twice.

November 25—18 drove 14 from cage 1 twice. 14 pecked 18 once on perch 1 and once on perch 3; fought back at 18 for the first time in a month.

November 27—18 drove 14 from cage 1 once and pecked her once on perch 4. 14 pecked 18 six times on perch 1, three times on the floor, and once on perch 3. 14 was now able to hold perch 1.

November 28—18 did not peck 14. 14 pecked 18 four times on perch 1 and once on perch 4.

November 29—18 pecked 14 twice on perch 1 and once on perch 4. 14 pecked 18 three times on perch 1 and once on the east wall. 18 was again partially able to hold perch 1.

November 30—18 pecked 14 six times on perch 1 and once on the floor. 14 pecked 18 once on perch 1 and once on perch 4. 14 was now beginning to build in its own nest in cage 5. 18's dominance on perch 1 was now almost completely restored.

December 1—18 pecked 14 on perch 1 once.

December 2—18 drove 14 from cage 1 once.

December 5—18 drove 14 from cage 1 twice.

December 7—18 laid its first egg in nest 1. No more contacts were observed between 18 and 14 until Christmas day, when 18's young were four days old; then 14 started building on top of 18's young again and the same kind of conflict as the above started all over.

It is observed in this case that female 18 did all of the defense of cage 1 from the intrusion of female 14. This may have been due to the polygamous behavior of 98 in regard to 14. Of these discussed here, 98 (mate of 18) is the only male which fed, mated, and carried cotton at all regularly to any other female than its own mate; 14 was the only other female which received this attention. Territory is usually defended by the male but due to 98's peculiar behavior, 18 was left to defend cage 1 against 14.

Relation of Rank to Number of Pecks Dealt

Schjelderup-Ebbe reports that chickens at the top of the peck order do less pecking than lower-ranking ones. Masure and Allee (1934 a and b) find the opposite to hold in their study of the same species and likewise with

pigeons and parakeets. Among canaries the ranking birds were also observed to have more contacts as shown by Table 8 where 97 and 98, the two highest-ranking birds based on either method of ranking, dealt far more pecks than lower-ranking birds. This difference between the findings of Schjelderup-Ebbe and those of our laboratory may be due to the fact that in a larger pen his lower-ranking chickens were better able to avoid contacts with the higher-ranking ones.

TABLE 8

Comparison of Rankings According to Different Criteria

Ranking according to number of birds dominated during largest number of months	Ranking by number of birds dominated as shown by one dealing larger number of pecks to other over total time	Ranking according to pecks dealt (not number of birds dominated)	
		Total	Homosexual
97	98	98 (2431)	97 (2021)
98	97	97 (2363)	98 (1901)
55	58	55 (1225)	55 (977)
58	55	39 (1117)	58 (729)
39	39	58 (1076)	39 (727)
19	15	14 (737)	14 (556)
17	19	15 (699)	15 (514)
15	17	19 (357)	19 (269)
18	14	17 (290)	18 (209)
14	18	18 (288)	17 (178)

Effect of Age on Dominance.—In December and January several young were produced and they were left with the adult birds until the cage became too crowded. While with the adults, while they are being fed by their parents and for a short period afterward, pecking observations were made on the young also. Comparison of the number of pecks dealt by young to adults and by adults to young gives information as to the effect of age on dominance in the peck order. Observations were made on nine young males and five young females. Age made very little, if any, difference in dominance either in males or in females. Although the observed differences are not large, males tended to dominate females no matter what the age. Male dominance over females must therefore appear very early since the oldest young were removed at fifty-one days of age. The first contacts were observed when the young were twenty-six days of age. Even at that age young pecked adults as frequently as adults pecked young.

Effect of Body Weight on Dominance.—Apparently no correlation exists between body weight and dominance as seen in Table 9. The lowest and highest ranking males are about equal in weight and are the lightest males in the flock. Similarly, the ranking female is the lightest and the heaviest

female is next to the lowest in dominance. Though males regularly dominate females they average slightly less in weight. This weight difference in favor of the females conforms to similar differences in averages of weights of about seventy-five canaries.

