AGONISTIC BEHAVIOR IN THE HOUSE FINCH
Part II: FACTORS IN AGGRESSIVENESS AND SOCIALITY

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In the first part of this paper (Thompson, 1960), the main features of the annual cycle of behavior of wild House Finches (*Carpodacus mexicanus*) were described. This part is concerned with dominance and related factors in sociality and with the possible relations of social organization to populations in the field.

Methods and materials were discussed in Part I (Thompson, 1960). In this part, numbers of tables and of figures continue the series of Part I.

SPATIAL AND SEASONAL ASPECTS OF AGGRESSIVENESS

The problem of the effect of space on the frequency of aggressive encounters was approached by varying the number of pairs of birds confined in a constant space. One, two, three, and four pairs of House Finches were placed in four equal-sized cages with dimensions of 4×8×8 feet. Each group was watched for one hour each day between 8 a.m. and 12 m. for four consecutive days, from February 4 through 7, 1959. The time of observation was rotated, so that each cage was observed at a different time on different days. This rotation was intended to minimize variations in the morning activity cycle. Figure 7 illustrates the results of this experiment. If the space available per bird is calculated by dividing the total space in the cage by the number of birds, it is apparent that fighting increases as space decreases. The increase of fighting with increased population density is not directly proportional to the space reduction, however, but it increases sharply where there is less than 60 cubic feet of space per bird.

Aggressive action occurs more frequently among caged birds than it does in wild birds. This may result from the reduction of space available per bird and from the increased frequency of contact between individuals. Between February 10 and March 19, 1959, records of aggressive encounters between wild House Finches were compared with records of such encounters between 11 birds confined in one cage for the same period. House Finches often congregated in an isolated elderberry tree on the study area, and because of the ease of observation the records of aggression among wild birds were taken from observations of birds in this tree.

The total number of encounters between wild individuals recorded during 8.25 hours of observation was 83, or 10.1 encounters per hour. For the caged birds the total number of encounters recorded during four hours of observation was 145, or 36.2 encounters per hour. The picture is greatly complicated by the varying numbers of wild birds present during any period of observation. If the maximum number present during five-minute intervals throughout the period of observation is recorded, it is possible to arrive at a fairly accurate figure for the mean number present throughout the time of observation. This calculated mean is 4.5 individuals. If we assume that the space available to these birds is equal to the volume of the portion of the tree used by the House Finches, roughly the upper half or 1188 cubic feet, the space available for each bird is roughly 264 cubic feet. Comparison of these numbers with figure 7 shows that they fall within the range of variation which might be expected if the curve were extrapolated. The curve should be thought of not as a single line but as a band which allows for some variation in the number of aggressive encounters which occur at any one concentration of individuals within a given space. There are still too many uncontrolled variables involved in the relationship between density and the amount of aggression to allow the construction of a precise curve to illustrate this relationship. Much more work is needed to clarify the issue. The evidence obtained from caged and wild House Finches does, however, suggest that the greater aggressiveness of caged birds is associated with the decreased amount of space available to them.

Annual variation in frequency of agonistic behavior of nine caged birds in 1954–55 and eight in 1957–58 is shown in figure 8. The tallies of aggressive encounters on which these figures are based were obtained in the course of observations originally intended merely for determining the dominance hierarchy. Because of this the observation sessions were not always of the same length. For the purpose of obtaining the range of variation in number of encounters recorded during any one four-week observation period it was necessary to adjust each observation session to a standard period of time. Since the greatest activity usually occurred near the beginning of the observation session at the time the birds were fed fresh vegetable material, it was decided that an adjustment of each session to a period of 20 minutes did less violence to the original data than expansion of some of the shorter sessions to one hour. Although the patterns of variation shown for the two years differ, the general trends are the same, with peaks in late fall, a marked depression in February, the suggestion of a second peak in early spring, and another depression in late May and early June. The longer record for 1958 suggests a third peak in late June, followed by a depression in July and August. The correspondence of these fluctuations in two different groups of birds in two separate years is considered significant. The most obvious cause for the seasonal fluctuations would be weather, but figures 9 and 10 suggest no correlation of agonistic behavior with either precipitation or temperature.

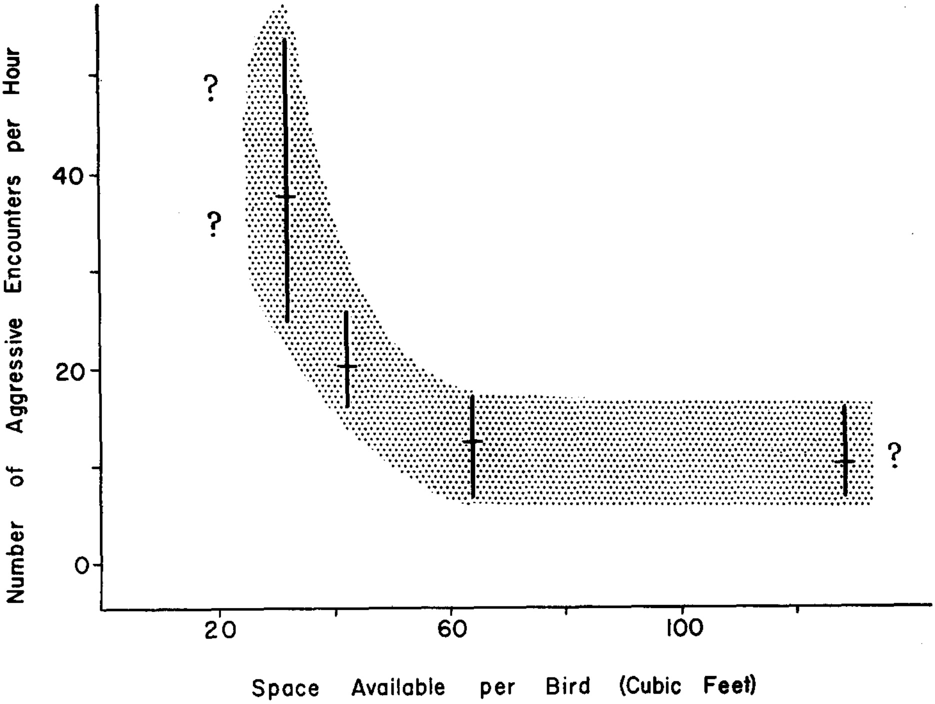

Fig. 7. Decrease of aggressive behavior of House Finches with decrease of population density within cages. Vertical lines indicate the range of total encounters per hour during four one-hour observation periods. Cross bars represent the mean number of encounters per hour.

There is another possible cause of the marked drop in the number of aggressive encounters recorded in certain intervals. At about the end of January and in early February, continuing on through March, there is an increased degree of restlessness, taking the form of aimless flying back and forth from perch to perch, corresponding to the "Zugunruhe" of migratory birds. Possibly some of the caged birds were winter residents in the Berkeley area, which would have moved to distant localities during the spring. Or it may be that this activity is merely an expression of a dispersal mechanism which tends to break up winter flocks and scatter the birds for breeding. The movement of wild birds at this time of year is documented by the increased numbers of unbanded birds which appear at feeding stations usually frequented by marked individuals. At

