SOCIAL ORGANIZATION AND BEHAVIOR IN A FLOCK OF CAPTIVE, NONBREEDING RED CROSSBILLS

By HARRISON B. TORDOFF

Analyses of flock organization in social birds have received much attention and have advanced knowledge of the behavior of animals in general. Although social organization has been observed in many kinds of birds, studies have been concentrated on a few species. Notable among these have been domestic chickens, *Gallus* (literature reviewed by Guhl, 1953), pigeons, *Columba livia* (Masure and Allee, 1934*a*), and shell-parakeets, *Melopsittacus undulatus* (Masure and Allee, 1934*b*). Within the Passeriformes, few social structures have been studied in detail. One exception is the study by Shoemaker (1939) of social hierarchy in the Canary (*Serinus canarius*). Shoemaker's results are especially important to the studies reported herein because both the Canary and the Red Crossbill (*Loxia curvirostra*) are members of the same subfamily of finches, the Carduelinae. Comparisons between the two species, therefore, should be instructive.

In 1953 at Lawrence, Douglas County, Kansas, Red Crossbills were first reported on November 5, when James S. Findley saw one male and approximately four females on the campus of the University of Kansas. The same flock, presumably, remained on the campus for a week and then moved three-fourths of a mile to some Scotch pines (*Pinus sylvestris*) at the residence of Theodore G. Metcalf. By late November, the flock numbered fourteen individuals—six males and eight females, not counting two males collected on November 12 and 13. On November 30, a live male with a broken right wing was obtained. Using this male as a decoy and hemp seeds as bait, I trapped two females on December 12 and then used the females as decoys and trapped the remainder of the flock in the period from December 18 to 20. All birds trapped, except one, are referable to *Loxia curvirostra benti*; the exception is an immature male which seems to be *L. c. stricklandi* (wing, 97 mm.; tail, 56; culmen, 20.8; depth of bill, 11.7). This male is orangish-yellow with a very few scattered reddish feathers; the other males at the time of trapping were rose-red. Although the male *stricklandi* was killed by accident on December 27, I observed it long enough to note some interesting differences between the two subspecies. In addition to its orangish-yellow color, this male was readily distinguishable from the rest of the birds by its larger size, much more nervous behavior, and especially by its call notes, which were lower pitched and harsher than the calls of the other birds. It would have been interesting to observe the position of this bird in the peck-order.

It seems worth emphasizing that the crossbills studied for this report constituted a nearly complete flock formed under natural conditions in the wild and that they had an "acquaintance" with each other previous to their capture.

METHODS

Trapping.—The birds were trapped in a simple drop-trap, ten inches square and four inches high, made of half-inch hardware cloth. They showed little hesitation in going under this trap. As birds were trapped and added to the cage containing the decoy birds, it became progressively easier to trap the remainder. The last few birds repeatedly started to leave, only to be lured back by the calls of the captives.

Marking.—On December 23, the crossbills were transferred from a small, indoor cage to a larger cage out-of-doors. They were marked with colored bands on December 30, as follows: Males were banded on the left leg only—aluminum ("A" in the discussion that follows), white (W), blue (B), orange (O), green (G). Females were

banded on the right leg only—orange (OR), white (WR), red (RR), tan (TR), green (GR); or on both legs—right orange, left aluminum (OA); right red, left aluminum (RA). Note that the designations for males are single letters, in contrast with the two-lettered designations of the females.

The flock as studied consisted of five of the original eight males and seven of the original eight females. At the time of banding, one female had scabby feet. This bird was liberated to avoid infection of the other crossbills.

Food and housing.—The crossbills were housed in a cage measuring six feet by nine feet by six feet high. The cage was constructed of separate panels, each six feet by three feet, joined together with carriage bolts. The panels were framed by two-by-twos and covered with one-fourth inch mesh hardware cloth. One panel had a door in it. An advantage of a cage of this construction is its adaptability. The cage can be enlarged or made smaller by adding or removing panels. The floor consisted of hardware cloth to exclude burrowing predators while permitting the birds access to vegetation and soil.

Perches and cover in the cage were provided by a Scotch pine four feet tall planted in the cage, by foliage-bearing branches of red cedar (*Juniperus virginiana*), and by sticks placed in various parts of the cage. Roosting boxes, open at the bottom and front and divided into compartments three to four inches wide, were placed along one side of the cage near the top. Water in an open pan and food were available at all times. Through most of the period of observation, the principal food was seeds of hemp (*Cannabis sativa*) and sunflower (*Helianthus annuus*), although piñon (*Pinus edulis*) nuts were also used late in the period. The seeds were available in automatic feeders. Because of the well known propensity in carduelines for eating salt, a small block of mixed salt and minerals was made available. Cuttle bone and grit also were regularly taken.