TABLE 9

Dominance and Body Weight

Sex	Ranking by dominance	Ranking by weight: Bird	Ranking by weight: Weight in grams	Average weights
	97	55	20.4	
	98	98	18.2	
Males	55	58	17.5	17.7
	58	97	16.4	
	39	39	16.0	
	19	18	19.4	
	17	15	19.2	
Females	15	14	19.1	18.4
	18	17	18.3	
	14	19	16.1	

Relation of Dominance to Behavior in a Simple Problem Box.—From June 27 to October 6, except for a few days in late August and early September, the five adult males and five adult females described were tested daily in a simple two-alley problem box. These birds had previously been trained to go down the alley with the red or green colored light by being released from the box after a correct performance. The construction of the box has been described previously by Allee and Masure (1936) and except for one change that description still holds. This change involves the insertion of a door at the entrance to each alley from the main runway. As soon as an error was made the door to the alley involved was closed for a few seconds and then opened to release the bird into the runway. It was then closed to prevent repetition of the error and thus only one error could be made at any one run. Table 10 shows no apparent correlation between dominance and behavior in the problem box either with smallest number of errors or shortest time spent in each run. These figures do not represent errors required to learn the problem since all of the birds were familiar with it at the beginning of the experiment. The superior performance of the males over the females is in accord with the results of Allee and Masure (1936) with Shell Parakeets.

Other Factors affecting Dominance.—The reversal making 98 dominant over 39 was gradual and lasted over a period of about three months. At an intermediate time during this reversal 39 was found to be able to win in approximately half of the contacts. During this time it was found that late in the day 98 won all of the contacts except those in the nesting territory of

39. This loss of dominance by 39 in the evening may have been due to a lower resistance to fatigue. Also when two birds were closely matched and one became incapacitated in flying by having the feathers wet from bathing the other often took advantage of it.

TABLE 10

Dominance and Problem Box Behavior

		Ranking by errors occurring in seventy-nine trials			Ranking by time in box	
Sex	Ranking by dominance	Bird	Errors	Per cent errors	Bird	Average time
	97	39	3	3.8	39	4.3
	98	98	3	3.8	98	4.4
Male	55	58	4	5.1	58	4.4
	58	97	5	6.5	55	4.5
	39	55	6	7.6	97	5.1
	19	17	6	7.6	19	5.6
	17	19	7	8.9	15	9.8
Female	15	15	7	8.9	17	11.9
	18	18	7	8.9	14	12.0
	14	14	10	12.6	18	15.2

An observation, which has no ready explanation, is the severe flogging occasionally given the mate by a male just previous to nesting. This may be immediately preceded or followed by the usual gentle pecking by which the females dominate their mates. The two types of contacts have no comparison in severity since in the former the male often held the female in its claws and dealt severe pecks at the head and eyes. Masure and Allee (1934b) describe regular dominance of the male over the female in parakeets during nesting. By pecking, the male parakeet drives the female to the nest. This does not explain the floggings in canaries since the male usually coaxed the mate to the nest by posturing to the nest, sitting on the edge, and uttering the sounds which accompany feeding. In parakeets the females dominate the males except during the breeding season.

DISCUSSION

Various explanations of the results may be offered which seem to differ from those described in the more fixed type of social hierarchy of the fowl. Cases in which a canary with a morsel of lettuce, too large to be eaten at one bite, ran away from inferiors were observed. Such cases were not counted.

Cases of pecks dealt by a maturing bird to a superior preliminary to the actual revolt have been observed in fowls. This possibility was ruled out

because young birds were not included in the experiment except in the one section on effect of age. They are not included in the figures which show the incomplete dominance characteristic of the species.

Subordinate fowls, at times, ate food from the bills of resting superiors and this might have been confused with a peck. If such occurred among the canaries it was not counted as a peck.

When a strange bird is introduced into a flock it may win the first few fights but, being outnumbered by resident birds, is weakened in fighting so that all come to dominate it in a short time. Such a condition could not have existed in this experiment since strange birds were never introduced after the experiment began.

Pecks dealt in play and sham battles have been suggested as an explanation but it was impossible for the author to distinguish a sham battle, if such existed in canaries, from a real battle. As for pecks dealt in play, the nearest approach was the gentle pecking of a male by its mate, in response to which the male postured away a short distance instead of fleeing in the usual manner.

So it appears that canaries follow the same type of social organization as described for pigeons and Shell Parakeets. The rule that one bird invariably dominates or is dominated by another must indeed be taken with a large grain of salt if applied to all birds.