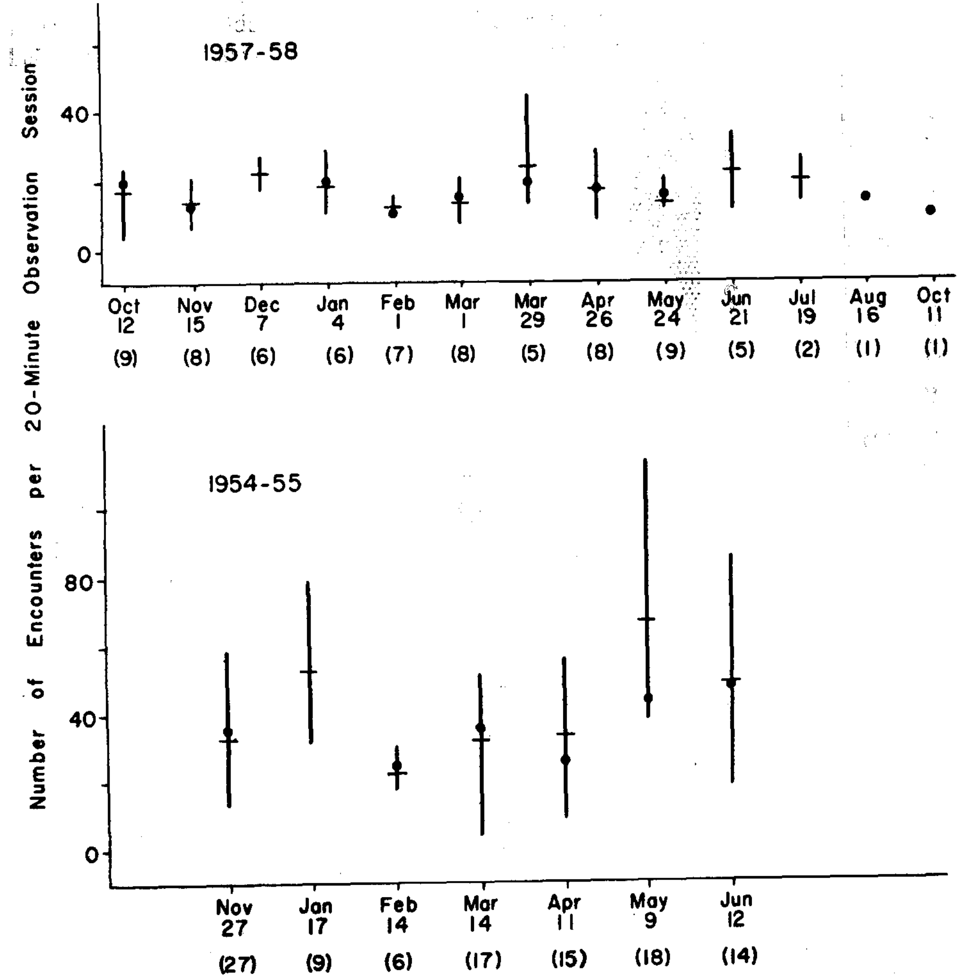

Fig. 8. Seasonal variation in the total aggressiveness of all caged birds, 1954–55, 1957–58. Vertical lines represent the range of total encounters per twenty-minute observation session. Cross bars represent the mean number of encounters per twenty minute session, and dots represent the mode. Dates represent the midpoint of four-week observation periods. Numbers in parentheses indicate the number of adjusted observation sessions (for explanation see text).

any rate, this extreme restlessness masks aggressive encounters between birds. The observer experiences great difficulty in recognizing such encounters amid the frantic flying about. The February dip may, therefore, be "unreal" in terms of the actual occurrence of aggressive encounters at this time.

The cause of the June depression is not apparent. It may also reflect a wandering tendency on the part of adults after the first brood has left the nest. This, also, was indicated in the virtually complete absence of House Finches from the study area, where they had been so abundant, during late May and early June.

Table 3[1]

Distribution of Wins Throughout the Test Groups in 1954–55 and 1957–58

Midpoint of observation period	Total wins	Number of individuals responsible for:					
		25 per cent		50 per cent		75 per cent	
		♂	♀	♂	♀	♂	♀
1954–55							
Nov. 27	989	1	1	1	2	3	3
Jan. 17	470	1	1	1	2	3	3
Feb. 14	300		1	1	1	3	3
Mar. 14	1133	1		2		2	2
						or 3	1[2]
Apr. 11	1023	1		2		2	
May 9	1981	1		1		2	
June 12	1733	1		1		2	
1957–58							
Oct. 12	457		1		2		3
Nov. 15	323		1		2		4
Dec. 7	202	1	1	1	2	1	3
Jan. 4	195		2		3	1	4
Feb. 1	148		1		2	1	3
Mar. 1	193	1		1	2	2	3
Mar. 29	197	1		1	1	2	3
Apr. 26	246	1		1	1	2	2
May 24	185	1		1		1	2
June 21	165	1		1		1	1
July 19	58	1		1		1	1
Aug. 16	40	1		1		1	1
Oct. 11	50		1	1	1	1	1

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[1] Tables 1 and 2 appeared in Part I of this paper.
[2] During this period a male and a female were tied for fourth place.

There is a marked difference in the number of aggressive encounters recorded in the two years. The peaks in 1955 are much higher than in 1958. There was one more bird in 1955 than in 1958; and, moreover, differences in individual aggressiveness would be expected apart from those induced by difference in group size. Another factor is difference in cage size. The effect of crowding on the incidence of agonistic behavior has already been mentioned. It is possible that some differences are also due to cage location. In 1955 the cage, although covered by a roof and exposed to direct sunlight only a short time each day, was in much brighter surroundings than the cages of 1957–58, which were located under oaks and were partly shaded throughout the day. Wild House Finches usually stay in the tops of trees and feed in open areas, avoiding the deep shade of dense woods. The cages of 1957–58 were therefore in a suboptimal habitat.

A bird is said to win an encounter if it causes its opponent to retreat. If all members of a group of eight caged individuals were equally aggressive, two, four, and six individuals would be responsible for 25, 50, and 75 per cent, respectively, of the total number of aggressive encounters recorded for a given period of time. It is possible to obtain some measure of how the test group conforms to or departs from this distribution. Table 3 shows the distribution of wins throughout the test groups in 1954–55 and 1957–58. During November and January of 1954–55 the figures agree closely with the expected distribution. The ratio 2:3:6 is well within any variation which might be expected on the basis of chance. The June distribution, on the other hand, is radically different. At this time one individual is responsible for 50 per cent of all wins, and two are responsible for 75 per cent of all wins. Likewise in 1957–58, the October-November distribution is not far from the expected ratio. The prominence of females in aggressiveness within a caged group is noteworthy in 1954–55. In the spring one male is responsible for 50 per cent of all wins, and the male and his mate for 75 per cent of the total, as in 1954–55. It is clear, then, that the increase in the total aggressiveness of the group

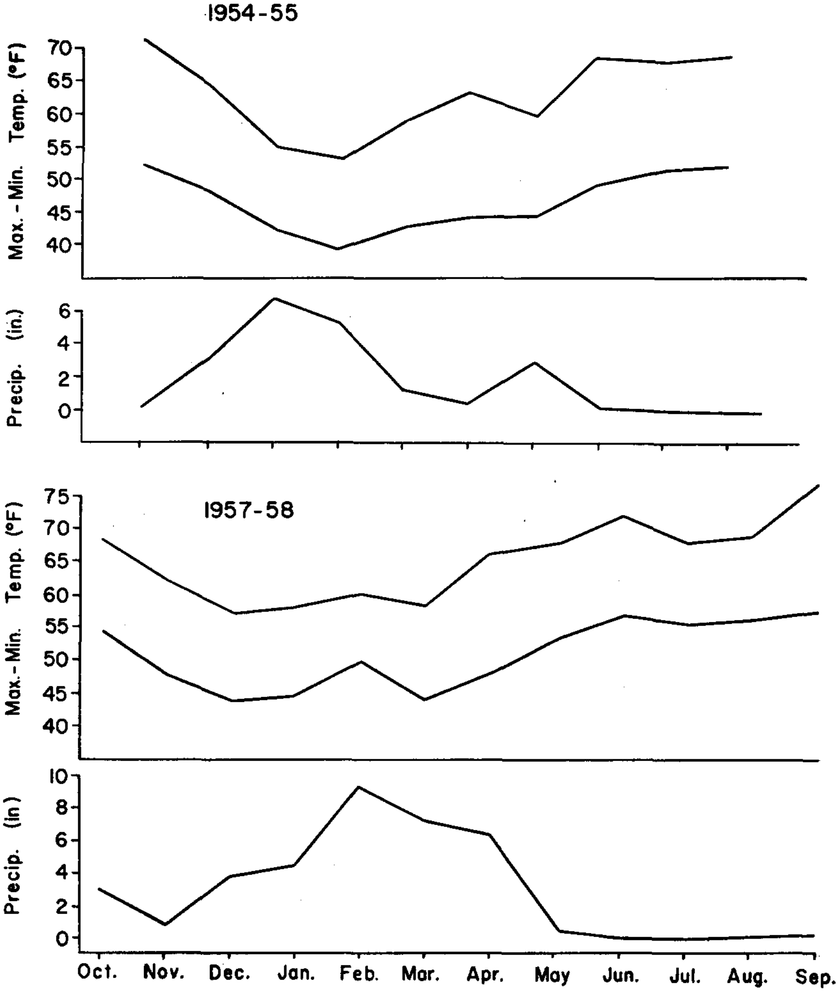

Fig. 9. Weather data for 1954–55 and 1957–58.

