AGONISTIC BEHAVIOR IN THE HOUSE FINCH
Part I: ANNUAL CYCLE AND DISPLAY PATTERNS

By WILLIAM L. THOMPSON

The primary purpose of this study is to describe the agonistic behavior of the House Finch (*Carpodacus mexicanus*) with an emphasis on aggression and dominance relations. By "agonistic behavior" is meant fighting or hostile behavior, including avoidance and fear reactions which may occur in hostile encounters between birds. The annual cycle of House Finches for the area near Berkeley, California, is described briefly as background for the discussion of behavior. Social hierarchies of wild and caged birds are analyzed, and factors involved in their determination are discussed. Additionally, to determine the effects of sex hormones on aggressive behavior and on social hierarchy, the behavior of male castrates both with and without treatment with testosterone were compared with the behavior of intact males; these results will be reported elsewhere.

Collias (1944) summarized the literature on aggressive behavior in vertebrates, and an overall review is not called for here. Probably the most conspicuous expression of aggressiveness in wild birds occurs in the course of territorial defense. Several recent reviews summarize the extensive literature on territory in passerine birds (Nice, 1937; Hinde, 1955; Tinbergen, 1957; Carpenter, 1958).

Another basic aspect of aggressive behavior is the formation of a social hierarchy or peck order. This was first described by Schjelderup-Ebbe in 1922 for chickens, and the extensive literature relating to their social behavior has been summarized by Wood-Gush (1955). Masure and Allee (1934) extended the study of social organization to pigeons and parakeets. Shoemaker (1939) described a peck order in small flocks of caged canaries. Since 1940, peck order has been described for several other passerine species, both as captives and in the wild. Odum (1941–1942) and Hamerstrom (1942) found a definite social hierarchy in flocks of wild Black-capped Chickadees (*Parus atricapillus*); Colquhoun (1942) describes a similar situation in wild Blue Tits (*Parus caeruleus*); Hinde (1952) includes data on social organization and on specific patterns of aggressive behavior for the Great Tit (*Parus major*) and other parids; Sabine (1949, 1959) found a well-established peck order in the Slate-colored Junco (*Junco hyemalis*), Oregon Junco (*Junco oreganus*), and Tree Sparrow (*Spizella arborea*); Hinde (1955–1956) mentions peck order and aggressive elements in the courtship behavior of several fringillids; Tordoff (1954) studied the peck order of a small winter flock of captive Red Crossbills (*Loxia curvirostra*), Nicolai (1956) of captive Bullfinches (*Pyrrhula pyrrhula*), and Marler (1956) of captive and wild Chaffinches (*Fringilla coelebs*). In addition, a series of recent papers in the field of comparative ethology too numerous to list here have dealt in part with the agonistic behavior of various species, particularly passerines.

MATERIALS AND METHODS

Observations of both wild and caged birds form the basis of this report. Observations of wild birds were made in Strawberry Canyon on the University of California campus, at a feeding station in a residential area of Berkeley, and at the Hastings Natural History Reservation, Carmel Valley, California. In addition brief observations were made at various other places throughout the San Francisco Bay area. Birds were watched using 7 × 50 binoculars. Notes were recorded directly in the field at the time of observation. No specific routine of observation was followed, and length of time spent observing depended largely on the activity of the birds and on the schedule of the observer.

Wild-captured, color-banded, adult House Finches were used for observations of behavior in captivity. In 1954–55 a flock of nine birds was placed in a cage of ½-inch mesh screening seven feet long, three feet wide, and three feet high. The back and floor were wooden. Several wooden perches were

placed at varying heights and positions in the cage. A wooden nest box, open in front, was used during the winter as a roost, and during the spring as a nest site. The cage was located in a shelter in the courtyard of the Life Sciences Building on the University of California campus. The shelter was provided with a white-washed glass roof and hardware cloth walls. The birds received direct sunlight for at least part of the day throughout the year. Length of day and temperature were therefore approximately the same for the caged birds and for wild birds in the Berkeley area, although light intensity was somewhat less in the cage than out-of-doors. The birds were observed through a "one-way glass" window at one end of the cage.

In 1957–58, four cages eight feet high, four feet wide, and four feet long were employed. Three of the four cages contained four pairs of birds, while the fourth contained one male and two females. These cages were located in Strawberry Canyon on the University of California campus, in an area inhabited by many wild House Finches. The cages were built under live oak and laurel trees and were shaded during most of the day, but some direct sunlight did reach the birds. Wooden perches were placed at varying heights. Shelter was provided by an 18-inch wide wooden roof over one side of the cage. The birds were observed through a three by five-inch opening at one end of each cage.

At all times, water, gravel, and a seed mixture consisting of canary seed, oat groats, and rape were available. Several times each week lettuce and apple or orange slices were also provided. During the spring and early summer, dry grass, string, and fresh green vines were placed on the floor of the cages, and were used by the birds as nesting material.

Three eight-day-old sibling House Finch nestlings were hand-reared. At first they were fed a soupy mixture of milk, cooked egg yolk and whole wheat bread crumbs, and were kept together in a covered box. When two weeks old, they were placed in a wire cage, and canary and rape seeds were introduced into the food mixture. When the birds were three weeks old, the egg and milk mixture was discontinued and they were fed a mixture of water-soaked bread, and canary and rape seed. A dry seed mixture was placed in the cage, along with daily rations of lettuce and/or apple, but the wet mixture continued to be available until the birds were ten weeks old, by which time they were feeding almost entirely on the dry seed, fresh fruit and greens.

A standard form was used for recording aggressive encounters among caged birds. A double-columned sheet was used to record the color-band combinations of the attacker and the bird which was attacked, and which avoided the attacker. The form which was used in 1954–55 provided separate columns for different perches in the cage in order to reveal any territoriality in relations between individuals in the cage. Since none developed no provision was made in later forms for the localization of aggressive encounters in different parts of the cage. Occasional observation sessions were devoted entirely to the recording of descriptions of postures, call notes, and activity patterns. The length of observation sessions varied from 10 to 60 minutes. Observations were made both in the morning and afternoon in 1954–55, but only in the morning in 1957–58. Since there were four cages to be watched in 1957–58 the sequence of observation of the cages was varied so that each cage was observed at a different time on consecutive mornings. In this way the effects of morning cycles of activity and inactivity were reduced, and the records for different cages were made more comparable.

An encounter between two individuals was recorded as an aggressive encounter if one either pecked the second, or if it threatened the second by moving toward it as if to peck, or performed one of the aggressive intention movements described subsequently in the text, or if it supplanted the second individual. Often it is possible to determine the dominance relationship between two individuals by the avoidance of one by the other, but this is not so reliable an indication of subordinate position as an actual flight or avoidance of a peck or threat by another bird.

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HABITAT AND FOOD

A compact statement of habitat of the House Finch is given by Grinnell and Miller (1944:454). Its geographic distribution has been mapped by Salt (1952). Water needs of House Finches and their adaptability to desert and dry summer regions has been studied by Bartholomew and Cade (1956). Eating of salt by House Finches has been noted in the literature (Peterson, 1942; Linsdale, 1957) and also by the writer.

House Finches are primarily seedeaters (Roessler, 1936) but they also eat fruit, and are considered a pest by fruitgrowers. Beal (1904) reported that the animal intake of House Finches amounts to little more than three per cent of the yearly food intake. It consists primarily of plant lice (aphides). Probably these insects are taken by accident along with vegetable material. Large numbers of House Finches are attracted to fields of blooming and fruiting wild mustard (*Brassica campestris*) and radish (*Raphanus sativus*) in the spring. In the fall, great numbers congregate at stands of ripe thistle (*Cirsium*) and other composites. The race from San Clemente Island makes use of cactus fruit as a food source (Grinnell and Miller, 1944).

House Finches usually nest in dense foliage and often build in ivy under the eaves of a building, if such a site is available. In the absence of dense foliage or a man-made structure, they may nest in crannies on cliffs. In many ways House Finches are similar to House Sparrows (*Passer domesticus*) in their nesting requirements, and the two species may compete for nest sites (Evenden, 1957; Gilman, 1908). Keeler (1890) wrote about the House Finch that "wherever it is scarce the English Sparrow is proportionately abundant and it seems not impossible that one may supercede the other in course of time." Gilman found House Finches able to defeat House Sparrows unless outnumbered by them, but observations in Berkeley have indicated that it is more often the somewhat larger and heavier House Sparrow which wins fights between the two species.

ANNUAL CYCLE

Agonistic behavior may be observed throughout the year among wild House Finches. It occurs primarily at resting or roosting sites, where several birds are perched near each other preening, calling, or singing. It occurs less frequently while birds are feeding in the open. Even when many birds are feeding in close proximity, as in the large feeding aggregations of adults and juveniles in late summer, there is very little aggressive behavior. Agonistic behavior does, however, take place regularly at feeding stations where food is available to only a few individuals at a time.

In early spring when pairs are forming, aggressive behavior reaches a peak. Increasingly, males become intolerant of other males perched near them. Males, when they have secured a mate, defend the area around the female, in the same way as Twining (1938) describes for a race of the Gray-crowned Rosy Finch (*Leucosticte tephrocotis*). For the most part this amounts only to an increase of individual distance, and the degree to which such an area is defended varies from time to time with any individual. A bird which is resting or preening near its mate may tolerate other individuals or pairs within a few feet, and then, after stretching, yawning, and rousing itself, it will begin to patrol the vicinity, chasing away other House Finches, without any sort of evident provocation on their part.