Methods of observation.—Systematic observations, made inside the cage, totalled 26 hours in the period from December 31, 1953, to March 25, 1954. The presence of the observer in the cage seemed not to affect the behavior of the crossbills, which in captivity are very tame. Casual observations of general behavior more than quadrupled the total time of observation but were not recorded in detail.

Notes were kept of courtship feeding, singing, pre-roosting activities, and other aspects of behavior. Most detailed notes, however, were made of encounters between individuals in which dominance was displayed. The dominance-submission rôles of individuals were recorded for each encounter as follows: W>B, where male W dominated male B; OA>GR, etc. This method made possible measurements of aggressiveness, based on frequency of encounters, as well as determination of peck-order. I had no difficulty in deciding which individual was dominant in any encounter. Behavior in this respect was obvious, as is described beyond. A total of 2,144 encounters was recorded.

GENERAL BEHAVIOR

The crossbills became accustomed to confinement in a few days but did not become indifferent to outside stimuli as caged birds sometimes do. They reacted to hawks passing overhead by becoming motionless, peering at the hawk, and giving a single low note which can be described as *tuck, tuck, tuck.* They resumed their normal activities within a minute after the hawk passed from view. Sometimes the hawks were so high as to be scarcely visible to the naked human eye. In the daytime, domestic cats, dogs, cars, airplanes, children, and birds of other species drew little attention from the crossbills. At night cats crawling on the cage caused the birds to fly about in panic but this was soon stopped by trapping the cats. On December 25, an immature male Baltimore Oriole (*Icterus galbula*) was placed in the cage and dominated the crossbills completely. They

seemed afraid of its aggressive advances and it did, in fact, peck some of them. The crossbills reacted to the oriole with threat displays but invariably retreated from it. The oriole was removed from the cage on December 26.

Feeding.—Red Crossbills have been known to eat sunflower seeds in the wild but my birds fed adeptly on them only after considerable practice. At first, the crossbills picked up sunflower seeds, manipulated them in the bill, and dropped them unopened. After a day or two, most of the birds learned to crack the seeds between their tomia but did this much less expertly than Cardinals (*Richmondena cardinalis*). Later the birds were seen to open sunflower seeds in a new manner: the crossbill held the seed against the perch with one or both feet and bit at one end of the seed with the tips of the bill until the husk was pierced. The tips of the mandibles would then be inserted in the crack and pried apart, exposing the kernel to the long, agile tongue. The birds have continued to open sunflower seeds in this way, which is of interest in that it employs the same peculiar lateral separation of the mandibles that is used in opening pine cones.

Pine cones were constantly available in the cage and the crossbills spent hours working on them even after the few seeds were removed. Baily (1953:39) recently described the use of the bill in opening pine cones (there is a large literature on the subject) but my observations do not agree with his. My crossbills simply inserted their bills, with the tips approximately opposing each other, under the cone scales. This necessitates partial opening of the bill; it remains open throughout the operation. The scales are then raised by lateral abduction of the lower mandible, that is, toward the side to which the mandible is deflected; this motion is produced by the powerful, asymmetrically developed muscles on this side of the skull. While the tips of the bill hold the cone scales apart, the tongue is inserted to probe for and remove the seeds.

Regardless of sex in crossbills, the direction of crossing of the bill is approximately evenly divided. In half of the birds, the lower mandible, which deviates more from the midline than the upper, passes to the right of the upper, in the other half, to the left. I was surprised to find that this morphological asymmetry of the bill is correlated with "right- or left-handedness" of the individual bird, at least in its opening of pine cones. When a crossbill feeds on a cone, the long axis of the bird's head is approximately at right angles to the long axis of the cone. The bird orients itself so that the tip of the lower mandible is on the side toward the distal end of the cone. When the bill is inserted beneath a cone scale, the tip of the lower mandible presses toward the central axis of the cone, in the lateral motion described above, while the scale is raised by the essentially stationary tip of the upper mandible. I saw no variation in this.

Known cases of "right- or left-handedness" are rare in birds. Parrots often favor one foot for clutching objects, but no morphological basis for the preference is apparent. In the Wry-billed Plover (*Anarhynchus frontalis*) of New Zealand, the bill is always bent to the right and the species is said to probe under stones, around which the birds run in a clockwise direction. The bill and skull of oyster-catchers (*Haematopus*) are bilaterally asymmetrical as a result of, or perhaps as an adaptation to, their peculiar method of prying invertebrates from rocks, but here again the asymmetry is in the same direction in all individuals (Webster, 1941:177). In Limpkins (*Aramus guarauna*) the bill is slightly bent near the tip but I know of no careful study of the significance of this asymmetry. *Loxops coccinea,* of the Drepaniidae, has slightly crossed mandibles. Nothing is known concerning possible "right- or left-handedness" in this species. Crossbills seem to be the only birds so far studied in this regard in which individuals are either "right- or left-handed," depending on the form of the bill.