It is possible, other things being constant, that any one of several factors such as body weight, intelligence, metabolic rate, age, fatigue, or amount of sex hormone present could be shown to be correlated with social dominance. But due to the fact that several factors are operating at once, and the improbability of keeping the other factors constant taken together with the small numbers which can be followed at any one time, it is difficult to find a very significant correlation of social dominance with any one of these factors. Except for sex and breeding activity, which are discussed at length above, the correlation between social dominance and any one factor in the physiology of the canary is probably slight. This view is supported by the frequent occurrence of triangle situations which must be due to coincidences as described in the introduction and could not possibly be due to the physiological vigor of all three birds at any one moment. These coincidents are perpetuated in the conditioned behavior of the birds. No single physiological factor could logically bring about a triangular situation such as 98 pecks 58, 58 pecks 97, and 97 pecks 98. For example, 98 is heavier than 58 and 58 is heavier than 97, therefore 97 could not be heavier than 98. However, the above triangle existed during August, September, and October, as can be seen in Text-figure 3, and the differences in the numbers of pecks are too large to be due to chance in sampling. This example is explained in such detail to emphasize the importance of coinci-

dences affecting the nervous system and perpetuated beyond the time when the fighting ability establishing it may have changed.

The correlation of dominance with sex and breeding activity suggests the possibility that social dominance is in some manner under the influence of a sex hormone. In 1936, following this suggestion, castrate and normal female canaries which were not in breeding condition were injected with estrone. No changes were observed in their social dominance or breeding activity. Working with the lizard, *Anolis*, Evans (1936) finds that the urge to fight is inhibited by hormones secreted by the ovary since normal females do not express dominance but castrated females do. He also has some evidence that injection of testis material into normal females stimulates fighting. Domm (1937) finds that injection of the gonadotropic substance, hebin, increases the fighting and produces precocious sexual behavior in baby chick males but not in females. Domm (1927) also finds that capons do not fight as vigorously as cocks. He states that the female fowl, while actively laying, has been shown to produce male hormone as well as female hormone. It is this male hormone which induces the characteristic comb growth in laying hens, since injection of female hormone is shown to have no such effect. Female canaries are frequently observed to sing as well as to fight much more while coming into the laying condition. One female canary while in this condition was frequently observed to tread other females and in their absence to tread males. Soon afterward it reacted as a normal female to the treading of a male, laid eggs, hatched, and reared young. This happened to this female each time before laying. It logically follows that singing, fighting, and masculine mating behavior may also be due to male hormone produced by the ovary of the female canary and by the testis of the male. Experiments to test this theory by injecting male hormones into female and male canaries are being planned.

The field study of 'territory' has attracted much attention of students of bird life for many years. It has been shown that birds fight much more violently in the vicinity of their nests. This area defended from intruders has come to be known as 'territory' in a rather technical sense. Howard (1920) has come to the conclusion that all fighting in birds is 'territory' defense. This extreme view was apparently a reaction from another held by Darwin, that fighting is primarily in reference to the mate. Craig (1921) takes a much broader view that "the animal fights in order to gain or to retain possession of that which is of value to him, such as food, mate, or nest." Though he recognizes the importance of territory, Tinbergen (1936) cites the case of the Snow Bunting in which a male, wandering into the territory of another, will not attack the resident male unless the former is accompanied by its mate. It is this fighting, whether it be in the vicinity of the nesting territory, food, bathing dish, or mate, which forms the basis

of social dominance. Cases were observed in the canaries where fights have obviously originated over each of these. The contacts originating in response to territory defense, however, far outnumber all the others. The expression of territory defense is of great importance in the study of the social hierarchy in the canary since a bird which is dominant to another in neutral territory normally becomes subordinate in the nesting territory of the other bird. This factor of territory alone would be sufficient to explain the occurrence of a 'peck-dominance' type of social hierarchy in the canary instead of the 'peck-right' type as described for fowl.

SUMMARY

1. A social hierarchy of the 'peck-dominance' type exists among canaries, rather than the 'peck-right' type as described for fowl.

2. Age, body weight, and problem-box behavior show no correlation with the position in the social hierarchy.

3. Birds ranking high in dominance deal more pecks than lower-ranking birds.

4. Males regularly dominate females except their own mates during time of breeding, when dominance is reversed for mated pairs.

5. Position in the social hierarchy fluctuates with breeding activity. Male hormone is suggested as controlling the mechanism.

6. Birds subordinate in neutral territory become dominant in their nesting territory. This factor alone would account for the 'peck-dominance' type of social organization.

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