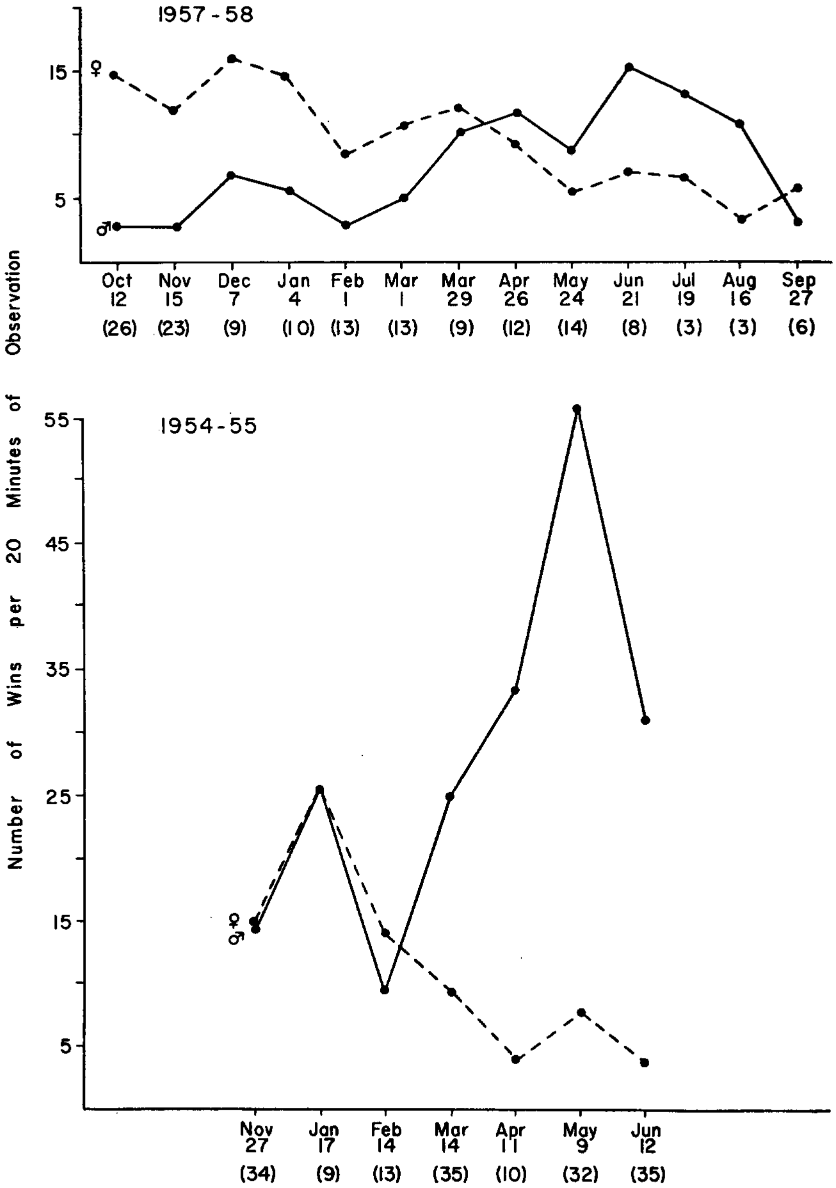

Fig. 10. Seasonal variation in the total aggressiveness of nine caged male and female House Finches in 1954–55 and eight caged males and females in 1957–58. Numbers in parentheses indicate the number of 20-minute observation sessions per four-week period.

during the breeding season is due primarily to an increase in the aggressiveness of a few individuals rather than of the group as a whole (see also fig. 13).

A breakdown of the data on total aggressiveness into male and female components indicates the varying roles of the two sexes throughout the year. In these data, shown in figure 10, the total time of observation is divided into 20-minute segments instead of adjusting each of the observation sessions to a 20-minute period. The number of wins per 20 minutes of observation is then calculated. Again the graph for 1955 is the more striking because of the great increase of male aggressiveness in spring. A corresponding increase of male belligerence and a simultaneous decrease in female hostile behavior was found in 1958, but to a much smaller degree than in 1955. This rise of male aggressiveness is undoubtedly related to the defense of mate and territory. A male becomes most aggressive when his mate is building a nest and beginning incubation. This may be observed in wild as well as in captive pairs. It is very noticeable in a cage, when the male whose mate is nesting begins to chase all the other birds in the cage, except his mate, as if defending a territory. Whereas previously he might supplant another male only if it was in his way on a perch, he now makes long detours to supplant subordinate males. This increase of male aggressiveness with sexual activity is illustrated in fig-

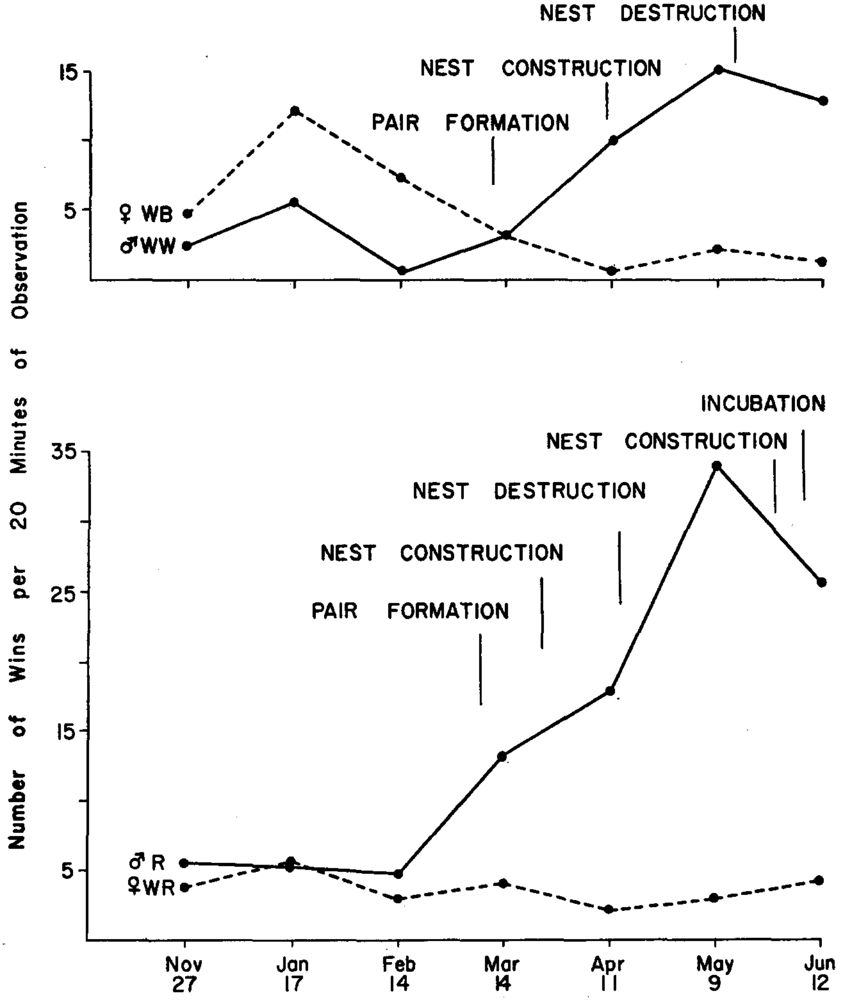

Fig. 11. Seasonal variation in the aggressiveness of two caged pairs of House Finches in 1954–55. The times of pair formation and other events in the annual cycle are indicated.

ures 11 and 12, in which the hostile activity of active pairs in 1954–55 and 1957–58 is diagrammed. In almost every case there is a marked increase in fighting from the time of pair formation. Another increase is noticeable (with the exception of male WP) at the time of nest construction and the beginning of incubation. These increases accord well with the increases in fighting observed in the wild. The apparent reason for the extreme increase in fighting behavior observed in male R, and to a lesser degree in the other males is that the entire cage becomes the territory of the male and female building a nest. The limits of the cage are well below the usual territorial limits, and hence the owners of the territory are continually being stimulated to chase away "intruders." In the wild state such territorial defense is mild, but when the intruders are unable to leave the area, the hostility increases markedly. The variable nature of this defense "drive" is shown by the highly variable degree to which a male chases his cage mates. Periods of resting and preening alternate with periods of feeding and violent supplanting attacks and chases. The male usually accompanies his mate wherever she goes, and

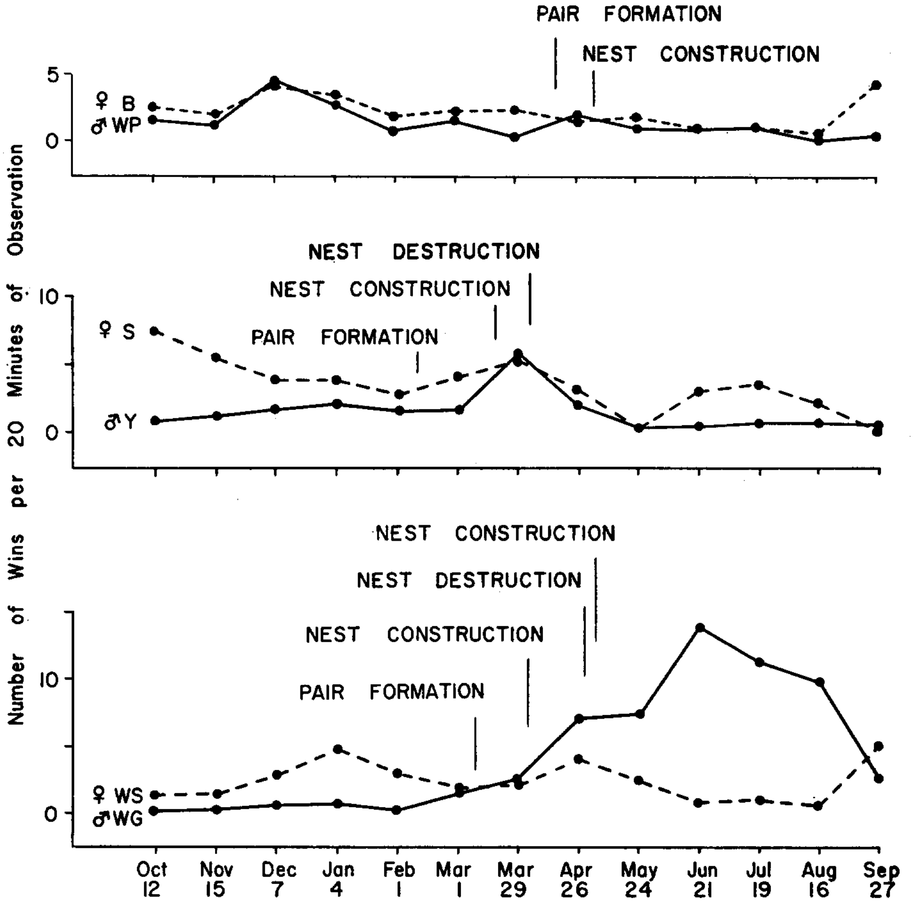

Fig. 12. Seasonal variation in the aggressiveness of three caged pairs of House Finches in 1957–58.

when she becomes active, his aggressive behavior increases. After a series of violent attacks, the male and his mate usually perch quietly side by side, preening, or just resting, for the most part ignoring the other birds in the cage.