Hemp seeds were cracked and shelled between the tomia of the bill. The crossbills

fed also on flowers and seeds from maples and elms which fell on the top of the cage. The crossbills nearly denuded the Scotch pine planted in the cage and regularly stripped the cedar branches put in to provide cover. Bits of pine needles and perhaps also cedar needles were eaten, but most of the "chewing" seemed to result from a compulsion to twist, pry, and bite at objects—almost any objects—with the bill. This urge probably is largely satisfied in the wild by normal feeding on cones. The crossbills reduced branches up to a half-inch in diameter to slivers; they shredded tough pine cones; they chewed the lumber in the cage until the edges were rounded; they pried endlessly in cracks. All these activities seem to keep the tips of the bill from becoming too long—a real possibility in this species with non-occluding mandibles. One male (A) in which the upper mandible reached an abnormal length pried especially vigorously and finally broke three millimeters off the horny tip, thereby restoring it to normal appearance.

As mentioned earlier, salt was continuously available to the crossbills. They picked at the salt block regularly; each bird probably ate some salt every day. Commercial canary foods of various sorts were ignored by the crossbills. The birds were unable to crack the husks on piñon nuts but eagerly ate the nuts when I cracked the husks.

Several times I have seen wild crossbills carry pine cones in their bills. My captives did this to get cones from the ground up to the perches where they pecked at the cones held by means of their feet. Pine cones and other objects carried in flight are held in the bill. Some cones which the crossbills carried weighed 12 grams. This seems to me a remarkable feat since the birds weigh only 30 to 35 grams, the cones are held far from the bird's center of gravity, and many of the flights with cones were almost vertical.

Soon after the crossbills were captured, the prenuptial molt began. It agreed with that described earlier for this species (Tordoff, 1952:202-203) and was completed on schedule; this seemed to me evidence of the general good condition of the birds. Feathers lost accidentally were quickly replaced. One female (RA) replaced two rectrices to full length in 30 days from the time of their accidental loss.

Bathing and sun-bathing.—Red Crossbills are vigorous bathers. Once or twice a week I flooded the ground in the cage with an inch or more of water. The crossbills, at the sight or sound of the running water, while still on the elevated perches, often began to flutter their wings, and otherwise act as though bathing. One of the birds would then fly down to the water and the others would follow. Vigorous bathing would then ensue until the birds were so drenched that they could barely fly; some were forced to crawl up the sides of the cage to the perches. As in most other activities, the crossbills were strongly imitative in their bathing and followed the lead of one or a few birds. Air temperature seemed to have no influence on their readiness to bathe. Dust bathing was not observed, but conditions for dust bathing in the cage were not good.

Sun-bathing in Red Crossbills is highly ritualized and regularly performed. I observed it only in late morning on bright days. A bird, after quietly preening and scratching, would raise its feathers and then, usually with its back to the sun, spread its primaries by extending the wrist. The tail was spread in such a manner that all tail feathers were at least partly exposed to the sun. Then the head was drooped and so turned that the sun's rays shone directly into one eye, the bird now appearing to be staring up and back over its shoulder. Finally, the bill was opened in such a way that the tips were about opposite each other, thus exposing the tongue, the lining of the mouth, and one side and base of the bill to the sun. The bird would then sit motionless for up to four or five minutes, staring with wide open eye into the sun. Some birds, at least, blinked the eyelids at intervals of a second or two. The "objective" clearly was to expose the greatest possible amount of skin and epithelial tissue to the sun. I saw no bird change from one eye to the other while staring at the sun.

This performance was carried on socially, that is, when one bird began to sun-bathe, others followed suit. Sun-bathing usually was terminated by preening and scratching.

Roosting.—Competition for roosting sites was severe. The crossbills preferred to roost in thick foliage of pine and cedar branches, but they so rapidly bit off twigs and needles that cover of this type usually was not available. I was unable to replenish this cover at the frequent intervals required by the birds' defoliating activities. Consequently, the roosting boxes already described were used. An original, uncompartmented box with, to my eyes, sufficient perch space soon was judged inadequate because of the intense fighting, which usually started as much as an hour before actual roosting. I added roosting boxes which, finally, contained a total of 20 compartments. Even this did not appreciably reduce the fighting. Perhaps strife over roosting sites is a normal part of pre-roosting behavior; it seemed to be in this captive flock.