This peak of aggressive activity continues through the selection of a nest site and the construction of the nest, but it begins to wane by the time the nest is completed. The area around the nest is defended rather sporadically and weakly. Vigorous displays are rarely observed in territorial defense. Usually the defender merely flies to a perch near the intruder and sits until the latter moves away. There are no sharp territorial boundaries, such as are found among Song Sparrows (*Melospiza melodia*), Snow Buntings (*Plectrophenax nivalis*), and many other passerines. Once incubation has begun there is little territorial defense, and it is therefore possible for nests to be built within a few feet of each other, with little or no interference from neighbors if they are in different stages of the breeding cycle.

The distance from the nest to the farthest point from the nest which is defended may be taken as a rough approximation of the radius of the territory. On the basis of territory defense in six nests during the period when territory defense was most vigorous, the average radius was 14 feet, the range 6 to 30 feet. This would give an average territory size of 642 square feet. This figure may be compared with approximately 158 square feet for the House Sparrow (Owen, 1957) which has similar semi-colonial nesting habits and indefinite territorial boundaries.

In the remainder of this part of the paper, particular phases of the annual cycle and the repertoire of displays will be described. In part II, agonistic behavior in caged birds and its significance in social and broader ecological contexts will be considered.

Flocking and movements.—During winter, aggregations of House Finches may be observed in rural and suburban areas. Groups of four, five, six or more birds are sometimes seen perched a few inches apart on power lines beside a highway. In towns, the clumping of birds is less noticeable, although there may be small aggregations at choice feeding areas or favored roosting sites.

The relative sedentariness of local populations of House Finches can be shown best by taking available banding records and analyzing them for evidence of long-distance movements as between breeding and nonbreeding seasons. Records of the recoveries of banded House Finches from 1923 through 1958 in files of the Fish and Wildlife Service were examined for this purpose. Table 1 shows the latitudes at which the 6004 recovered or recaptured House Finches were banded. Most (96.8 per cent) of these were recaptured at the place where they were banded. Column two presents the percentage of individuals that were recaptured or found dead somewhere other than the place where they were banded.

Banding records show that House Finches have been banded in the northern part of their range (up to 48°N) throughout the year, but this does not entirely rule out the possibility that some individuals may leave the breeding area in winter. If those banding records are selected in which one date, either of banding or recovery, falls within the breeding period (March through July) and in which the second date, again, either of recovery or banding, falls within the nonbreeding period (August through February), it should be possible to rule out the likelihood of recaptures of any individual within a single breeding or wintering period. Such recaptures would tend to obscure any evidence of long migratory movements of the population as a whole by emphasizing the percentage of individuals that remain on their breeding area. Column three lists the record of birds banded and recovered in opposite seasons at each latitude for which there are banding records.

If the northern populations tended to migrate south during the winter, the percentage of foreign retraps should be markedly higher for the selected group of birds than for the total except where the numbers in columns one and three are about the same, as at latitudes 50° and 49°N. The percentages are in general not markedly higher for

Table 1

Numbers of Birds Banded at North Latitudes and Distances of Recovery from Place of Banding

Latitude (°N)	Total banded and recovered	Per cent recaptured elsewhere	Banded and recovered in opposite seasons	Per cent foreign recaptures	Longest distance traveled (miles)	> 200 miles	100–200 miles	50–99 miles	25–49 miles	10–24 miles	5–9 miles	1–4 miles
50	1	0	1	0								
49	10	0	9	0								
48	97	0	49	0								
47	0	0	0	0								
46	2	0	1	0								
45	1	0	0	0								
44	8	0	7	0								
43	0	0	0	0								
42	2	50.0	0	0	51			1				
41	4	25.0	2	50.0								
40	133	2.3	41	7.3	15					1		1
39	54	1.9	18	0	9						1	
38	254	1.6	85	1.2	98			1			3	
37	451	4.9	210	6.7	290	1	1	2	3	3		9
36	20	0	11	0								
35	42	16.7	12	6.7	18					1	5	1
34	4261	2.6	2023	3.5	800	6		3	11	24	39	26
33	353	1.1	158	0	87			1				3
32	311	0.6	125	1.6	680	1		1				

this selected group, and furthermore the percentage of foreign recoveries does not increase toward the northern end of the range as would be expected if these northern populations were migratory. Those latitudes which do show a high percentage of foreign recaptures are represented by small samples and the high recapture percentage is probably due to chance. It is true that the banding records do not give an adequate sample of the total House Finch population, since the northern part of its range is poorly represented. Also, recoveries of banded House Finches in proportion to the number banded are very few at any latitude. The larger proportion of recovered birds toward the southern end of the range is undoubtedly a reflection of the greater number of banders in the southern part of the range, particularly in the San Francisco Bay area (37°N) and the Los Angeles area (34°N).

The available evidence indicates that House Finches generally remain on or wander about near their breeding area during the autumn and winter months rather than migrate over a long distance to a wintering place farther south. The few instances of a very long distance (over 200 miles) between the place of banding and the place of recovery may have resulted from man-provided transport.

Pair formation.—In areas such as Strawberry Canyon where House Finches are not winter residents, females become associated with males about a week after males become established on their breeding areas and begin to sing frequently. Males and females fly together and perch together. Since none of these wild birds was banded, it was not possible to determine whether the same birds remained together. About the time the females appear, the males begin to chase each other. Two males may sing from opposite sides of a tree. Soon one may hop across to the other side and supplant the other on his

perch in the same tree. The first may not molest him further. Sometimes, however, the dominant individual will chase the other to another tree. During these chases the birds give a short, staccato call note, repeated in rapid succession. Females become more constantly associated with particular males, and after pair formation has occurred, the two individuals are almost always together until egg laying and incubation.

The details of pair formation are not clear. Since the males do not stake out territories and remain on them until a female appears, it is impossible to observe a wild male or female House Finch continually during this or any other phase of the annual cycle. Pair formation probably takes place as in other birds which mate in winter flocks (Lack, 1940:279), that is, "the members of a pair gradually come together, using many small interrelated mutual actions, with intervals when they move apart again" without either member of the pair appearing to subdue the other, that is, without any simple "sexual dominance." Bergtold (1913) suggested that House Finches remain mated over the winter because he saw the birds in pairs at feeding stations in winter. In Berkeley the close association of the pair so striking during the breeding season is not at all evident during fall or winter. Caged birds do seem to retain some remnant of the pair bond, and billing has been observed during late fall, even between male castrates and intact females. Here it appears that habit and forced proximity may be motivating influences.

In town where both males and females are present through the winter it is difficult to establish the presence or absence of a continuous recognition of the mate as such. In the Coast Range foothills, however, there is some indication that the pair bond is not continuous from year to year. As mentioned above, males begin to appear on breeding areas in mid-February, followed a week or so later by the females. This difference in arrival time would suggest that the birds are not paired when they arrive on the breeding area.

At this time males and females associate in small groups, and the membership of any one group appears to be fluid. Within a few days, however, males become associated with certain females. It is common to see one female accompanied by two males. The males often show no hostility toward each other at first. Frequently the female is the leader in these threesomes. The characteristic flight formation is single file. Soon one male begins to attack the other, and finally only one male remains with the female.

These early stages of pairing are not detectable among caged birds because the individuals are forced to be together and to perch nearer each other than is usual in the wild. Beyond this stage, however, observations of captive birds have helped considerably to fill in the picture. After a few weeks of close association the members of the pair begin a mandibulating activity or billing ("kissing" of Conder, 1948) which leads to courtship feeding. As is true in other phases of the breeding cycle, finches in Strawberry Canyon begin courtship feeding later than do those in town. Conder (1948), in describing the development of courtship feeding in the Continental Goldfinch (*Carduelis carduelis carduelis*), distinguishes four stages which follow each other at intervals of about two days: (1) kissing (or billing), (2) female crouched while kissing, (3) mock feeding, and (4) true feeding. A similar sequence of developmental stages can be observed in House Finches.

The first evidence of pair formation in captive House Finches is billing, accompanied by soft twittering. The male leans toward the female, or *vice versa*, and gently pecks at the closed beak. Usually the bird being pecked leans slightly away from its mate, indicating an avoidance tendency still remaining. Later the birds lean toward each other, both open their beaks slightly, and the male may insert his into that of the female. In the House Finch the "kissing" gives way to mock feeding before the female crouches. Still later the male accompanies this mock feeding with regurgitating movements of the

throat, but no food passes into the female's open mouth. At this time the female usually begins to beg from the male, assuming the customary passerine begging posture and giving loud, rapidly repeated call notes, almost in the same rhythmic pattern as the male song, but in an apparent monotone. The tarsometatarsus is held almost parallel to the ground, the tarsal joint flexed more than usual, and the tail may be lifted 35° to 45° above horizontal or may sometimes be held horizontal. Often the tail is flicked vertically in rhythm with the calling. When this behavior pattern first appears, the female may stretch her neck toward the male, having her beak slightly opened and her head about on the same level as her shoulders. Later in the development of courtship she retracts her neck and tilts her head almost vertically so that the male points his beak downward to feed her. At about the time of nest building, the male actually feeds the female regurgitated material, just as both parents later feed the young. The calling is continued while the male is feeding the female, but the sound becomes very faint while he is stuffing food into her mouth. When the birds are not visible, it is possible to detect feeding by the periodic, sudden muffling of the call note, followed by a rise in the dynamic level after the female swallows. The male usually regurgitates and thrusts his beak into the open mouth of his mate several times during a single feeding, and the begging call of the female becomes a sequence of alternating groups of loud and soft call notes.