Several caged pairs attempted to nest at the same time as another, more aggressive pair. These were never successful, but their efforts to take over the nest already being used, or to build near the same site, always increased the amount of fighting. Notice the succession of peaks of hostile behavior of individual males and females in 1957–58 (fig. 13). No two birds of the same sex reach their peak of aggressiveness at the same time. Figure 12 illustrates in a different way the same range of variation which is shown by the vertical lines in figure 7.

There is, nonetheless, much individual variation in male fighting, and it is not clear why some peaks occur where they do. The maximum in June of male WG, for example, is not correlated with any nesting activity, because his mate was not sexually active at the time; his hostile behavior rose above its level during nesting.

Figure 10 shows a decline in female group hostility at the same time that male group hostility is increasing. The decrease may be seen in the behavior of the individual females (fig. 13), as well as in the group as a whole. Despite this downward trend from the winter state, there is usually an increase of aggressiveness during nest construction and incubation. This, too, is in agreement with the behavior of wild birds, because much of the early territorial defense is initiated, if not taken over completely, by the female. Wild, incubating females have little occasion to show hostile behavior, isolated as they are, but captive females show extreme aggressive behavior when off the nest. The two females which incubated in captivity did not usually move from the nest even if other birds came up to the rim of it. In one instance a pair attempted to build a nest within four inches of the one occupied by female WR and were not often bothered by her. When the captive incubating females were off the nest to eat or drink, however, they were often belligerent toward other birds of either sex.

DEVELOPMENT OF AGGRESSIVE BEHAVIOR IN YOUNG BIRDS

Three House Finches reared by hand showed no signs of hostility toward each other until four weeks after hatching. Before this they had pecked at food particles on the feathers or beak of their companions, but the one pecked did not seem to recognize any hostile intent, and the pecking appeared to be primarily a matter of curiosity or feeding on the part of the bird which pecked. The first aggressive encounter seen was a vigorous peck by one of the males, P, at the female, O. Within a day or so, W, the other male, also began to peck at O, and within a week he pecked both O and P vigorously, chasing them from perch to perch. The pecks and supplanting attacks were accompanied by the same *chip* which is characteristic of adult quarrelling.

On June 8, ten days after the first aggressive encounter, female O began to peck both males. She was less aggressive than male W but pecked at either of her companions which perched near her. She was particularly hostile toward W.

On June 18 the young House Finches, seven weeks old, were released in the house in the company of an adult male canary. Male W performed a high intensity head-forward display, including the raising and extension of first both wings, then only one.

Wild adult House Finches often retreat from an approaching juvenile. Juveniles just out of the nest show a marked tendency to fly directly toward an object, landing on top of it instead of perching beside it. The hand-reared nestlings demonstrated this behavior and one would frequently knock another off a perch by flying directly at it and landing on top of it. When they first begin to fly, the young birds do not brake well

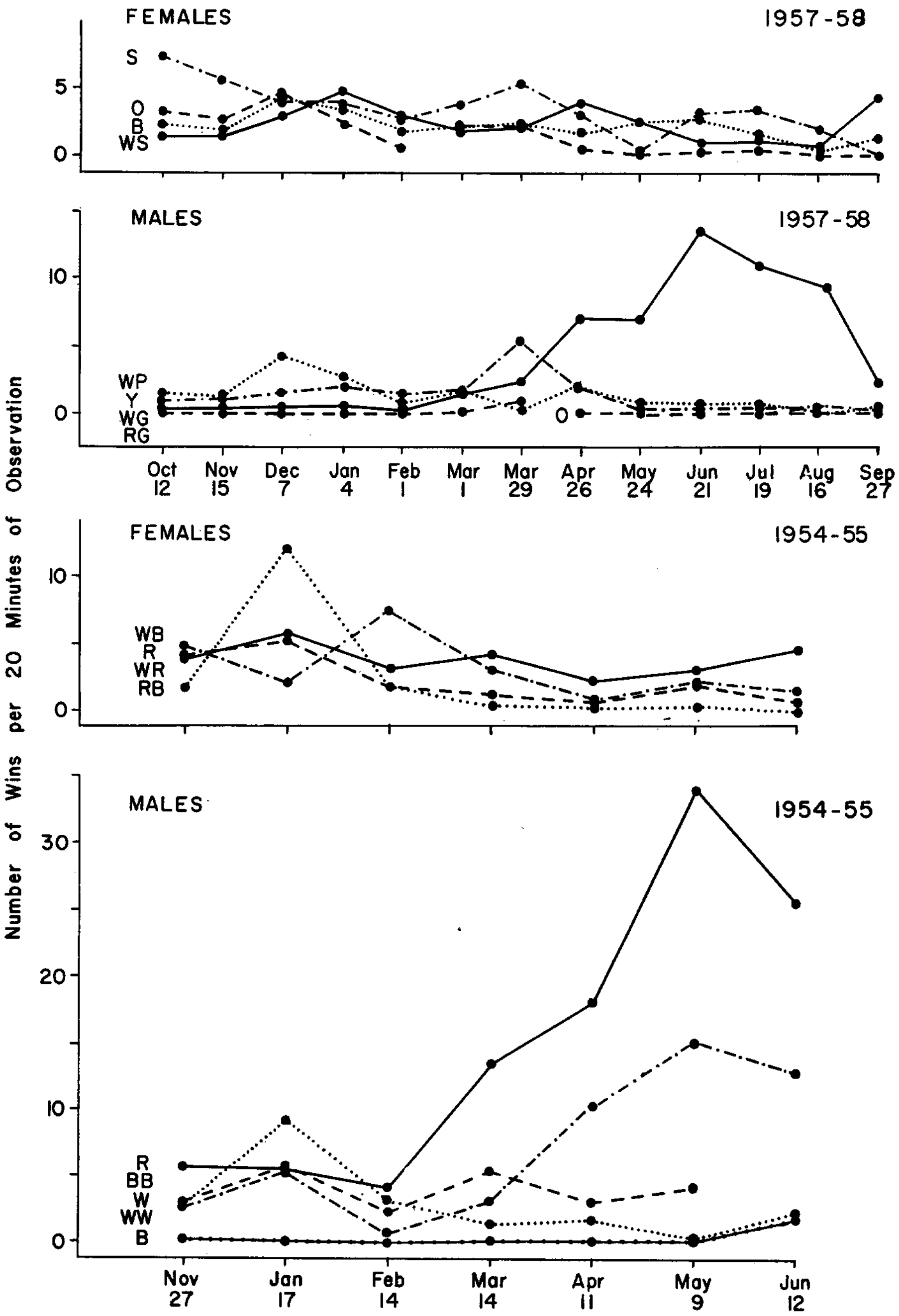

Fig. 13. Seasonal variation in the aggressiveness of individual caged male and female House Finches in 1954–55 and 1957–58.

when landing and tend to overshoot the perch. This forward momentum contributes to pushing the companion off the perch, since its hold is not very tight at this stage in development. Fledglings just out of the nest show this same tendency to fly directly toward the adults to beg for food. Usually the adult will hop to one side to avoid being hit. Since the juveniles have the same plumage pattern as the female, the adult male may mistake the oncoming bird for an adult female, and since, as will be mentioned later, males usually retreat from attacking females, he may avoid what appears to be a female attacker. The impression of attack may be heightened by the lack of fear which the juveniles display. On the other hand the behavior of the adult male may be only an attempt to dodge the approaching fledgling, learned from experience with birds just out of the nest.

Table 4

Developing Behavior Patterns in Three Juvenal House Finches

Days after hatching on which new behavior was recorded	Behavior
0	Hatched
9	Taken from nest; preening, gaping, begging responses developed
12	W sleeps with head under scapular tract, whose feathers are out of sheaths
13	W and O fly well, P not well; all flap and flutter wings vigorously from time to time
15	Wing fluttering just developed to accompany begging
16	W drinks water; all three peck at seed on floor of cage
17	Birds very restless at dusk, then settle on perches to sleep
18	Begin feeding themselves to some extent; still beg
20	Birds near full size; rectrices almost full length
21	Flight still erratic
29	P singing—monotone of rapidly repeated notes
32	First bathing from rim of water dish; P pecked O, causing her to retreat
39	W pecks P, P pecks O
41	O pecks P, P pecks W
43	O pecks W, W pecks P
51	W gives complete, high intensity head-forward display to canary
54	W singing loudly—adult song posture; song more rambling and disconnected than that of adult wild male

Table 4 lists developing behavior patterns in three juvenal House Finches.