When the crossbills roosted in the pine, they settled in thick clumps of needles at the ends of branches. Here they looked remarkably like pine cones and it is easy to visualize the protection afforded by this habit. No more than one or two birds roosted on the same twig.

Activity preceding roosting consisted of rapid flying about the cage with rapid, "excited" calling. This flying may have been an expression of the flight to roost trees in the wild. Dominant birds repeatedly chased others out of roosting compartments. The last birds to settle down each night were invariably the females lowest in the peck-order.

After the birds finally settle in their roosts and before they go to sleep, they extend and retract their long tongues in a deliberate manner. The flickering of the pale pink tongues in and out of the mouths of the birds at the rate of three to five times a second is very striking. This performance is continued for perhaps three to five seconds, followed by a pause of several seconds, and then is repeated. Individual birds continued the flickering of the tongue for at least several minutes. It is extended on both sides of the upper mandible, although not strictly alternately, and when it is fully extended it reaches well beyond the end of the bill. After a minute, more or less, of this performance, a sizable cluster of white, frothy bubbles collects on the outside of the bill where the tips cross. These bubbles seem to be saliva. After cessation of protrusion and retraction of the tongue, the bubbles soon break, leaving the bill wet and shiny.

Coincident with the manipulations of the tongue, although at a slower rate, the crossbills open and close their bills in a manner suggesting that they are stropping the edges together. An amazing feature of this "stropping" was that the birds actually crossed their bills in the "wrong" direction! Knowing of some early literature in which it was suggested that crossbills were unable even to oppose the tips of the peculiarly formed bill, it was astonishing to me to find that they could not merely oppose the tips but actually could cross their bills in either direction. When the bill was closed on the wrong side, as was frequently the case for several seconds, the mouth did not close evenly, causing the birds to look most peculiar.

The movements of the tongue and bill possibly clean the bill, although crossbills habitually wipe their bills in the same fashion as other passerines after feeding. A second possibility is that the appearance of stropping may not be accidental, that is to say, the activities may be performed specifically to reduce certain parts of the bill by abrasion. I think that the latter is the correct interpretation of the performance. In other birds, overgrowth of the tomia is prohibited by the occluding surfaces, but in crossbills the tomium of the upper mandible does not occlude on the side opposite the tip of the lower mandible nor does the tomium of the lower mandible occlude on the side opposite the tip of the upper mandible. These edges are most effectively rubbed together in the re-

versed crossing of the bill. Examination of study specimens readily reveals the effect of the stropping. The two surfaces just described are so obviously worn down in crossbills that the reverse crossing of the bill might well have been predicted from the examination of study skins alone. The moisture from the tongue seemingly lubricates the bill to make the stropping more effective, much as oil or water lubricates a whetstone.

The twisting and prying at objects and the stropping of the bill not only counteract the tendency for overgrowth which is inherent in the non-occluding bill, but have permitted crossbills to develop the bizarre bill and, thereby, to exploit a new food source. It would be interesting, indeed, to know when these traits appear in the ontogeny of crossbills; possibly they appear at the age at which the tips of the bill start to cross. Judging by the shape of the bill, the White-winged Crossbill (*Loxia leucoptera*) prevents overgrowth of the bill in the same manner as the Red Crossbill.

Loxia is a recognizable genus primarily because of the unique bill. In other respects, crossbills might well be included in *Carpodacus* or *Spinus*. In crossbills the prying and stropping are correlated behavioristic traits that seem to have made possible the existence of a morphological generic character, namely the crossed bill.

SOCIAL ORGANIZATION

Establishment of peck-order.—A fairly rigid peck-order was already established at the time of capture of the birds. Certain changes in peck-order occurred, for reasons discussed later, after the birds were in captivity, and these changes make it possible to visualize the establishment of peck-order in newly formed wild flocks and the integration of newcomers into established wild flocks.

Peck-order was of the rigid, essentially straight-line type but with some triangles of dominance. There were three social hierarchies: a peck-order in the males, a peck-order in the females, and general dominance of all males over all females (but see exceptions to latter).

Peck-order probably was established by fighting and threat displays and was maintained primarily by threat displays. Fighting in Red Crossbills involves mainly attempts to bite; in severe fights, the combatants may fly into the air, facing each other in a nearly vertical position, and attempt to bite and perhaps strike each other with feet and wings. Crossbills pulled clumps of feathers from their opponents on several occasions. Three times I observed perched, dominant crossbills seize subordinates by the primaries and hold the birds suspended in the air for a few seconds.