A case of mistaken feeding by the male may shed some light on the combination of stimuli adequate to release feeding in the male. A mated pair was observed feeding at a trapping station. The female was caught and began struggling to escape. She gave a low-pitched *chip-chip-chip* call, slower than the usual twittering of courtship feeding, but of similar quality. She frequently looked up at the top of the trap. Her beak was open because of the heat, and her wings, held slightly out from the contour feathers, fluttered periodically during her struggles to get free. Her mate became noticeably excited, hopped around the cage giving a version of the mild alarm call, then hopped onto the cage, peering down at her. Her posture in the cage resembled vaguely that of a begging female (body crouched, head tilted back, beak open, tail slightly spread, wings drooped and fluttering), and this apparently provided an adequate stimulus to cause the male to feed her. He began to twitter and attempted to feed her through the screen of the trap roof, actually regurgitating. The female did not respond to his attentions, however, and he swallowed the food again, then wiped his beak. At this point, he was startled and flew away, whereupon the female was removed from the trap.

Nest building.—Pairs make investigating forays to prospective nest sites, then frequently return to a communal roosting tree to rest and preen for a few minutes before leaving to feed or look at nesting places again. In the Poultry Husbandry area of Strawberry Canyon, a single elderberry tree served as a communal resting place where several pairs of House Finches, along with Brown Towhees (*Pipilo fuscus*), Song Sparrows, and goldfinches, rested, preened, and sang. The birds did not, however, roost there at night and no nests were built there.

It appears that the female makes the final choice of nest site. The male may lead the female to several possible nest locations, sometimes carrying nesting material, but often he merely follows her as she moves from place to place examining sites which appear to be of general suitability. Sometimes the female carries nesting material while inspecting nest sites. Although there is considerable variation in the kind of place chosen by House Finches for a nest, it is usually built under the cover of a roof overhang or in dense foliage. One of the commonest nest locations is an ivy-covered wall, the nest often being built just under the eaves. A drain pipe or rafter just under a roof overhang is also a frequently used location. Where sites are not available on or in man-made buildings, dense foliage or cliffs may be chosen.

When a nest site is picked the female begins to collect nesting material. A great variety of materials may be used. It appears that the birds utilize almost any pliable material of appropriate size that is locally abundant. Dry grass stems, roots or leaves, and plant fibers stripped from the woody stalks of weeds or bushes are commonly used in the Berkeley area. Green vines and sprigs of Scotch broom (*Cytisus scoparius*) blossoms have also been found as nest components. Hair, feathers, cotton, string, thread, soft paper, frayed cigarette filters and very fine plant fibers may be used for the lining.

During the early part of the breeding season both males and females may be seen picking up twigs or grass, leaves, stems, or other material, but dropping them almost immediately, or carrying them only a short distance. This sort of behavior was also described for the Song Sparrow by Nice (1943). Captive, hand-reared juvenal birds perform the same action, picking up pieces of paper or feathers from the floor of their cage. In the male this behavior is continued through nest construction, whereas in the female it matures into actual nest construction.

The male accompanies the female on each trip she makes and may sit watching her, peck at the ground as if eating, or collect nesting material himself. Only rarely does he carry material to the nest, and then it is apparently not used in construction. My own observations differ in this respect from those of Evenden (1957) who reports active participation by males in nest construction. Grinnell and Linsdale (1936) suggest nest building by males. Their description of the male accompanying the female as she collects nest material, picking up material himself and sometimes carrying it to the nest, are in accord with my own, but I have never seen the male deposit the material carried in his beak on the nest. Usually he drops any object he has picked up before arriving at the nest, or he may take it into the nest, then come out still carrying it. Captive, adult males have been observed to follow the female onto the nest she is building, pick up the piece of grass she had just deposited, and fly off with it, sometimes returning it, sometimes not.

The frequency with which females bring material to the nest varies both throughout the day and with the stage of construction of the nest. During the early part of nest construction the female of pair 4 (1958) returned to the nest at intervals of one to three minutes for most of the morning. Spurts of fairly intense nest building alternated with periods of rest, particularly in the afternoon hours, when the frequency of carrying material to the nest dropped off considerably. Two days later, when the nest was about finished except for the lining, female 4 returned every ten to fifteen minutes, with some shorter intervals during spurts of intense building. Female 3, whose nest was discovered while she was lining it, likewise returned to the nest about every ten minutes, remaining on it from one to five minutes to work the plant fibers into the nest cup. Female 8, in the early stages of construction, brought nesting material on the average of every 3.5 minutes for 30 minutes or so, then was away for 15 to 20 minutes, after which she resumed her building. The data are insufficient to make more than an estimate of the time consumed in nest construction, but it appears that about four to seven days elapse between the beginning of nest building and the laying of the first egg. After the first egg or several eggs are laid, materials may be added to the nest.

Three caged females built complete nests. One of these repeatedly attempted to construct a nest in one corner of the cage, but the grass kept falling off the platform. A larger support was provided and a pile of grass crudely arranged in the form of a nest was placed upon the platform. The female took possession almost at once, crouching and twisting her body in short arcs to mold the cup and rim, and adding a lining to the cup. Seven days later the first egg was laid. Similar crude nests were provided in each of the other cages, but in every case the pair owning the nest site pulled out this artificial nest,

even if it was firmly attached to the platform. Some individuals later began construction on their own, some did not. One female repeatedly attempted to construct a nest. At times she would bring a piece of grass to the nest site, place it on the pile of material already in place, go off the nest, approach it by another route, and take off the same piece she had just deposited. This deposition and removal of a single item was continued for several minutes, then the material was dropped to the ground, and the bird fed or preened for a few minutes before resuming her attention to the nest. She frequently performed the crouched, twisting movements of molding the nest cup, even when there was very little material present to mold. Indeed, she sometimes appeared to be performing the movement on the bare platform with only a few isolated pieces of grass at the edge.

This same female was plagued by the depredations of her mate. He followed her onto the nest and disarranged the material she had just arranged, sometimes removing some of it. Both birds inspected the nest frequently without adding or removing anything. This nest was never completed.

House Finches almost always build a complete new nest for each brood. There are records of their use of the nests of other birds. Shepardson (1915*a*, 1915*b*) notes the laying of House Finch eggs in nests of the Black Phoebe (*Sayornis nigricans*), Cliff Swallow (*Petrochelidon pyrrhonota*), and Hooded Oriole (*Icterus cucullatus*). Robertson (1931), Hanna (1933) and Hensley (1959) recorded the parasitization of House Finch nests by cowbirds.

Copulation.—Copulation begins during the later stages of nest construction, several days before the first egg is laid, and recurs several times each day until the clutch is completed. It usually takes place in the early part of the morning. Marler (1956) describes its occurrence in the Chaffinch as in the very early morning shortly after sunrise. House Finches in Strawberry Canyon do not generally become very active until an hour or so after sunrise. Blanchard (1941) reports the occurrence of copulation in the White-crowned Sparrows (*Zonotrichia leucophrys*) throughout the day but most frequently during the half hour before sunset.

Egg laying and incubation.—Eggs are laid early in the morning. They are laid on consecutive days until the complete clutch of three to seven eggs is finished. Bergtold (1913) reports the average clutch in Colorado as being four with a range of two to seven. Evenden (1957) gives 4.2 as the average clutch size, with a range of four to six, on his study area in Sacramento, California. The nests examined in Strawberry Canyon averaged 4.7 eggs per clutch, with a range of three to six.

Bergtold (1913) mentions a special call used by the female while laying and distinguishes this from the call note given by the female while she is incubating. I have been unable to make such a distinction.

Michener (1925) reported a case of polygyny in which a male and two females "worked together" to build a nest. Ten eggs were laid; one of them was crowded out of the nest. Finally one female left the area and six of the eggs hatched.

On the day the first egg is laid the female may spend some time on the nest, apparently incubating. Certainly incubation begins before the last egg is laid. Evenden (1957) found the female on the nest only very early and late in the day during the early part of the laying period, but as the clutch neared completion she remained on the nest for increasing periods of time and sometimes began full-time incubation the day before the last egg was laid.

There is sometimes a marked difference in the size of young House Finches in a single nest, although Evenden did not find such a difference in the nests he studied. It is possible that this size difference, when present, is due to brief intervals of incubation

before the clutch is finished. Precise hatching dates and times are needed to answer this question about House Finches. Nice (1943) reported that the female Song Sparrow usually begins incubation the day before the last egg is laid. Marler states that the female Chaffinch may sit on an incomplete clutch up to 30 minutes after bringing material to the nest.

On the nest the female utters a soft *chee-chee-chee, chee-chee-chee* continuously, the notes characteristically in groups of three with pauses between groups. There is some variation in pitch, but the general impression is that of a monotone. The dynamic variation, however, is more marked. The reason for this variation is not apparent. The call seems to serve as communication between the female and her mate. On two occasions incubating females were heard calling softly in this way, then increasing both volume and to some extent frequency of the notes. When caged females produce this call, it usually incites the male to strenuous chasing of the other birds in the cage.

Bergtold (1913) gives the incubation period for Denver as 14 days, sometimes more (up to 17), rarely less (13). Keeler (1890) reports the incubation period as 13 days. Evenden (1957) records a mean incubation period of 13.27 days, with extremes of 12 to 16 days.

While the female is incubating the male spends most of his time feeding and preening, often in company with other males. Some females whose first nesting attempts have been unsuccessful or which have not begun nesting may join these largely male assemblages in feeding areas often some distance away from the nest location. These assemblages resemble those of autumn and winter in their loose organization. One such company of 20 to 25 birds observed at the Hastings Reservation in June, 1958, moved as a loosely integrated flock feeding on the ground in a recently cut field. There seemed to be units of two or three birds which stayed close together. Feeding and resting periods were broken for males by occasional trips to an elevated perch to sing. Once the entire group flew up, circled back and alighted on power lines and adjacent trees. After a few minutes of singing and preening the flock, composed primarily of males, but with a few females as well, moved back to the ground to continue feeding. First one bird, then several, then a few more flew down from the elevated perches, until the entire group was on the ground again.