SOCIAL HIERARCHY

There is a well defined social hierarchy, or peck order, in flocks of House Finches. It is particularly noticeable in small groups of caged individuals. The hierarchy is fairly stable, but changes do occur from time to time. In the social hierarchy, a bird is said to be "dominant" if it can be expected to win in hostile encounters with another "subordinate" individual. The dominance described here is of the peck-right type, but occasional reverses may occur under exceptional conditions. A bird is said to win an encounter if it causes its opponent to retreat. Such hostile encounters involve the various forms of aggressive behavior already described here and in Part I.

Peck order in caged groups.—In caged groups of House Finches in winter, females are generally dominant to males. Figure 14 shows the heterosexual aggressiveness of both sexes throughout the year by indicating the number of wins of either sex over the other for every 20 minutes of observation. A comparison of the two graphs in figure 14 reveals that the patterns of male and female dominance throughout the year are not identical in 1955 and 1958, but that the general, overall patterns are about the same.

During the breeding season the females as a group are no longer dominant to the males as a group, but each mated female remains dominant to her mate. This is unlike the conditions described by Hinde (1955–1956) for some other passerine species in which the female is dominant to her mate during the breeding season, but the male is dominant to the female in the winter. It is not likely that the birds are behaving sexually throughout the year, since the gonads of both sexes regress during the winter months. Other manifestations of sexual activity such as male courtship display, courtship feeding, and full song do not occur in the winter, at least in caged birds. Also, a hand-reared, immature female was found to be dominant to immature males during the first winter.

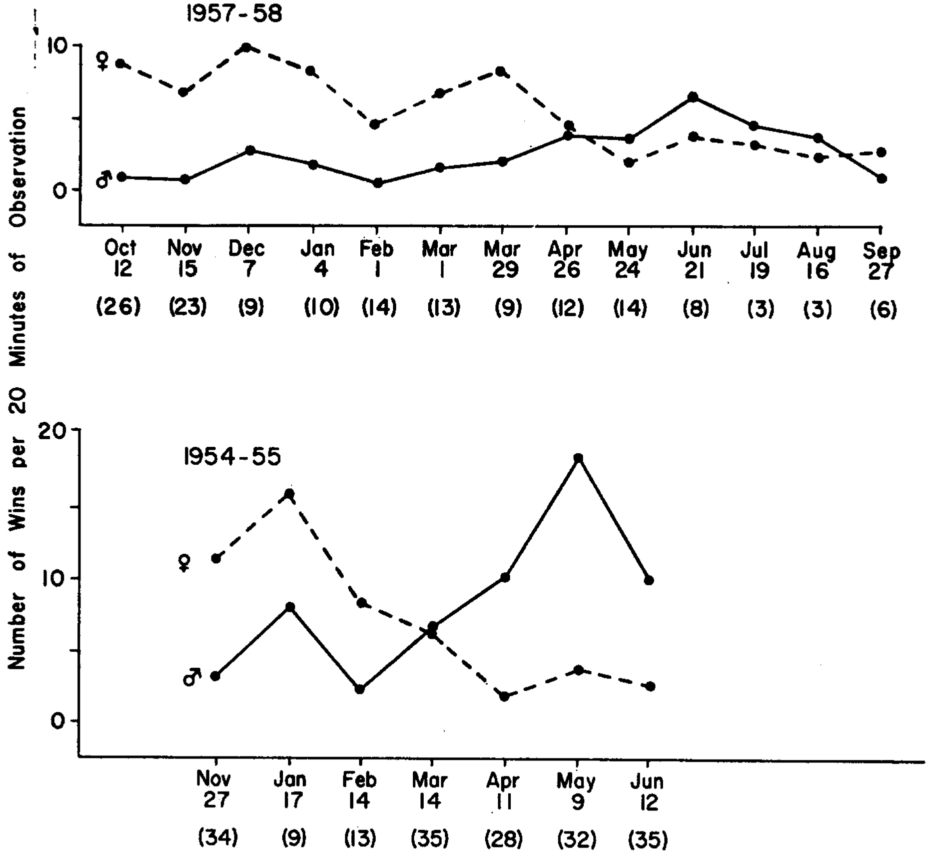

Fig. 14. Heterosexual aggressiveness of caged male and female House Finches in 1954–55 and 1957–58. Numbers in parentheses indicate the number of 20-minute observation sessions per four-week period.

There must be something other than a hold-over of sexual motivation responsible for this female dominance in winter. The dominance pattern in House Finches, therefore, is different from that of most other passerine species which have been studied, although a somewhat similar situation has been described for the Bullfinch, *Pyrrhula pyrrhula* (Hinde, 1955–1956; Nicolai, 1956). The detailed differences in dominance of males and females in 1955 and 1958 are probably related to the same factors which were discussed previously with regard to the differences in the incidence of total aggressiveness in the two years.

The dominance of females as a group over males as a group may be observed in the hierarchies shown in table 5. The first two sections represent the hierarchies during December, 1954, and December, 1957. These show that some of the males are dominant to individual females, but in general the females are dominant as a group. One group of four pairs of House Finches was continued almost intact for over a year in order to observe dominance changes. At the end of the year, instead of returning to the typical winter pattern of females winning over males, a somewhat jumbled social structure was maintained. For the most part it represented the same social hierarchy as during the breeding season. It would appear, in this case, that once the birds learned a hierarchy they tended to continue it even in the absence of the stimuli which helped establish it in the first place. This same sort of phenomenon has been described in hens by Allee (1942). In January, 1959, in order to test this interpretation, three groups of House

Table 5

Social Hierarchies of Mixed Groups of Caged Male and Female House Finches in Winter

Read from left to right in the horizontal rows. The numbers indicate the number of wins by the bird in question. For example, in the first hierarchy, RB won 7 observed aggressive encounters with WB.

November 14 to December 17, 1954

		RB	WB	R♀	WR	R♂	W	WW	BB	B
RB	♀		7	14	12	2	1	9	6	6
WB	♀			19	39	20	0	34	23	34
R♀	♀				28	28	23	23	21	18
WR	♀		1			42	2	47	1	39
R♂	♂	16	1	1	1		24	62	26	62
W	♂		29		20			21	15	16
WW	♂			1			2		26	60
BB	♂		1	2	33	1	1	2		60
B	♂			1			6			

November 24 to December 21, 1957

		S	O	B	WS	Y	WP	WG	RG
S	♀		8	4	5	8	5	3	3
O	♀			15	5	9	7	4	2
B	♀				15	16	0	3	4
WS	♀					9	10	3	4
Y	♂						11	3	2
WP	♂			25				7	7
WG	♂								5
RG	♂								

January 3 to January 31, 1959

Group A

		I	L	LW	RN	RB	SO	G	SR
I	♀		7	10	7	4	6	3	7
L	♀			3	0	3	4	3	1
LW	♀				4	0	1	4	2
RN	♀					0	1	5	10
RB	♂				1		0	2	1
SO	♂		1	2	1			1	5
G	♂								1
SR	♂				1				

Group B

		WS	B	S	PG	R	SG	GS	W
WS	♀		10	1	4	12	3	5	3
B	♀			1	2	11	2	4	2
S	♀				0	3	1	1	0
PG	♀					6	2	2	2
R	♂						6	2	3
SG	♂							2	7
GS	♂								6
W	♂								

Group C

		R	L	GB	WG	GR	WP	Y	O
R	♀		1	2	0	4	2	3	2
L	♀			2	1	2	1	1	1
GB	♀				7	7	4	6	10
WG	♀	2				6	8	8	5
GR	♀				1		3	2	5
WP	♂							8	1
Y	♂								3
O	♂						9		

Finches were mixed, the males of one group joining the females of another, and all were placed in cages which were unfamiliar to them. The results are shown in table 5. In all three groups females were dominant over males, and in only one was a male (WG) dominant over females (R and GR) in the beginning. Within a few weeks several males had begun to win encounters with females, but in all cages the females as a group remained dominant over the males as a group.

Comparisons with wild birds.—In contrast to the dominance of females in caged birds, encounters between wild birds, at a feeding station from September through January, were won by males more often than by females. Of 84 hostile encounters between males and females, males won 50 and females 34. Seven females and eight males were involved as winners in these 84 encounters. In the wild there appears to be no marked dominance of one sex over the other, such as is indicated by data obtained from captive individuals. Males made 6.3 attacks per bird as opposed to 4.9 attacks per bird made by females during observations at a feeding station. The reason for this difference in behavior of wild and captive birds is not apparent. The behavior of the wild birds is more like that of other passerines described by Hinde (1955–1956), but it still differs somewhat because of the frequent wins by females. It would be just as unwarranted to assert that males as a rule are dominant to females in wild winter flocks as to state the reverse.