Most of the aggressive activity, however, took the form of threat displays, the main elements of which involved an advance with head lowered, neck outstretched, and bill widely opened in such a manner that the tip of the lower mandible was well below the tip of the upper (fig. 1). In some cases, a high-pitched, buzzy note accompanied this display. The buzzy notes characterized more aggressive displays and were always used in fighting. Less vigorous threat displays always included opening of the bill toward the subservient bird and sometimes included lowering of the head and stretching of the neck. The widely opened bill provides an effective-appearing threat; the two curved and pointed parts of the bill look to be capable of inflicting a severe bite. Actual biting followed threatening only occasionally. Threat display, alone or with the buzzy warning note, usually caused the inferior bird to retreat. When an inferior approached a dominant bird in possession of a disputed roosting site, the dominant bird would gradually open its bill as the other bird approached; actual aggressive display depended on the closeness of approach. No fixed distance of tolerance was noted; if the birds were agitated, they seemed to seek encounters with birds lower in the peck-order, often chasing them

vigorously around the cage. When the crossbills were loafing, preening, or sun-bathing, approaches as close as four inches were frequently tolerated or reacted to only mildly. Many encounters involved no obvious threatening at all; subordinate birds simply avoided dominant birds or moved away as the latter approached them.

It was clear that the head, face, and bill are the parts of the bird possessing the highest valence in recognition of individual crossbills by one another. All displays involved

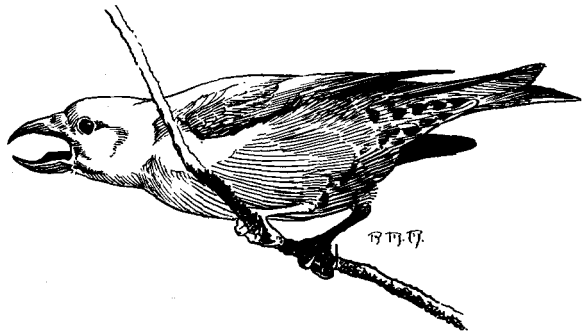

Fig. 1. Threat display in a male Red Crossbill; sketched from life by Robert M. Mengel.

face-to-face postures. It may be significant that the prenuptial molt, because of its variable extent and replacement of red feathers with green feathers in the males, increased the ease of recognition of individuals, at least to human eyes. This increased ease of recognition may be of value in maintenance of the mating bond.

The importance of features of the head and, to some extent those of the neck, in individual recognition in domestic chickens has recently been shown experimentally by Guhl and Ortman (1953).

Peck-order in males.—The five male crossbills included four first-winter birds and one adult (B), judging by the color of the edgings of the tail feathers (Tordoff, 1952: 201). All had essentially red body plumage although two (O and G) had some "orangish" feathers. When observations were begun on December 31, the males had an established peck-order as shown in table 1. This hierarchy contained one triangle of dominance—male G, second from the bottom of the peck-order, dominated W, otherwise at the top

Table 1

Peck-order in Male Red Crossbills, Based on 404 Encounters

	December 31–January 12						January 14–March 25			
Male	Dominates						Dominates			
W	—	B	A		O	—	B	A	G	O
B		—	A	G	O		—	A	G	O
A			—	G	O			—	G	O
G	W			—	O				—	O
O					—					—

of the peck-order. On January 13, G suffered a head injury as a result of being frightened into flight at night by domestic cats. On January 14, G was poorly coordinated, flew erratically, and seemed to lack good depth perception. W seized this opportunity to dominate G and maintained its newly won dominance even after G recovered. I saw no effort by G to dispute W's dominance after January 14. It is noteworthy that O, the lowest bird in the peck-order, did not climb in the rankings at G's expense. Even on Jan-

uary 14, when G seemed severely handicapped, we recorded G as dominant over O in one encounter. The effect of the loss of dominance by G over W was to resolve the peck-order into a straight-line system of dominance.

Aggressiveness of males.—Table 2 illustrates the aggressiveness of the individual males. The degree of aggressiveness of males with other males is directly correlated with position in the peck-order. The despot, male W, was especially active in dominating

Table 2

Aggressiveness in Male Red Crossbills Based on 404 Male-to-Male and 620 Male-to-Female Encounters

Male	Per cent of all ♂-to-♂ encounters in which ♂ indicated participated as dominant bird	Per cent of all ♂-to-♂ encounters in which ♂ indicated dominated next lowest ♂	Per cent of all ♂-to-♂ encounters in which ♂ indicated dominated lowest ♂ (O)	Per cent of all ♂-to-♀ encounters with ♂ dominant in which ♂ indicated participated	Per cent of all ♂-to-♂ and all ♂-to-♀ encounters with ♂ dominant in which ♂ indicated participated as dominant bird
W	51	23	11	26	36
B	28	6	11	19	22
A	10	3	7	10	10
G	11	9	9	16	14
O	0	....	....	29	18
Totals	100	41	38	100	100

second-ranking B, but the other males did not pay particular attention to dominating their immediate subordinates; only 41 per cent of all male to male encounters involved birds adjacent to each other in the peck-order. On the other hand, the four top ranking males were approximately equal in their aggressiveness toward the lowest male (O). This male was one party to 38 per cent of all recorded encounters between males.