During the incubation period the male stays away from the vicinity of the nest most of the time, and almost never is heard to sing near it. He does come regularly to feed the female, at least during the early part of the incubation period. In most observed instances the female did not leave the nest until called from it by the male or unless she was frightened off. The male flies to a perch a few feet from the nest and calls *cheep, cheep,* slowly and softly. Some females fly out at once to be fed, but others wait for several minutes before they leave the eggs. In only a few instances was the female fed on the nest. Usually the male accompanied the female back to a perch near the nest but seldom went to it himself. If for some reason the male did not come back within about an hour, the female might fly off on her own to look for food, or she might remain sitting for a longer time than usual. One female was observed to stay on the nest for two hours. Her mate rarely summoned her to be fed, and she frequently left alone. This individual was well along in incubation, and it may be that the male attends the female less regularly at this time. There is considerable variation from pair to pair in this regard.

Most pairs begin nesting and hence reach the incubation stage at about the same time. The males tend to aggregate at feeding areas during the intervals between feeding of females at the nest, and perhaps for longer periods if, as has been suggested, this regular feeding of the female breaks down in the latter part of the incubation period. Some pairs begin nests but do not lay eggs or may not incubate them if laid, and these

pairs may join the male flocks to forage. During the breeding season these sizeable flocks are often encountered in open fields or other suitable feeding areas.

At this time of year, also, communal roosts in dense foliage may be used by the males and non-nesting females. The male of a pair may roost near the nest, but more often he roosts at some distance from the nest, as Evenden (1957) points out. On the Strawberry Canyon study area, the dense foliage of three *Eugenia* trees served as a roosting place for more than 20 birds a night during late spring. Individuals slept within three inches of each other, and there was much chattering and supplanting as the birds settled down just before dark.

Hatching and care of young.—Evenden (1957) notes that the female remains on the nest much of the time for the first few days after the young hatch. This was also true for nesting observed in this study. After this time, however, the young are brooded very briefly, if at all, at the time of feeding. At two nests beyond brooding stage, at which observations were made intermittently, feeding occurred about every 30 minutes (15 records of intervals). At some nests the young are fed almost exclusively by the female, whereas in others the male may also take an active part. The male fed the young at a nest which was watched for ten hours, starting at 8:10 a.m. on April 23, 1955. The nest contained five young about seven days old. The female fed 10 times, the male 13. Feedings occurred at about 25-minute intervals. The interval away from the nest was about 55 minutes for both male and female (57.6 and 54.7 minutes, respectively). The female remained on the nest to brood the young for an average of 5.1 minutes, whereas the male remained at the nest an average of less than a minute. Evenden also found both parents feeding, but Keeler (1890) reports only the female feeding young. The male of one pair in Strawberry Canyon fed the young alone after his mate disappeared when the nestlings were a week old. The nestlings are fed entirely by regurgitation, as are the begging adult females. Apparently no insect or other animal food is brought either to adult females or to nestlings. While the parent is feeding them the nestlings produce a rapidly repeated, high-pitched, but soft, *cheep*, *cheep* call.

Evenden (1957) found young leaving the nest from 12 to 18 days after the date of hatching. His observations give an average initial flight of 49.3 feet with extremes of 12 and 125 feet and an average gain in altitude of 1.6 feet. My own more limited observations were as follows:

Date	Distance	Height gain or loss
June 11	15 ft.	+ 3 ft.
June 13	15	+ 3
	40	+10
	15	− 1
Averages	21	+ 3

In each instance the bird flew to a nearby perch. In one, the fledgling followed the female parent from the nest and settled down near another adult. The initial flight distance undoubtedly varies with the surroundings of the nest. The young are not usually enticed off the nest, but they may follow one of the adults as it leaves. In three instances, the young left with no apparent external provocation. After leaving the nest, fledglings begin to *cheep* softly. They beg from any adult which comes near them. They hop or fly directly toward the adult, or even toward other juveniles.

Post-breeding activities.—It is not known what happens to the young just after they leave the nest, but they probably do not join large feeding flocks during the several weeks when they are fed by both parents. Later on juveniles and adults may assemble where food is plentiful. On July 8, 1958, the hills east of the Poultry Husbandry area,

on the south side of Strawberry Canyon, were covered with dense stands of thistles bearing ripe heads. About half an hour before sunset a large aggregation of 200 to 300 birds was seen feeding on the ripe seeds. Most of them were adult and juvenal House Finches, together with a few Brown-headed Cowbirds (*Molothrus ater*) and American Goldfinches (*Spinus tristis*). The ratio of adult male-plumaged to female-plumaged House Finches was approximately one to five. Birds with female plumage may be either adult females or juveniles of either sex. There are differences in the degree of wear of the feathers of an adult female and a juvenile at this time of year, but from a distance these differences are not apparent.

Every few minutes a small segment of the aggregation, 10 to 20 birds, would become alarmed and fly up, but they would settle down almost immediately a short distance from their original feeding locality. Although the intervals between individuals were short, only two to four inches in many cases, there appeared to be no aggressive behavior whatsoever—no pecking, no supplanting.

After sundown the assemblage began to disperse. Singly and in groups they left the feeding area, flying down the canyon, some going toward Berkeley, others going over the southwest ridge toward Oakland. One large group of 50 individuals and other small groups of two or three, flying down the canyon toward town, met and passed other birds flying up the canyon to the feeding area.

Salt (1952) mentions that the large autumn aggregations may move to elevations higher than their breeding areas and then move back down as winter progresses. During mid-October the number of House Finches to be seen in Strawberry Canyon decreases markedly, and by November the species is scarce. In residential areas of Berkeley, Oakland, and adjoining towns, the House Finch population seems to change little with the seasons. Birds in town may spend the winter on or near their breeding area and do not gather in large flocks, although small groups of birds are often seen. Usually rural flocks, also, are of small size, perhaps because the local concentrations of food which attracted large numbers of individuals into small areas in the fall are not available and because food is more widely dispersed during the winter.

Molt.—The Micheners (1940) give the period of molt in the vicinity of Pasadena, California, as May 1 to late November. In the Berkeley area, however, molt appears to be more restricted to the period from September through early November. For an individual the molt lasts about 105 days, varying from 90 to 120 days. Most males assume the adult male plumage at the time of the postjuvenal molt, but some (van Rossem, 1936) retain the female pattern through the first year. The latter condition is more typical of the other members of the genus, including the American species, the Purple Finch (*Carpodacus purpureus*) and the Cassin Finch (*C. cassinii*), as well as most Eurasian species (Dementiev, 1954).

Figure 1 summarizes the sequence of events in the annual cycle of the House Finch in the San Francisco Bay area.

Comments on nesting success and timing.—Of 11 nests begun in the Strawberry Canyon study area, 10 were completed. Eggs were laid in at least eight of these, and incubation was begun in all eight. All but two nests were abandoned after a few days of incubation. Eggs had disappeared from three when they were found to be abandoned. Small mammal nests were constructed over three of the deserted structures, in one nest on top of the eggs. More hair, paper, fine plant fibers, and other soft materials were added to the lining and a roof was constructed of the same materials. The owners were never identified. Probably feral house mice (*Mus musculus*) were responsible.

The eggs of only two nests were known to hatch. The young of one nest fledged but were fed rather irregularly by the male parent only and left the nest prematurely, ten

days after hatching, remaining for several days in vines below the nest. Their fate and that of the other young was unknown.

It is possible that high density of breeding pairs on an area so small as that used in Strawberry Canyon made nest robbing easier for whatever it was that destroyed clutches and caused nests to be abandoned. Steller Jays (*Cyanocitta stelleri*) are abundant in the area and are on record as nest robbers (Bent, 1946) although not specifically as robbers of House Finch nests. Cats are common, but most nests were probably out of their reach. Nests were located on an average of about 30 feet apart, with some in clusters much closer together. Of the nests begun during the five-year period of his observation, Evenden (1957) found 48 per cent destroyed or abandoned.

During 1958 there was evidence of second broods at the Hastings Reservation, but in the Strawberry Canyon study area there was no evidence of more than one nesting, although Keeler (1890) reported that two broods are produced in the San Francisco Bay area. For several weeks after most of the nests were abandoned near the end of April, House Finch activity in Strawberry Canyon was greatly reduced. Very few birds were in evidence, and very little singing was heard. On May 22, however, there was a heavy rain during the night. The following day was clear and warm, as in the early part of the breeding season. Several pairs investigated vines as if seeking nest sites, and several males were singing vigorously. It was at this time that nest eleven was begun. After several days this activity again declined. Sporadic interest in nest sites continued into June, but no new nests were found on the study area.