Table 6

Dominance Within Pairs of House Finches

Pair		Dec.	Jan.	Feb.	Mar.	Apr.	May	June
♂	♀							
R	WR	♀/♂	♀/♂	♀/♂	♀/♂	♂/♀	♀/♂	♀/♂
WW	WB	♀/♂	♀/♂	♀/♂	♀/♂	♂/♀	♂/♀	♀/♂
BB	R	♀/♂	♀/♂	♂/♀	♂/♀	♂/♀	♂/♀	....
Y	S	♀/♂	♀/♂	♀/♂	♀/♂	♀/♂	♀/♂	♀/♂
WG	WS	♀/♂	♀/♂	♂/♀	♂/♀	♀/♂	♀/♂	♀/♂
WP	B	♂/♀	♂/♀	♂/♀	♀/♂	♀/♂	♀/♂	♀/♂

Table 7 illustrates the social hierarchies of the 1955 and 1958 caged flocks during the breeding season. There is no clear-cut dominance of one sex over the other. The members of one pair usually occupied about the same level in a hierarchy, with the female usually dominant to the male. Unmated birds fell to the bottom of the hierarchy.

It is possible that in a fairly stable, resident population, members of the population recognize each other and maintain a fairly constant hierarchy throughout the year, carrying over into the winter months, at least in part, the same rank they had during the breeding season, much as was the case in the caged birds. This explanation seems unlikely, however, since the amount of population mixture and turnover, as indicated by banding records, appears to be great. Only a small proportion of the House Finches which are banded during the year at a given place are seen there again. It is true that a core of resident birds does remain throughout the year, and many of these were involved in the encounters observed, but of 31 pairs involved in such recorded encounters, only 12 were recorded more than once. The largest number of encounters recorded for a given pair is four (for three pairs), and in every instance these were recorded in a single day. In only one pair were the members seen to fight each other on more than one day. Several of the birds involved in encounters in January had been banded as juveniles in the previous year and so could not have been a part of the breeding hierarchy at that time. Previous experience in a breeding population hierarchy does not appear to be a plausible explanation for this lack of conclusive female dominance in the wild population.

Dominance within pairs and within a given sex.—In five out of six caged pairs observed the male dominated his mate for a brief period just before pair formation (see table 6). The reason for this is apparently that the male was initiating pair formation by the billing performance. The female is less resistant to the male's advances than at other times of the year and allows him to approach closely to bill. She usually avoids the male if she is not receptive instead of supplanting him directly, as would be the normal procedure outside the breeding season. The actual basis for the change in aggressive motivation is not known, but it appears to be related to changes in levels of the sex hormones.

Table 7

The Relation of Weight to Position in Social Hierarchy

Bird	Sex	Rank in hierarchy	Rank in weight	Bird	Sex	Rank in hierarchy	Rank in weight
RL	♂	1	2	R	♂	1	2
SB	♂	2	3	WW	♂	2	1
BW	♂	3	4	W	♂	3	4
PL	♂	4	1	B	♂	4	3
GL	♂	1	2	WR	♂	1	2
GW	♂	2	1	WB	♀	2	3
OR	♂	3	3	R	♀	3	1
BR	♂	4	4	RB	♀	4	4
OS	♂	1	4	R	♂	1	3
OP	♂	2	2	WR	♀	2	4
RL	♂	3	1	WW	♂	3	1
WO	♂	4	3	WB	♀	4	5
				R	♀	5	2
P	♂	1	1	W	♂	6	7
G	♂	2	2	B	♂	7	6
R	♂	3	4	RB	♀	8	8
SB	♂	4	3				

Male WP was dominant to female B throughout the winter. Later, she became his mate. In this case the dominance of the male lasted for a much longer time than usual.

Besides the dominant-subordinate relation of the two sexes toward each other, there is the question of the causes of dominance relations between individuals of the same sex. Factors such as breeding condition of the individual, general state of health, age, weight, the shade of red of the plumage of males, territory, and "native belligerence" or genetic background of aggression, in addition to the previous experience of the individual, all might play some role in determining position in the social hierarchy.

Breeding condition is particularly important in determining social rank during the breeding season, and it is especially noticeable in the males, which may move from near the bottom of the peck order in a cage in winter to the top of the hierarchy in the spring. Birds that come into breeding condition first and become mated rise in the hierarchy more rapidly than other males which are slower to reach full gonadal development, fail to obtain mates, or for some other reason are retarded in developing sexual behavior.

Male B in 1955 was an example. Although he was at the bottom of the social order in the fall and winter, he might have been expected to rise in the hierarchy as did the other males during the spring. Instead he remained at the bottom of the scale. In April and May he became active in courting a female which was already mated. When her mate escaped from the cage in June, B became paired with her and immediately assumed a higher position in the hierarchy.

Male WG in 1958 serves as another example. He moved from next to last to second in the hierarchy, dominated only by his mate (WS).

Females, likewise rise in the hierarchy in the spring according to their breeding status. Female WS just mentioned rose from last place in the female hierarchy to the alpha position for the entire flock. This is not to be confused with the change of rank which Lorenz (1952) described in the Jackdaw (*Corvus monedula*), in which the one member of the pair rises at the time of pair formation to the same status as the other member. In the House Finch both members of the pair rise in the hierarchy, but they do not necessarily rise to the same level. Only male WG in 1958 rose to the level of his mate, and he remained subordinate to her, not of equivalent status. Male Y, which in 1955 came closest to equaling WG's rise in social position, out-ranked only one female, which was unmated and was added to the flock six months after it was established. Even at the time male Y chased the other males vigorously, while his mate was building a nest, he was still subordinate to three females, including his mate.

For the most part all the caged birds appeared to remain in good health. Those which showed illness usually died very shortly, before any changes in social status were evident. Schjelderup-Ebbe (1935) states that the usual outcome of fights between healthy and unhealthy individuals is success for the healthy one. Allee (1942) has suggested that fatigue or illness at the time of some initial encounters may produce the triangles which occur so frequently in diagrams of social hierarchies. One member of the 1955 flock, female RB, had only one leg when captured. She was thereby at a disadvantage, but she won most of her initial encounters when placed with the other birds in the cage. Gradually, however, she lost her alpha position and sank to the bottom of the hierarchy, remaining dominant only to male B. She had lost many feathers so that bare spots of skin were visible on her head. She perched with difficulty because of the one leg and moved about only with great exertion. Probably she lost her original status because of her inability to move about as easily as the other birds and to attack others as readily as they attacked her. Probably, also, she became fatigued more quickly than her opponents. When male B finally found a mate, he, too, overcame RB and she remained in the omega position from then on. Allee (1942) suggests that other members of the flock are quick to recognize signs of weakness on the part of a superior and to take advantage of the weakness to overcome the opponent.

Age or maturity is sometimes considered a possible factor concerned with social status. Since all the birds studied in the caged flocks were adult when captured, this factor could be ruled out for the caged flock. Encounters between adults and juveniles have been observed in the wild, however, and juveniles have often won over adults. Absolute age seems to be of little or no importance in adult hierarchies, since few, if any, birds live to become old and feeble.

Weight or size would appear to be a likely factor in determining success in initial encounters. Table 7 presents the weights of all birds in the 1955 flock and those of all males in the 1958 groups. The correlation coefficient of weight and social status for all groups, obtained by using a measure for degree of relationship of ranks $(P=1-\frac{6(\Sigma D^2)}{N(N^2-1)})$, was 0.38, a very low degree of correlation. Collias (1943) using a different method obtained a correlation coefficient of 0.47±.073 between weight and social rank in hens.

By using the measure for relationship of ranks, the correlation of the shade or intensity of red in the male plumage with rank in the male hierarchy was determined (table 8). Again a low correlation coefficient of 0.2 was obtained. The relative unimportance of color may be shown more strikingly perhaps by noting that the first male to obtain a mate and to become the alpha male was a pale yellow color, whereas two of his companions had bright red plumage on head, breast, and rump. Also, male B in 1955, the omega male, was second in intensity of color. Color, then, seems to be of small importance, if indeed it plays any role, in determining social status.

Familiarity with the area has been shown by Schjelderup-Ebbe (1922, 1935) and others to be of great importance in determining which one of two birds will dominate the other. This has been borne out to some extent in the present study but not to the degree which might be expected. Individuals which were introduced into the caged flocks after others in the flock were well established usually assumed a position near the bottom of the social hierarchy among members of their own sex. For example, female PG was added to one caged flock six months after it was first established. She assumed a position second from the end of the female hierarchy, but she was dominant to all the males except WG. Male X was introduced seven months after the establishment of the flock, and he assumed second place in the male hierarchy, dominated by all females. Male O was introduced one month later and took the omega position in the hierarchy. Several factors probably contributed to this in addition to unfamiliarity with the new surroundings. By this time the other three males were mated and probably partly because of this, they dominated the unmated male O. In addition, first male Y and then male WG patrolled the cage chasing other males vigorously, and singling out O as the particular object of their aggression. Probably fatigue from the almost continual chasing and supplanting by the dominant males, as well as the unfamiliar surroundings, and the lack of the boost of aggression which pair formation seems to provide contributed to the maintenance of O in the omega position.