The domination of female crossbills by males in non-breeding flocks provides an outlet for aggressive drives in the males ranked low in the male peck-order. Table 2 shows that male O, at the bottom of the male peck-order, was the most aggressive male in dominating the females, participating in 29 per cent of all male to female encounters. Second was male W, with participation in 26 per cent of such encounters. When all encounters in which any male participated as the dominant bird are summarized, it turns out that A is the least aggressive male. He ranked third in the peck-order of males; next in order of increasing aggressiveness was fourth-ranking G, followed by O, B, and W in that order.

Peck-order in females.—At the beginning of observations, the seven females were arranged in a hierarchy, as shown in table 3. This peck-order included two triangles of dominance and one bird (RA) figured in both. Female RA ranked fifth at this time, although in table 3 RA is listed fourth, which was her ranking at the close of observations. But RA dominated first-ranking OA and was in turn dominated by sixth-ranking RR. In the night of January 2-3, the then fourth-ranking female TR received a severe head injury through disturbance by domestic cats. On January 3, TR was unable to fly or even to feed properly and was persecuted by all females and males. I removed TR to prevent the other birds from killing her. On January 1, TR was placed back in the cage although she was still very poorly coordinated. Again she was vigorously attacked by the other birds and was removed once more. On January 6, TR was once more placed in the cage where she seemed capable of feeding and avoiding most of the other birds. Female RA, however, repeatedly sought out TR and attacked her. In this period, RA attained dominance over TR and ascended to fourth place in the peck-order where she

remained throughout the remainder of the period of observations. By January 7, TR was again exercising her dominance over females RR and OR.

One consequence of TR's efforts to regain her position in the peck-order after her injury was an increase in her aggressiveness. Through her increased aggressiveness she attained dominance over male G. This dominance was maintained uneasily until March 7; G frequently fought back unsuccessfully. On this date G began to contest TR by violent fighting. This fighting continued intermittently until March 15, when, after a particularly violent fight, TR seemed to have been reinjured and died in a few hours. I do not know whether G inflicted the injury or whether TR flew against some object while fighting. Her death was caused by hemorrhage in the brain.

Table 3

Peck-order in Female Red Crossbills, Based on 1,120 Encounters

Female	December 31–January 2 Dominates							January 3–March 31 Dominates						
OA	—	GR	WR		TR	RR	OR	—	GR	WR		TR	RR	OR
GR		—	WR	RA	TR	RR	OR		—	WR	RA	TR	RR	OR
WR			—	RA	TR	RR	OR			—	RA	TR	RR	OR
RA	OA			—			OR	OA			—	TR		OR
TR[1]				RA	—	RR	OR					—	RR	OR
RR				RA		—	OR				RA		—	OR
OR							—							—

[1] TR died March 15.

All changes in peck-order thus far described have been attributable to injuries that impaired the ability of the injured bird to coordinate properly. In fact, the clearly abnormal behavior—convulsions, coma, and the like—of TR after her injury stimulated vigorous aggression by all other birds. In contrast to this was the behavior of female GR, which injured one hallux so badly that I was forced to amputate it. The injury and subsequent amputation were a heavy drain on the vitality of GR. For about two weeks, GR avoided the other crossbills and spent most of the time perched in a corner of the cage. In spite of her obvious disablement, no crossbills challenged her high position (number two) in the peck-order. When approached too closely, GR responded with a threat display in normal fashion. Seemingly, an injury must impair the ability of the crossbill to react normally in individual encounters if the injured bird's position in the peck-order is to be affected. Another case in point is that of male A, the bird originally captured with a broken wing. I saw no evidence that A was handicapped in any encounters because of its injury, which ultimately healed sufficiently to permit fairly good flight.

Aggressiveness of females.—Comparative aggressiveness of the female crossbills is presented in table 4. The frequency of dominant participation in encounters is directly correlated with rank in the peck-order, as was true also for the males. One exception is provided by female GR, however, which ranked second in the peck-order but fourth in aggressiveness. The females also agreed with the males in that aggressive behavior did not seem directed disproportionately to either the lowest ranking female (OR) or to females immediately subordinate to the aggressor. (It should be noted that the percentage figures in tables 2 and 4 are not directly comparable. Other things being equal, percentages for the females would be smaller than for the males because the flock contained seven females and only five males.)