During the spring of 1959, heavy rains were over by April 1. Nesting was underway by April 9 and continued until early July. There were no breaks in nesting activity such as were observed in 1958, and song and activity of House Finches around nest sites continued for a longer period in 1959. The cessation of activity coincided with the onset of the foggy mornings which are characteristic of Berkeley summers. In 1959, the weather

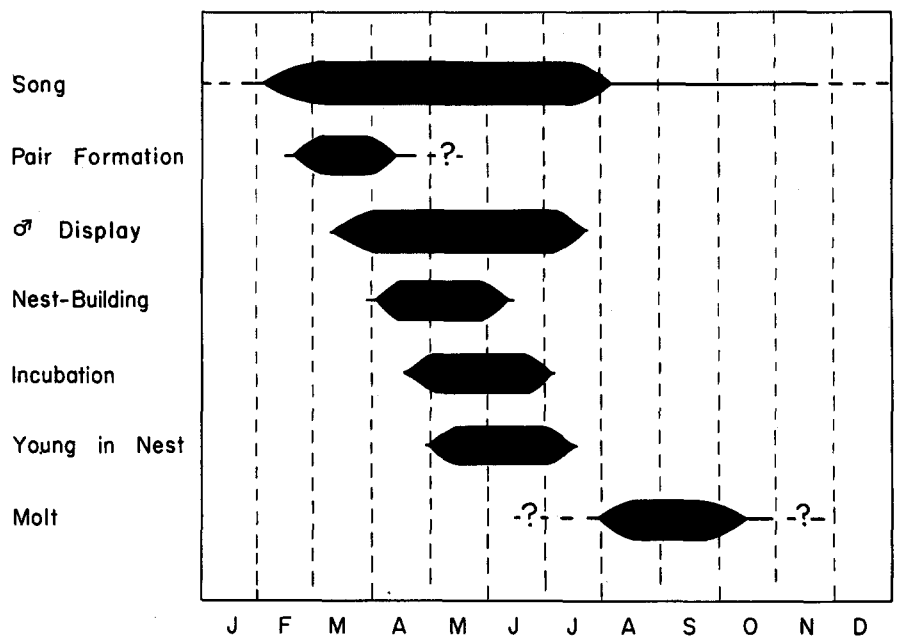

Fig. 1. Sequence of events in the annual cycle of House Finches in the San Francisco Bay area.

was unusually warm and clear during May, June, and early July. An explanation for the nesting calendar of 1958 therefore presents itself. Nesting began to wane in late May as a result of cool, foggy mornings during which song and breeding activity were noticeably decreased, and the second surge in breeding activity in June of 1958 may be explained as a result of a break in the series of cool, overcast mornings which inhibited nesting activities. The recurrence of foggy mornings a few days later terminated the breeding season in the study area.

The surge of breeding activity after the early April rains in 1958 may be interpreted as a result of delay imposed by the heavy precipitation. Photoperiodic influences may be supposed to have brought many of the birds into breeding condition before the end of the week of rainfall, but the unfavorable weather inhibited the building of nests. John Davis (personal communication) tells of having observed similar increase of nesting activity of Brown Towhees after heavy rains had prevented nest building. Observations of nest building in 1959 indicated that several pairs of House Finches began to build at about the same time but not with such synchrony as in 1958. The return of clear weather after the last heavy spring rain that year apparently served as a stimulus for several pairs to begin at about the same time.

PATTERNS OF AGGRESSIVE BEHAVIOR

The term "aggressive" refers strictly to attack, whereas the term "agonistic" includes escape, defense, and passivity, as it was defined by Scott and Frederickson (1951). Both terms will be used throughout the discussion in a fairly strict sense.

Supplanting attack.—The simplest and most direct form of hostile behavior is supplanting attack. One bird flies to the perch where a second is sitting, flying directly toward the second individual or to a point just beside it. The second bird usually flies or moves away before the aggressor alights. Occasionally the attacker is itself attacked by the perched bird, and violent combat usually follows. Marler (1956) describes how the attacking Chaffinch fixates its victim, calls, may tail-flip, and then flies to attack, but there is seldom any evidence of special behavior prior to supplanting attacks of House Finches. Likewise the victim shows no sign of fear or avoidance before moving, unless it has been chased or supplanted by the same individual just previously. Occasionally the sequence similar to that described for the Chaffinch may be observed in the House Finch in captivity, but it has been observed only rarely in the wild. Like the Chaffinch, House Finches show little sign of conflict in their behavior, either as aggressor or victim, and no displays result from supplanting attacks, except for the infrequent occasions on which the attacker misjudges its victim and is itself supplanted by the intended victim.

Often supplanting attacks occur without accompanying call notes, but occasionally the attacker will employ the *chit-chit* call characteristic of "head-forward" displays and attacks (table 2). Supplanting attacks occur most often at feeding places but may also take place at favorite perches, or in the territories established by breeding pairs in the spring. When the attack is made at a feeding place the primary incentive seems to be the food itself, rather than attacking the victim. In territorial defense, however, the intruder becomes the main incentive. Some birds appear to be unusually aggressive and interrupt feeding to supplant others several feet away.

As Marler (1956) and Hinde (1955–1956) suggest, a supplanting attack is often a more confident expression of hostility than any other form of aggressive behavior. The attacker does not hesitate to fly directly at another bird. If it does hesitate, it pauses in an intention movement of flight toward the opponent, which produces the display described below as the "head-forward" display.

Table 2

Summary of House Finch Postures and Associated Call Notes

Posture	Call notes	Circumstances in which given
Aggressive or avoidance		
Supplanting attack	"chit-chit," or "cheee"	At limited food source or favorable perch
Head-forward	"chit-chit," "cheee," or "tzeep"	At limited food source or favorable perch
Actual combat	"chit-chit," or "cheee"	Failure of "victim" to yield to attacker after head-forward display or supplanting attack
Beak-fencing	"chit-chit," or "cheee"	Failure of "victim" to yield to attacker after head-forward display or supplanting attack
Avoidance	none	When perched near a superior
Fear reaction	"zeet" (very soft)	When frightened by a loud noise or some other disturbance
Struggling to escape	"keeeeet," or "ahnn....."	When caught or held, or fighting while confined in a small space
Non-aggressive		
Begging by female or fledglings	"chee-chee-chee"	Young off nest, or female before and during incubation
Billing	twitter	Courtship, pair formation
Perching, legs extended	"keet," "coot," or "kweet" (interspersed with other call notes or given alone)	Curiosity, or mild alarm
Perching upright	"cheeup"	Mild alarm, isolation, location of companions. Sometimes given in chorus.
Courtship display, dance	song, with stressed "tzeep"	Courting strange female
Song flight display	song	Flying from one song post to another. Rarely used before supplanting another male.

Head-forward display.—A common form of hostile display between perched birds is the head-forward display (Hinde, 1955–1956; Dilger, 1956). Depending on the circumstances and the degree of hostile motivation, the display may take several forms. Two arbitrary positions in the gradient of postures from no hostility to extreme hostility will be described. These are referred to as (a) low intensity head-forward display and (b) high intensity head-forward display.

(a) Low intensity head-forward display. The body of the aggressor is slightly tipped toward the horizontal (see fig. 2A). The legs may be flexed slightly more than is usual when standing, the neck is stretched toward the bird about to be attacked, and the beak may or may not be opened. The wings usually remain in place partially covered by the contour feathers. The body feathers are usually sleeked, but occasionally, particularly if the attacker is a female, the breast, forehead, back, and upper belly feathers will be "shuffled," to use the term suggested by Moynihan and Hall, 1954 (see fig. 2B). The bird may hold this posture momentarily, then move toward the other individual if it has not moved away at the first sign of head-forward display.

Usually the low intensity head-forward display is accompanied by no vocalization. It occurs most frequently when a bird of lower rank comes too near a superior at a feeding place, or on a perch, violating the minimal limits of individual distance, an area around the individual which is free of all others. Individual distance, as described by Conder (1949), is a variable quantity in the House Finch, which changes according

to the "mood" of the bird and the circumstances. Birds may roost in contact with each other, although usually there is some space between them. In the daytime, however, the minimum individual distance observed in resting birds is about 15 centimeters. Individual distance of males increases during reproductive activity and when a male is near his

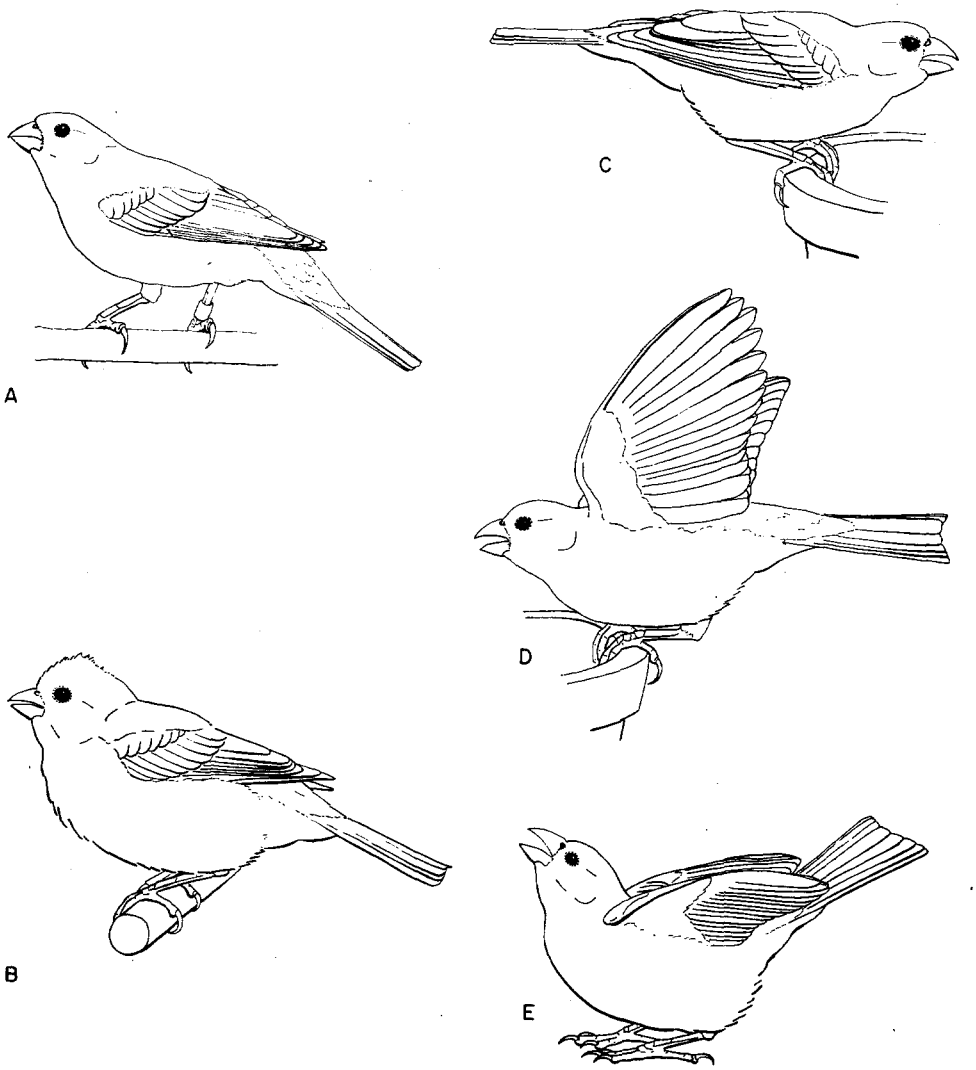

Fig. 2. A and B, forms of low intensity head-forward display; C, D, and E, forms of high intensity head-forward display.

mate he may supplant another bird that comes within 15 to 20 feet, or even more. Territorial behavior is extremely variable in any one individual from one time to another.