Table 8

The Relation of Plumage Color of Males to Position in Social Hierarchy

Bird	Rank in hierarchy	Rank in color
R	1	1
WW	2	3
BB	3	4
W	4	2
WP	1	2
Y	2	3
WG	3	1
RG	4	4
P	1	3
G	2	4
R	3	1
SB	4	2

When 11 males were placed in one cage, in which four of them had been previously, three of these four won encounters with all the strangers. The fourth lost to only two of the new individuals. This bears out quite well the accepted idea of the importance of familiarity with surroundings in determining the outcome of aggressive encounters between individuals. A week later the more aggressive, introduced individuals were beginning to climb in the peck order.

Somewhat related to this familiarity with an area is the matter of territoriality or the ownership and defense of an area. The caged House Finches observed in this study did not establish separate territories within the cage, as Shoemaker (1939) recorded for his canaries and Bennett (1939, 1940) and others for pigeons. Instead, the alpha pair acted as if the entire cage were their territory. The beta pair was prevented by the alpha pair from breeding. They displayed a strong inclination to nest, however, inspecting nest sites, particularly the nest of the alpha pair, and chasing birds subordinate to them in the hierarchy. They, too, showed signs of territoriality but to a much smaller degree than the alpha pair. The gamma pair showed very weak tendencies toward nesting, and they were much less aggressive than either the alpha or beta pair. The three pairs may be thought of as holding a single territory in common but defending it with varying degrees of aggressiveness. The alpha pair was the primary territory holder, the beta pair the secondary holder, and the gamma pair the tertiary holder. The two unmated birds were attacked by all others in the cage and may be thought of as intruders in the territory of each of the other pairs.

Writing about the peck order of canaries, Allee (1942:143) stated that "when they are confined in a small space, the social order becomes relatively simple and definite; it is little complicated by territoriality. Given more space, individual territories tend to become established in which the territory holder is usually supreme. . . . Even a socially low-ranking male normally dominates other males in some restricted space about his nest." In the case of the House Finches just described the effect is of a reduction of the available area until the territories of several pairs become contiguous.

Territorial behavior is characteristic of the breeding season when the different pairs are attempting to nest and their success in building a nest is dependent on their success in establishing a territory, but its relation to the dominance behavior observed in winter when there are no territories and the birds are in flocks is not clear.

Finally, there is the matter of "native belligerence," or the genetic background of the aggressive behavior of any individual. Potter (1949) demonstrated that hens of different breeds vary in their aggressiveness. Hens of some breeds consistently win in encounters and hens of other breeds just as consistently lose. Furthermore, this tendency to win is not necessarily related to weight or breeding condition (Ginsburg and Allee, 1942). Scott (1958) discussed the difference in aggressiveness of various strains of dogs. Leopold (1944) described a hereditary wildness factor in turkeys. In House Finches and in other animals, however, it is very difficult to separate the inherited from the learned behavior. Undoubtedly much of the difference in individual aggressive behavior is due to previous experience. The whole spectrum of motivational influences from physiological to learned factors is involved. But, as Scott and also Ginsburg and Allee suggest, apart from anatomical and physiological factors there is probably also some genetic control of the threshold of aggressive reactions to various situations and stimuli. It is true that the genetic differences described for dogs and hens are between distinct strains which do not usually interbreed and that such wide divergence would not be expected in a freely interbreeding population. Individual differences would be expected to occur in a panmictic population, however, and some would be almost if not just as great as those between separate breeds of hens. But there should be many more intermediate conditions between the two extremes. Variation in intensity of territory defense by different individuals of a given species may be observed in the field, and it is not impossible, or even improbable, that part of this variation has a genetic basis.

Interspecific relations.—At feeding places and on perches House Finches sometimes supplant other species and are sometimes themselves supplanted by other species. Species to which House Finches may be said to be dominant and species to which they are usually subordinate are listed here.

Species attacked by House Finches
Contopus sordidulus
Passer domesticus
Spinus psaltria
Serinus canarius
Junco oreganus
Zonotrichia leucophrys

Species which attack House Finches
Contopus sordidulus
Passer domesticus
Pipilo fuscus
Melospiza melodia
Chamaea fasciata

Usually a House Finch merely supplants an opponent of a different species, but occasionally head-forward displays may be performed in instances of strong conflict, as between House Finches and House Sparrows (*Passer domesticus*) at a feeding station. Hand-reared House Finches performed the extreme form of the head-forward display toward a canary.

DISCUSSION

Although hostile behavior occurs more frequently among groups of caged House Finches than among free-living ones, the same postures and call notes are employed in both situations. The significance of some aggressive patterns is not clear, however, until they have been studied under natural conditions. On the other hand, some behavior patterns become more understandable when observed more closely in captivity. The combination of field and laboratory study has proved to be almost essential in the description and interpretation of House Finch behavior.

The dominance pattern of the House Finch differs from that of the canary, Greenfinch (*Chloris chloris*), Continental Goldfinch (*Carduelis carduelis*), Hawfinch (*Coccothraustes coccothraustes*), Chaffinch (*Fringilla coelebs*), and Brambling (*Fringilla montifringilla*), as the males are not generally dominant to the females in winter. Captive female Bullfinches have been reported (Hinde, 1955–1956) to be on the whole dominant to the males in winter, and this resembles more the condition in the House Finch. The female of a pair of House Finches, however, remains dominant to her mate during the breeding season. In this respect, the House Finch resembles the species studied by Hinde. He reports that some male canaries may continue to make occasional attacks up to the time of copulation. A similar situation was observed in one pair of House Finches. These birds were confined in a very small (18 × 18 × 12 inch) cage, however, and the lack of space might have elicited abnormal behavior. Other wild and caged males were not seen to attack their mate after the pair bond was established. In general, the seasonal variation in dominance of male and female House Finches seems to agree most closely with that of Bullfinches.

Noble, Wurm, and Schmidt (1938) found that the male Black-crowned Night Heron (*Nycticorax nycticorax*) is dominant to the female during the breeding season, and they postulated that this male dominance was necessary if copulation was to be successful. Such a condition is not necessary for successful mating in many passerine birds, in which the dominance of the sexes is reversed from the pattern in night herons. Table 9 lists species in which the female is dominant.

In the House Finch, copulation usually occurs at the invitation of the female. In most other species the female may be stimulated to solicit by a male display or may solicit without male display. In either case actual copulation, when successful, is usually initiated by the female with no overt signs that the male is necessarily dominant immediately before the act.

Tinbergen (1939), Nice (1941), and Lack (1943) interpret the function of male bird song as a warning toward rival males or as a means of attracting females, or both.

Moynihan and Hall (1954) suggest that the term "song" be limited to vocalizations which serve both functions. This definition is followed by Smith (1959). Morris (1958), however, suggests that the earlier interpretation of song, as having either function or both, be recognized, and it is this definition which is used here. Although male song may sometimes lead to hostile encounters between male House Finches, this is of relatively rare occurrence, and it seems incorrect to imply that this is one of the major functions of House Finch song. The primary function appears to be the attraction of a female, because unmated males, or a male whose mate is incubating sings much more frequently and more vigorously than males in the company of their mates. It is quite possible, however, that loud singing by males may lead to some dispersal of individual males, because two singing males usually perch farther apart than when they are not singing. Probably, therefore, there is an aggressive element in vigorous singing by male House Finches, but it is never so apparent as in the song duels of the Snow Bunting (*Plectrophenax nivalis*) or Song Sparrow (*Melospiza melodia*).