The total number of female-to-female encounters was 1,120. The total number of

male-to-male encounters (with two fewer male birds than females) was only 404. If the 620 male-over-female encounters are added to the latter figure and the few female-over-male encounters are added to the former, aggressiveness in the two sexes is approximately equal.

Factors affecting social dominance.—Shoemaker (1939:404) found that male canaries regularly dominate females except during the breeding season, when dominance is reversed for the mated pair. In my crossbills, no actual mating took place in the period of observation. Female RR, however, was frequently noted in courtship feeding with males W and B and she dominated both males. It is interesting to note that RR ranked

Table 4

Aggressiveness in Female Red Crossbills, Based on 1,120 Female-to-Female Encounters

Female	Per cent of all ♀-to-♀ encounters in which ♀ indicated participated as dominant bird	Per cent of all ♀-to-♀ encounters in which ♀ indicated dominated next lowest ♀	Per cent of all ♀-to-♀ encounters in which ♀ indicated dominated lowest ♀ (OR)	Per cent of all ♀-to-♀ encounters in which ♀ indicated dominated most frequent opponent
OA	30	3	5	OA > RR 9
GR	13	4	1	GR > TR 4
WR	20	5	6	WR > RR 7
RA	21	11	2	RA > TR 11
TR	9	4	4	TR > RR 4
RR	7	2	2	RR > RA 5
OR	—	—	—	—
Totals	100	29	20	40

sixth among females while W and B were first and second, respectively, among the males. The total number of recorded encounters involving female RR and males W and B was 39; of these, RR dominated 36. It seems to me that RR may have achieved dominance over W and B through participation in the early stages of pair formation. Further observations should show the effect of mating on male-female dominance in Red Crossbills.

Age may be unimportant in determining position in the peck-order. Only male crossbills can be aged by plumage characters. The single adult of the five males ranked second. Shoemaker (1939:399) found that age made little, if any, difference in dominance in canaries.

Size, at least within one subspecies, seems also to play no part in determining dominance in crossbills. Female RR ranked sixth, yet was the largest of the females. Shoemaker (1939:399-400) determined that weight did not affect dominance in canaries.

Effect of captivity on peck-order.—A measure of the rigidity of the peck-order in my flock of crossbills is the fact that only 29 encounters of the total of 2,144 were recorded that involved reversals of the dominance situations shown in tables 1 and 3. No reversals were recorded between any two males. Of the 29 recorded for females, 14 were encounters in which TR dominated WR (WR dominated TR 17 times). Some of the others may have been the result of faulty observation or recording.

In wild flocks of crossbills peck-order is probably established and maintained as described here. Captivity may have caused the peck-order to be somewhat more rigid, however, by increasing the number of individual contacts. I recorded 2,144 encounters in 26 hours of observation—an average of 82 encounters per hour or 14 contacts per bird per hour, since each encounter involves two birds. In wild flocks, encounters are probably not nearly so frequent as in my captive flock. I have frequently seen threat displays and dominance, however, in feeding flocks of wild crossbills.

SURVIVAL VALUE OF SOCIAL ORGANIZATION

Some obvious benefits of social organization in birds have been noted by other authors. Guhl (1945:340) found that food consumption and egg production in domestic hens were higher in organized flocks than in flocks kept disorganized by introduction of new birds. Shoemaker (1939:381) remarked that social groupings may have survival value in several ways: "(1) greater defensive strength in numbers; (2) more eyes in more directions to detect predators; (3) heat conservation in severe weather; (4) ease of finding food to be shared by the group; (5) proximity of sexes insuring greater fertility; and finally, (6) group breeding may result in lessened mortality of the young."

Red Crossbills and other carduelines would seem to derive special benefits from their social habits in finding food. Characteristically, crossbills feed on seeds of conifers, especially pines. Many kinds of pines do not fruit each year and food for crossbills, therefore, often occurs abundantly but in small patches scattered over extensive areas. The gregarious nature of crossbills leads them to call to passing flocks, even while feeding. The passing flocks then often join the feeding birds and share in the food. The strong powers of flight of carduelines enable them to cover long distances in search of food.

The existence of a well defined peck-order would seem advantageous in simple economy of effort. The peck-order permits resolving of disputes with a minimum of effort. Considering the gregarious nature of crossbills, it seems that the peck-order prevents much fighting and consequent waste of energy.

I observed that social dominance was exercised in all situations. The clear benefits to the individual crossbill of high rank in the peck-order, however, were most evident in regard to food and roosting sites. When favored food such as piñon nuts was placed in the cage, the crossbills fed approximately in order of their rank in the peck-order. That is, the highest males fed first and the lowest females fed last.