(b) High intensity head-forward display. The body of the aggressor is held in a horizontal position, the legs flexed to such a degree that the tarsometatarsus is almost parallel to the axis of the body (see figs. 2C and 4B), the neck is stretched forward along the main axis of the body, and the beak may or may not be opened, but it is not snapped.

Usually the beak is opened at higher levels of aggressive motivation. The wings are usually held folded over the back in a normal resting position, partly covered at the wrist. Body and head feathers are usually sleeked, although rarely the shuffling feather posture may be used, as with low intensity head-forward displays. Tail, body, neck, and head form a straight line pointing at the bird which is being attacked. If the bird being attacked is above the attacker, the straight-line posture is changed, so that the head is pointed toward the second individual (see fig. 2E). When the head is raised, the tail feathers also may be raised slightly above the usual horizontal position. If the second bird does not yield at once, or if it offers a counterattack, the first usually lunges forward, either supplanting the other, or engaging in combat with it. Marler (1956) suggests that head-forward display as it occurs in the Chaffinch is associated with a conflict of some sort. As in the Chaffinch the most extreme form of House Finch hostile display occurs in the high intensity display and is apparently associated with conflicting motivation (see following). This display usually occurs at feeding stations or in cages where the individual distance may be violated.

A loud, harsh *chit* call is given during aggressive display. It appears to be a very abbreviated form of the customary flocking call. One female used a harsh *tzeep* or *tzeet* call when attacking other birds.

The most intense form of head-forward display is sometimes accompanied by a complete or partial extension of one or both wings (see fig. 2D and 4D). The wings may be fully or only partially extended. The wing is rotated at the shoulder and extended at both elbow and wrist, or only at the elbow. Sometimes the wings are just lifted from the supporting contour feathers and held in a horizontal plane, still folded. This is accomplished by rotating the wing at the shoulder but not extending the elbow or wrist. Wing raising is a flight intention movement commonly associated with high intensity head-forward displays (Hinde, 1955–1956; Marler, 1956).

Combat.—If a bird which is supplanted or which is attacked by another in head-forward display resists the attacker, actual combat may result, or the attacker may yield at once and move away. Usually combat consists in the pair's hovering in mid-air, loudly and rapidly calling *chit-chit-chit*, each pecking vigorously at the other's beak, and grappling at the opponent with the claws (see fig. 3C). Sometimes combat between males leads to vigorous singing by the winner or by both combatants after they separate.

A less violent form of combat is "beak-fencing," which is less common than the struggles just described. It is much like the "billing" which occurs during the early part of pair formation, but it is much more vigorous, and usually occurs between birds of the same sex. It, too, is usually accompanied by loud calling consisting of a sharp *chip* note given in variable series.

Physical combat is of relatively rare occurrence between House Finches, but it sometimes occurs in the early stages of a change in hierarchical status among caged birds, or in dispute at feeding stations among wild birds. It is of short duration when it does occur, and no serious injury seems to result.

Billing is a gentle pecking by a male at the bill of a female. It appears to play some part in the establishment of a pair bond. It gradually evolves into courtship feeding as the pair bond becomes stronger. The details of this transformation have been described earlier.

Avoidance.—There is no certain posture associated with avoidance behavior—one bird simply moves out of the way of another which is attacking or supplanting it. There appears to be no raising of feathers along a large part of the dorsal and ventral tracts as Marler (1956) describes for the Chaffinch, and there is very little evidence of the "shifty" gaze which the Chaffinch displays. Birds which are subordinate in the hierarchy

tend to stay out of the way of dominant individuals. If it eats at a feeding tray near a superior, a bird will pick up bits of food with quick lunges at the food source, withdrawing its head to eat, and often leaning or facing slightly away from the superior. Often a given individual will stay away from food or water, only just a few inches away, in order to avoid a superior. It is often possible to obtain a good estimate of a hierarchy

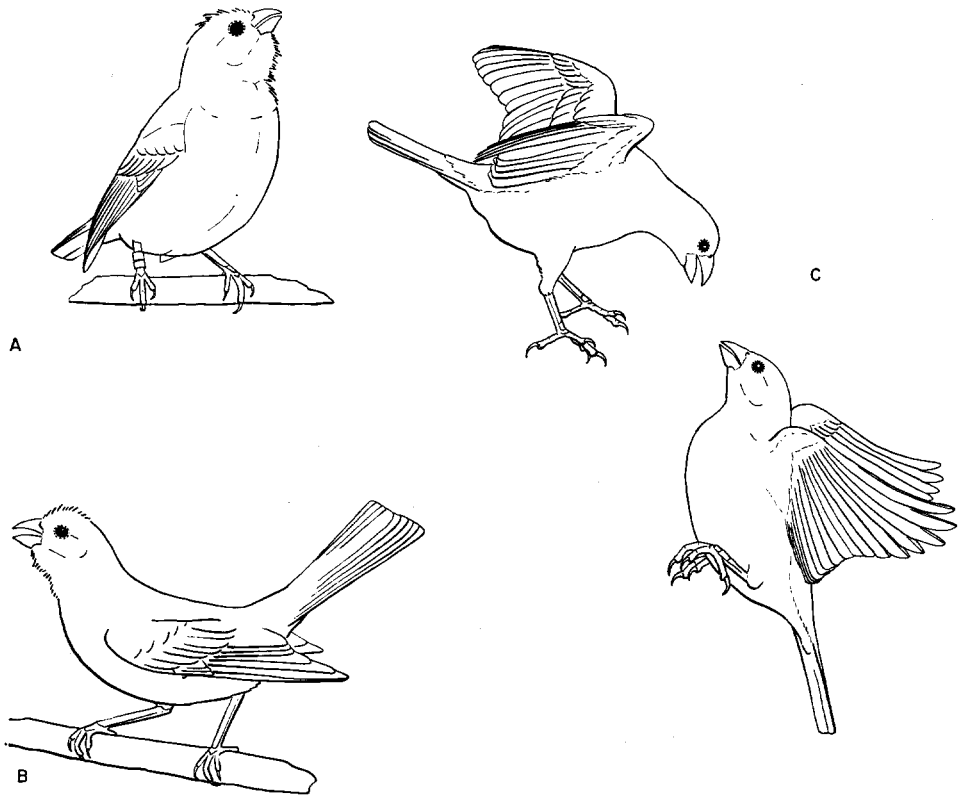

Fig. 3. A, typical song posture of male House Finch; B, "courtship" display posture of male House Finch; C, combat between two House Finches.

by noting the avoidance of certain birds by others, as well as the pecking or supplanting of some by others. Avoidance behavior is noted most often at feeding places or at water, wherever birds gather together. Marler has noted (1955) that avoidance behavior tends to be discarded during a period of severe hunger. A bird will endure much more abuse from a superior if starved.

As would be expected from a bird trying to remain inconspicuous and out of the way of another, no calls are associated with avoidance behavior.

Fright response.—The most frequently observed fright response in the House Finch is flight from wherever the bird was disturbed to an elevated perch nearby if the fright was mild, or to some distant place if the fright was severe. Occasionally a bird will crouch, with body noticeably tensed, neck extended slightly so that the head points forward in line with the body axis, and feathers sleeked. The posture is almost identical with the posture of an intense head-forward display. It is so little ritualized that it should be properly called a flight intention movement rather than a formalized display posture as is the head-forward display. Both postures have undoubtedly developed from

the same motor activity—flight takeoff—but are released by different stimuli. The fright reaction is often accompanied by a very soft *zeet*, sometimes given by only one of a group of birds.

Another possible expression of mild fright is an extension of both legs and the neck, so that the bird assumes a stiff-legged, erect posture (fig. 4A). This is a silent reaction which usually gives way to a more relaxed position and the usual conversational call notes, or to flight.

If a bird is caught and held in the hand it often utters a loud and nasal-sounding *ahnn-n* while it struggles to escape. Sometimes when several birds are confined in a small container they will fight, and one, apparently the loser, will utter this same sound.

Conflicting motivation.—Head-forward display is often accompanied by ruffling of the feathers of one or more parts of the plumage. Hinde (1955–1956) and Marler (1956) suggested that for other passerine birds this denotes a conflict in motivation, often between attacking and fleeing. The most vigorous head-forward displays of the House Finch are given in circumstances which suggest that there is some such conflict whenever the head-forward display is given instead of a direct supplanting attack. The forehead feathers are the ones most often ruffled when there is conflict between fleeing and attacking or feeding, or other tendencies. At times, however, the feathers over most of the body may be ruffled. It has been mentioned that attacking females sometimes ruffle during head-forward display (see fig. 2B). A caged, incubating female had occasion to chase intruders from the edge of her nest several times. Here the conflict might be between incubating and attacking. Other birds of both sexes which have ruffled plumage while in head-forward display might have had conflicting fleeing and attacking tendencies.