Table 9

Male and Female Dominance in Breeding Season, Especially during Copulation

Male dominant	
Pygoscelis papua	Roberts, 1940
Gallus domesticus	Masure and Allee, 1934*a*
Melopsittacus undulatus	Masure and Allee, 1934*b*
Nycticorax nycticorax	Noble and Wurm, 1940
Anas platyrhynchos	Allee, 1942
Larus atricilla	Noble and Wurm, 1943
Columba livia	Allee, 1942
Streptopelia risoria	Bennett, 1940
Plectrophenax nivalis	Tinbergen, 1939
Female dominant	
Chloris chloris	Hinde, 1955–56
Coccothraustes coccothraustes	Hinde, 1955–56
Fringilla coelebs	Hinde, 1955–56; Marler, 1956
Fringilla montifringilla	Hinde, 1955–56
Carduelis carduelis	Hinde, 1955–56
Serinus canarius	Hinde, 1955–56

Many of the fringillids which were studied by Hinde (1955–1956) perform a display somewhat similar to the display of male House Finches. The non-aggressive, sleeked, wings-raised posture which Hinde describes for the male canary resembles the House Finch display somewhat, but it is given under different circumstances, apparently involves a much stronger tendency to attack, and it may be performed rarely by the female. The sleeked, wings-raised display of the male Greenfinch (Hinde, 1955) and sleeked, horizontal posture of the male Hawfinch (Hinde, 1955–1956) likewise appear to involve a stronger aggressive motivation than the House Finch display, but they resemble it more closely than does that of the canary because the Greenfinch and Hawfinch displays, like the House Finch display, sometimes involve pivoting. Pivoting is a very conspicuous part of the displays of the Continental Goldfinch, but it is not combined with the wings-drooped posture which seems to correspond to the non-aggressive wings-raised posture of the canary and the display of the male House Finch. The dance of the male Bullfinch is reminiscent of the House Finch display, particularly in the circumstances in which it occurs, but the posture involved does not correspond very closely to that assumed by the House Finch. Similarly the lopsided, wings-drooped posture of the Chaffinch (Hinde, 1955, 1955–1956; Marler, 1956) has only a slight resemblance to the House Finch display. Of all these species only the Greenfinch and House Finch sing while performing the display, although the Continental Goldfinch may utter call notes, and the Bullfinch is said to give a coarse low warble. Horizontal pivoting and song are characteristic elements of some estrildine, pre-copulatory displays, but the postures of the birds generally are not like the House Finch display posture (Morris, 1958). It is of interest, although not necessarily significant, that the "courtship" posture most like that of the House Finch is the display posture of the male House Sparrow, a ploceid (Daanje, 1941; Summers-Smith, 1954).

In general the agonistic postures and behavior of House Finches closely resemble those of other fringillids (Hinde, 1955–1956). As Hinde remarks, these behavior patterns appear to be very widespread among all the passerines. Nevertheless, House Finch behavior suggests some alternate interpretations to those given by Hinde (*op. cit.*) and Marler (1956). According to their interpretation a horizontal body position as in head-forward display or fright is associated with a tendency to flee. As was noted previously, display is supposedly associated with conflicting motivation, and it might be assumed that a conflict between a tendency to attack and a tendency to flee would result in a head-forward display. As Hinde mentions, however, the bird with the more horizontal posture is the more likely to attack. This does not appear to be consistent with the idea that the horizontal posture is associated with a tendency to flee, since the bird with the more horizontal posture would be expected to be the one to flee, whereas in fact it is usually this bird which attacks. If on the other hand we think of the situation only in terms of conflicting motivation—both escape and attack tendencies strong and of about equal strength—then the bird with the more horizontal posture, that is, the one with the greater conflict, should not consistently attack or flee, but the outcome should be random, depending on which tendency is stronger. Because neither explanation seems to fit the observed behavior exactly, it is much simpler to think of the horizontal posture of either an aggressive head-forward display or of a fright reaction as merely an intention to fly. In either case—attacking or fleeing—the bird flies. Since in a head-forward display the body is pointed toward another bird, whereas in the fright reaction the body usually points away from other individuals toward a clear flight space, the birds should have no difficulty in distinguishing the two intentions. The different circumstances in which the two displays occur, the utterance of a loud call note with a head-forward display, and the silent crouch of the fright reaction, at least in the House Finch, must also make the meaning of the posture clear to other birds. Thus the two almost identical postures retain their separate signal function because of the different contexts in which they are given.

The fluffing of body feathers of subordinate individuals during conflicts with more aggressive birds has not been observed in the House Finch. Only feathers of the forehead may be slightly erected when a bird appears mildly afraid. Aside from fluffing by birds when resting, preening, sleeping, or when sick, fluffing occurs only in some head-forward displays. There is no direct evidence, then, that in the House Finch fluffing is associated with thwarted fleeing or that it serves as a submissive posture as Hinde suggests to be the case in the eight species he studied. It is possible, of course, that the fluffing which sometimes occurs during a head-forward display may result from a fleeing tendency which is blocked or overbalanced by an attack tendency. Or, this fluffing may be a ritualized pattern which has been carried over from the agonistic context in which it occurs in some other fringillids. More observation is needed to clarify this point.

The lack of a well-defined and stoutly defended territory beyond the immediate vicinity of the nest or the mate is probably associated with the close spacing of nests, although it is not possible to say which is cause and which is effect. The very mild aggressive element in male song is undoubtedly connected with the limited territoriality of the species. The lack of a conspicuous, pre-copulatory display, or the displacement of a phylogenetically earlier display of this sort into a different context such as seems to have occurred in the House Finch and House Sparrow, is probably tied in with the small size of territories and the continual proximity of nesting pairs. The importance of isolation for the success of coition has been pointed out earlier. It should be mentioned, however, that the need for isolation breaks down as the proximity of nests increases and a colony is formed. Colonial species do not require privacy for the successful performance of the sex act. The sight of copulation is not so stimulating to onlooking males that they attempt to interfere. The House Sparrow, a semicolonial species which nests in denser groupings than the House Finch, has reached this stage, but the House Finch has not.

The so-called "Darling effect," or the synchrony of the breeding activities of a colony, places a premium on mutual stimulation by members of a group (Darling, 1938). It is perhaps significant that three species which nest in loose groupings, the House Finch, Greenfinch, and House Sparrow, have a conspicuous display performance involving a "dance" and loud song. In at least two of these, the House Finch and the House Sparrow, the display may involve several males at one time. These communal displays may serve the same sort of function as the displays of members of a colony of sea birds in bringing about a close synchrony of breeding activity among the members of the group and in stimulating more birds to breed.

It is important to relate the display repertoire of any species to its ecology, insofar as this is possible. Most ethologists and ecologists would agree that the way of life of any successful species, including its various behavior patterns, is closely bound by selective forces to the environment in which it lives. There has been mention of several behavior patterns of the House Finch which can be tied to the semicolonial nesting of the species. What is there, then, about the ecology of the House Finch that causes it to form large flocks or feeding aggregations and to nest in loose clusters?

Nests are too widely spaced for the aggregations to be considered colonies, and the proximity of nests is undoubtedly due at least in part to the localization of optimal nesting sites. The territory of a pair of House Finches includes only a small area around the nest and does not include a foraging space. Other species such as the Song Sparrow include a foraging area inside the strongly defended territory limits. Most territorial species utilize a great variety of food items and are thus able to live within a small area. But House Finches feed exclusively on seeds and fruits and, unlike most other passerines, do not take insect food. They utilize only a small portion of the total available food types and have become adapted to moving from place to place to locate the proper items. Characteristically, large numbers of finches may be seen feeding in open fields where weed seeds or fruits are abundant. As soon as this food source is exhausted the birds move on to other, more rewarding sites. House Finches and other American members of the genus *Carpodacus* are commonly observed to fly long distances between feeding and nesting areas. A similar separation of defended nesting territory and neutral feeding area is described for the Scarlet Grosbeak (*Carpodacus erythrinus*) by Haas (1939). Bates and Lowther (1952) suggest a semicolonial nesting habit in the Scarlet Grosbeak much the same as is often found in the House Finch. Possibly the same factors of specialization in feeding and localization of optimal nest sites are involved in both species.

SUMMARY

This part of a study of the agonistic behavior of the House Finch is concerned with factors in aggressiveness and in sociality and with the possible significance of certain behavior patterns in free-living populations. (See Thompson, 1960:269, for a summary of Part I.)

Experiments with caged birds indicate that the incidence of aggressive behavior increases when the amount of space available to each bird is strongly decreased.

Observations of caged birds indicate that peaks of aggressive behavior occur in late fall, early spring, and late June. The cause of the peaks and the intervening troughs is not clear, but several factors are suggested. The increase in total aggressiveness of the group during the breeding season is due to an increase in the aggressiveness of a few individuals rather than of the group as a whole. Males were found to be more aggressive than females in the spring. This rise of male aggressiveness is undoubtedly related to the defense of mate and territory.

There is a well-defined social hierarchy in captive flocks of House Finches. Caged females generally are dominant to males in the winter. During the breeding season the females as a group are no longer dominant to the males as a group, but each mated female remains dominant to her mate. In contrast to the dominance pattern of caged birds, encounters between wild birds at a feeding station between September and January were won by males more often than by females. There is no clear pattern of one sex as a group being dominant to the other. The reasons for this discrepancy in wild and captive flocks are not apparent.

At feeding places and on perches House Finches sometimes supplant other species, and they in turn are sometimes supplanted by other species. Circumstances determining which species will win an encounter vary.

Factors which seem to have bearing on the position of an individual in the social hierarchy are breeding condition, general state of health, familiarity with the area, territory, native belligerence, and previous experience.

It is suggested that the horizontal posture of either a head-forward display or a fright reaction may be interpreted as merely an intention to fly rather than an indication of a tendency to flee.

Although the primary function of male song during the breeding season appears to be advertisement for a mate, song does seem to involve weak aggressive motivation, and it may lead to some dispersal of individual males.

The lack of a well-defined and stoutly defended territory beyond the immediate vicinity of the nest or the mate, the very mild aggressive element in male song, and the lack of a conspicuous, pre-copulatory display, or the displacement of an earlier display of this sort into a different context, may be related to the semicolonial nesting habits of the species.

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