The forehead feathers alone may be shuffled while a bird is feeding near an observation window where the observer is partly visible. Here the conflict would be between eating and fleeing. In the sexual display of the male the forehead and throat feathers are shuffled, and the rest of the display probably involves a conflict between fleeing and sexual tendencies, but these same feather tracts are also shuffled when the male sings by himself with no apparent cause for conflicts between either hostile, sexual, or fleeing tendencies. The motivation of this feather posture is undoubtedly related to the motivation of song, which at the present time is a much debated, but little understood phenomenon. Full House Finch song, whatever its motivation, does involve a considerable expenditure of energy and emotion, and this may involve sympathetic "pilomotor" activity as Morris (1956) describes.

Likewise, wing extension appears to be associated with conflict. Hinde (1955–1956) suggests that it is an expression of extreme hostility, and it does occur in the House Finch in circumstances which involve extreme hostility, but still there must be some element of fear, or tendency to flee, else the bird would attack without display, as is customary in the relationship of a high-ranking individual toward one lower in the hierarchy. If there were not some conflict, the intention movement of flight (wing raising and extension) would immediately be completed as an actual flight toward the opponent.

Head-forward displays are most often given toward strangers of the same or different species, or after long continued supplanting of members of a known group. In either case there is probably a conflict between attack and some other tendency—in the first, perhaps an uncertainty as to the aggressiveness of the opponent and fear to press an attack too fast; and in the second, increasing weariness and a desire to rest.

SONG

For the House Finch, song does not appear to have the strong connection with territory which it has for the European Robin, *Erithacus rubecula* (Lack, 1943) or the Song

Sparrow (Nice, 1943). Several males may perch in one tree, some preening, some chirping, and some singing loudly. In cages one bird may sing loudly for several minutes without receiving any special attention from his superiors in the flock hierarchy. At other times, however, a singing captive male may be chased by his superiors. House Finches were never seen to engage in song duels at the territorial boundaries such as are described for other species by Nice (*op. cit.*) and Lack (*op. cit.*). Usually, however, singing

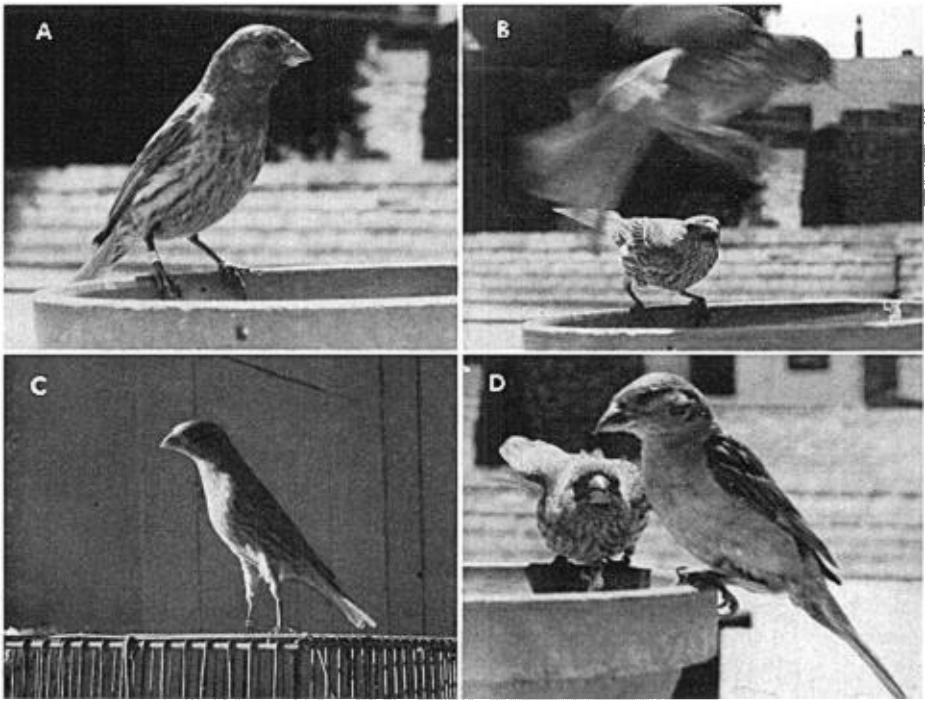

Fig. 4. A, stiff-legged erest posture of mild fright; C, stiff-legged erect posture of extreme fright; B and D, two forms of high intensity head-forward display. In D the female House Finch on the left is displaying toward a female House Sparrow.

individuals are spaced at greater intervals than individuals which are not singing. Males may sing as close together as 25 feet apart without interference, but one often supplants the other if they are closer to each other. Likewise, if two birds are singing simultaneously in a cage, one usually supplants the other.

The song of the House Finch may be described as a rambling warble, ending, when given with full intensity during the breeding season, with a final *tzeep*. This end syllable is given with a rising inflection. A sonogram of a characteristic House Finch song is illustrated in figure 5.

After a period of silence lasting several weeks during the molt, from about the end of July through the middle of September or the early part of October, relatively weak and incomplete song is heard irregularly from adult males. From then on it wanes but does not cease entirely. During most of the winter sporadic singing, usually by single males, may be heard during the day. It is heard more commonly on the lower campus of the University of California than in residential areas of Berkeley, although House Finches are still present in the residential areas. The song given at this time is less

vigorous than that of the breeding season and lacks the ending *tzeep* which is characteristic of spring song.

In the San Francisco Bay area House Finch singing begins to increase in early February. In residential areas the birds may group together in flocks, singing, preening, and feeding. During this period, song may be very loud and vigorous. The bird flies from perch to perch, almost as if claiming a territory, but no hostility is evident between individuals. A male may sing from a tree in which several other males are resting, without showing any aggressive inclinations toward them and without evoking any overtly hostile responses from them.

A male singing with full intensity stands in a posture characteristic of many passerines. Usually the tail is raised just above the line of the body axis, the head is tilted slightly and the beak is opened, sometimes partly opening and closing rapidly with the rhythm of the song. The wings usually are held in place under the body feathers

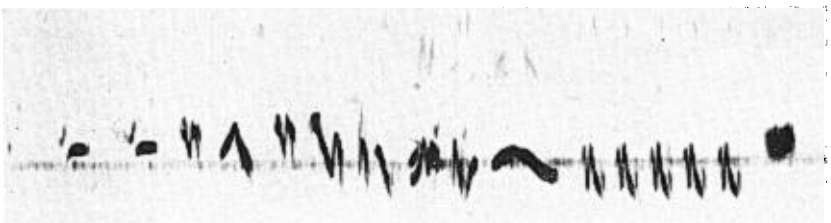

Fig. 5. Sonagram of complete adult male House Finch song, recorded by P. R. Marler. Duration, 2.1 seconds; frequency extremes, about 2000 and 5000 cycles per second.

(see fig. 3B) but rarely may be slightly drooped. The feathers of the chin and forehead are ruffled. Often the bird turns slightly from side to side with the rhythm of the song. Winter song and much of the singing done during the breeding season are given with lower intensity, lacking the final *tzeep*, and usually are shorter and softer than song of full intensity. When singing this "incomplete" song the bird usually perches with legs flexed in a normal perching posture, or it may be squatting on a perch resting the body on the feet, with feathers slightly fluffed. This posture is often observed in birds singing during mid-afternoon.

Females, too, may sing the "incomplete" song, most often during March and April. A hand-reared female kept indoors and exposed to a rather irregular schedule of illumination sang often during November and December. One captive female was repeatedly observed to sing softly, sitting on one foot, with her eyes closed. Female song has been observed in several different situations in the wild. In caged birds it was noted most often while the bird was resting. Wild females have been observed to sing both while alone and in the company of the mate, but in either situation it is of rare occurrence.

Males frequently sing or call while flying. A bird may fly long distances between song perches, giving a burst of song just after taking off. During such long flights the song may give place to the *cheep* call. When males are released after being banded or trapped, they often sing loudly during the flight from the trapping station. On several occasions females were observed to sing upon release.

Occasionally "song-flight" displays are performed by male House Finches. Usually these are short flights from one prominent elevated perch to another. The bird flies slowly with a "butterfly flight" such as is described by Conder (1948) for Goldfinches, Hinde (1955–1956) for canaries, and Marler (1956) for Chaffinches. The wings appear to be held more rigidly than usual and do not seem to make a complete downstroke. For the last 20 feet or so the bird glides with wings spread and held slightly above the hori-

zontal, still singing vigorously. Song flight has been noted early in the spring, before many birds were associating in pairs, and in June after the first broods had left the study area. The display appears to be performed most often, if not exclusively, by unpaired males. It is not associated with aggressive activity toward other males, as is the song flight of the Snow Bunting (Tinbergen, 1939), although on one occasion a male was seen to use this display when supplanting another male.

Marler (1956) describes a "whirring flight" used by Chaffinches when flying in very dim light or darkness. This type of flight is also used by House Finches under similar circumstances, as when they are disturbed at the roost.

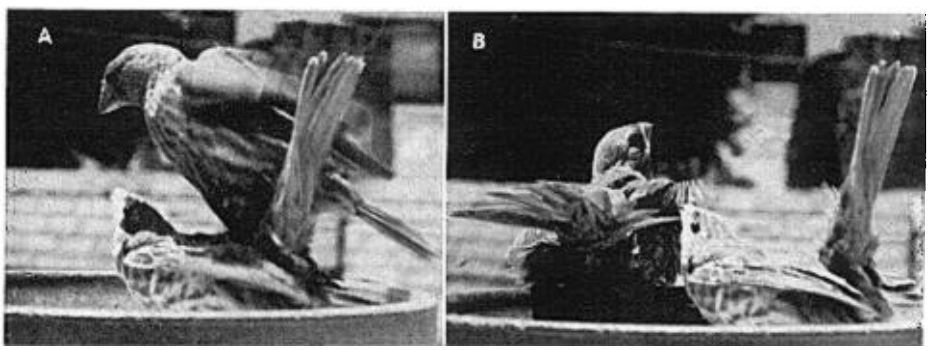

Fig. 6. A, copulation of male House Finch with dummy female; B, postcopulatory display of male House Finch beside dummy female.

COPULATION AND SEXUAL DISPLAY

Copulation itself does not appear to involve conspicuously overt elements of aggressiveness. The male House Finch, however, performs a display toward the female which evokes a hostile reaction from her, and since this display appears to be related to copulation, behavior leading up to and including copulation will be considered here.

Copulation normally occurs at the invitation of the female. Typically she pauses on a perch several feet from the nest, before entering with nesting material which she carries in her beak. The male is usually on another perch several feet away from her. She raises her tail to a vertical position, droops the wings and vibrates them as in courtship feeding, and retracts the neck slightly, at the same time tilting the head back, so that the beak points upward. The male may not notice her at once, and if he does not within a few seconds, she may resume a regular perching posture, fluff, shake, and proceed to carry her materials to the nest, or she may fly to another branch and repeat the invitation. If the male does see her, and he usually does, he flies to her at once, hops onto her back, his abdominal feathers fluffed, flaps his wings to maintain his balance, leans back, his tail pressed against the underside of hers, and apposes his cloaca to hers (fig. 6A). When he hops off or falls off, both birds may resume a regular perching position, fluff, and shake. The female then usually goes onto the nest. Frequently, however, the male, as soon as he hops off the female's back, especially if the copulation has been complete, assumes the same crouching posture as the begging female or juvenile—legs flexed, body held horizontal, feathers fluffed, tail slightly raised, and wings drooped and fluttered, head held back, but slightly up, uttering a soft twittering (fig. 6B). On two occasions the female then mounted and went through the motions of copulation, lowering her tail, flapping her wings to maintain balance, and touching the male cloaca with her own. After copulation both birds fluff their feathers and shake. The male may then preen, while the female flies to the nest to work into it the material she still carries in her beak.

Twice a male was seen to attempt copulation with a strange female which was preening and shaking her feathers. She was pulling her primaries and breast feathers alternately, shaking her body with tail held up, and wings fluttering, as in bathing. The male, whose mate was incubating, approached her with his neck stretched up as if about to mount, but she supplanted him. The male stood watching the female, which resumed her preening, again shaking with raised tail and fluttering wings. The male again approached her with head up, and legs extended stiffly as if to mount, but again she supplanted him and this time flew to another perch.

During the breeding season the male House Finch performs a display which does not appear to be involved in pair formation and which does not usually lead to copulation, but which does seem to have some sexual motivation. The male stretches his neck up and slightly back, with head tilted slightly upward, body feathers usually rather sleek, but forehead and chin feathers ruffled, wings slightly drooped, and tail raised to a vertical position slightly spread. The legs are usually flexed, thus placing the body in a horizontal position. The bird hops toward a female, turning slowly from side to side (pivoting), singing very loudly, and emphasizing the ending *tzeep* phrase. Sometimes several *tzeep* phrases are inserted between repetitions of the complete song. Usually this display is directed by the male to a female other than his mate. Although it does occur before the first nesting of the season, it appears most often and in its most intense form well along in the breeding season after most birds are paired, and so does not seem to be a common method of pair formation. The female as a rule repeatedly supplants the male when he comes within two feet or so of her, and if her mate is in the vicinity he usually supplants and chases away the displaying bird. Sometimes the noise attracts other males and the female may chase off several different males, each displaying to her one at a time. The female usually flies some distance away under these circumstances and is usually not followed by more than one male, if by any.

On one occasion a female did not supplant a male which was displaying toward her, and he approached to within six inches of her. When she neither supplanted nor solicited him he stopped his display and perched quietly beside her.

The display is apparently part of pairing and mating, as is demonstrated by the use of a stuffed female mounted in the invitation posture. Near the end of the breeding season in July, 1958, a stuffed female was placed at a feeding station frequented by House Finches. A male soon flew down to eat, landing two feet from the food tray on which the dummy was standing. He looked at the dummy for a few seconds, then hopped toward it. He stopped momentarily beside it, stretched his neck up, fluffed his belly feathers, dropped his wings slightly, and hopped onto the dummy, carrying out the complete copulatory act. Then he hopped down and crouched beside the dummy, twittering, as described above for reverse copulation. His abdominal feathers were still fluffed, the wings drooped, tail spread and raised, and he leaned away from the dummy, almost lying on his right side. He continued this for almost a minute, then stood up and began to display before the female dummy. He circled around it, going from the right side to the front, to the left side, and then hopped onto her back again. This time he stood with head and neck erect, belly feathers fluffed, tail spread and lowered, as before, but spent more time placing his cloaca in contact with that of the female. In so doing he caused the tail of the dummy to fall into a horizontal position. When he hopped down he stood looking at the female, still twittering, tail erect, body feathers slightly fluffed, but not crouching as before. After pecking at seed on the ground and chirping softly, looking at the dummy from time to time for several minutes, he began to sing and display again, but not so vigorously as before. He again hopped onto the dummy whose tail was still in a horizontal position, and attempted copulation, then jumped off and began to feed.

Daanje (1941) described a communal display of the House Sparrow in which several males, including the mate, may display before a female which is not in reproductive condition. Summers-Smith (1954) maintains that this display is not simply a nonfunctional performance retained from some time in the past history of the species when it had a functional significance in courtship, but that it still functions as a stimulus to the female, leading to reproductive synchronization of the two sexes. Daanje suggests that the display originated as an attempt by the male to induce the female to copulate. Armstrong (1947) and Darling (1938) have described the function of display in birds generally as bringing the individuals involved into reproductive rapport.

Perhaps the display of the male House Finch also originally had this function, but, as in the House Sparrow, it no longer occurs regularly in this connection, except in unusual circumstances such as the one just mentioned involving the dummy. We may ask why the sexual displays of males of both the House Finch and the House Sparrow have lost their supposed earlier function as a precopulatory display occurring at the onset of the breeding season as well as later. As Summers-Smith points out, the display is highly stimulating to males and attracts them from all around. The same is true with male House Finches. The sound of a male displaying to a female attracts males from some distance away. In a cage containing several pairs of House Finches, attempts at copulation are always unsuccessful because the male attempting copulation is always knocked off the female by the other males. A conspicuous precopulatory display in such a semicolonial species as either House Finch or House Sparrow would, then, be very dysgenic, and successful copulations in both species usually occur after a postural invitation by the female. The female House Sparrow employs the juvenal summoning call which probably is not sexually stimulating to other males in the vicinity, but it attracts the attention of her mate. The female House Finch assumes a silent soliciting posture. Copulation then usually proceeds without interference from neighbors.

From the evidence at hand it appears that the display may serve more to induce a second nesting than a first attempt, or especially to induce a second if the first attempt fails, since the display occurs most often near the end of the first nesting period. In view of the very limited number of second broods observed in the study area this stimulation of the female, when successful, may be very important to the species. It is not clear why the display does not occur more often early in the season before the first nest building. A possible factor is failure of the reproductive drive of the male to reach the threshold necessary to release the display at this time of pair formation. Experiments with a dummy female in soliciting posture indicate that the male can be induced to display only when the gonads are enlarged during the breeding season. It is possible that the almost constant contact with the female, involving billing and courtship feeding, provides an outlet for the sexual motivation building up before nest construction begins. Only after the female mate begins incubation is the sex drive thwarted, and the males may display toward any strange female they encounter. The display of the House Finch appears to be associated, then, with a strong and thwarted sexual motivation which, however, may lead to continued breeding effort, as discussed above. When the female does not permit the male to come near her, he performs the display toward her.

The pivoting of the male House Finch during his display probably involves the same alternate flying-toward and flying-away tendencies as the pivoting of other fringillid species (Hinde, 1955–1956). It seems likely that this hesitation in the approach of the male toward a strange female is related to the general dominance of the female over the males. Probably the display is not usually performed toward the mate because the male is accustomed to approaching close to her, and the conflict of approach and retreat tendencies does not occur.

SUMMARY

The agonistic behavior of the House Finch is described with an emphasis on aggression and dominance relations. Part I of this paper is concerned with annual cycle and display patterns. Both wild and captive birds were observed intensively in central coastal California, chiefly in Berkeley, in 1954–55 and in 1957–59.

Loose aggregations of House Finches may be observed in rural and suburban areas during the winter. In the Berkeley area, males become established on their breeding areas and begin to sing in late February and early March, and about this time pair formation takes place. Nesting begins in April and may continue into early June. After the young leave the nest and become independent, both adults and juveniles tend to aggregate in large groups where food is plentiful.

During early spring when pairs are forming, the aggressive behavior of wild birds reaches a peak. Males defend the area around a female, as well as a space around the nest, but there seem to be no well-defined territorial boundaries which are strongly defended. The average size of the territories observed was 642 square feet.

The simplest form of hostile behavior observed in House Finches is supplanting attack. Another common form of hostile display between perched birds is the head-forward display, which may be of either low or high intensity. Hostile displays may give way to actual combat, which may be a vigorous struggle or merely beak-fencing, or billing. Subordinate individuals avoid those above them in peck order; fright responses may by either immediate flight, crouching, or a stiff-legged, erect posture.

Ruffling of the feathers of one or more parts of the plumage, or extension of one or both wings may be associated with a conflict in motivation.

Copulation in the House Finch normally occurs at the invitation of the female. Occasionally reverse copulation occurs. The male performs a striking, sexually motivated display toward females and this may serve to bring the sexes into reproductive rapport.

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Museum of Vertebrate Zoology, Berkeley, California, April 4, 1960. (Present address: Department of Zoology, Wayne State University, Detroit, Michigan.)