In regard to roosting, I could not see that any sites offered special advantages over other sites. Even so, strife was severe and dominance was repeatedly exercised by the high ranking birds. Evening after evening female OR, the only bird in the flock that had no subordinate, was the last to find a place to roost. In general behavior, OR was a timid, poorly adjusted bird and this probably resulted from, or caused, her low rank in the peck-order.

The triangles of dominance deserve comment. The triangles seemed to result in decreased efficiency of the flock. As an example, when females OA, RA, and RR were searching for roosting sites, I noted that their dominance relationship (OA dominated RR, RR dominated RA, RA dominated OA) tended to keep all the females agitated. First, one of the three females would pick a roost, then in turn each of the three birds would evict its subordinate in the triangle and also other subordinate females. The triangles clearly promoted confusion and when female RA was removed, experimentally, strife over roosting sites was noticeably diminished. It is probably significant that the

changes observed in the peck-order in this flock were changes that tended to eliminate triangles and to promote a straight line system of dominance. In view of this, it is surprising that canaries (Shoemaker, 1939) do not establish a straight line peck-order but instead show "peck-right dominance," in which pecks are dealt by both members of most encounters, the bird which pecks the most being judged to be dominant.

ACKNOWLEDGMENTS

Glen E. Woolfenden assisted in trapping the crossbills and in recording and tabulation of some of the observations. For this help, I am very grateful. Additionally, I am pleased to express my gratitude to Mr. and Mrs. Theodore G. Metcalf for permitting us to erect a feeding tray and to trap the crossbills in their backyard, to Olin L. Webb for aid in construction of the outdoor cage used in this study, to James S. Findley for aid in some observations and for helpful suggestions, to Jean Tordoff for assistance in caring for the crossbills, and to officials of the University of Kansas for making funds available for purchase of materials and supplies.

SUMMARY

A flock of 12 Red Crossbills trapped in eastern Kansas was caged and studied, with the following results:

Individual crossbills in feeding on pine cones were found to be either "right- or left-handed," depending on the direction of crossing of the bill. Prying and "bill-stropping" seem to prevent overgrowth in the non-occluded bill.

Bathing and sun-bathing were usually performed socially.

Peck-order was established and maintained by fights and threat displays; peck-order was essentially the straight line type but with some triangles of dominance. Three hierarchies were present in the flock: (1) a peck-order of males; (2) a peck-order of females; and (3) dominance of males over females.

Some changes in the peck-order were directly attributable to injuries. Injuries affecting ability to coordinate and behave "normally" are more likely to affect rank in the peck-order than injuries such as a broken wing or damaged foot.

The top-ranking male was the most aggressive male and was especially active in dominating the second-ranking male. Other males seemed not to pay particular attention to their subordinates. The lowest male was dominated about equally by all four males above him and was a party to 38 per cent of all male-to-male encounters. The lowest-ranking male was most active in dominating females, followed closely by the top-ranking male.

Aggressiveness in females, as in males, was directly correlated with rank in peck-order and did not seem directed disproportionately to either the lowest ranking female or to the aggressor's immediate subordinate. Males and females were about equally aggressive.

Captivity was judged to have increased the rigidity of the social hierarchy through increasing frequency of individual contacts but it was thought not to have altered basic behavior patterns.

Social organization results in more efficient functioning of the flock as a unit and has definite survival value.

Triangles of dominance imposed on a basically straight-line peck-order are disruptive and disadvantageous, at least in small flocks. Observed changes in the peck-order tended to eliminate triangles of dominance.

LITERATURE CITED

Baily, A. L.
1953. The Red Crossbills in Colorado. Part Two. 1952 observations of the Red Crossbills. Denver Mus. Nat. Hist., Mus. Pictorial No. 9:33-63.

Guhl, A. M.
1945. Some observations and experiments on social behavior in the domestic fowl. Trans. Kansas Acad. Sci., 47:337-341.
1953. Social behavior of the domestic fowl. Kansas Agr. Exp. Sta., Tech. Bull. 73.

Guhl, A. M., and Ortman, L. L.
1953. Visual patterns in the recognition of individuals among chickens. Condor, 55:287-298.

Masure, R. H., and Allee, W. C.
1934*a*. The social order in flocks of the common chicken and the pigeon. Auk, 51:306-327.
1934*b*. Flock organization of the shell-parakeet, *Melopsittacus undulatus* Shaw. Ecology, 15: 388-398.

Shoemaker, H. H.
1939. Social hierarchy in flocks of the Canary. Auk, 56:381-406.

Tordoff, H. B.
1952. Notes on plumages, molts, and age variation of the Red Crossbill. Condor, 54:200-203.

Webster, J. D.
1941. Feeding habits of the Black Oyster-catcher. Condor, 43:175-180.

Museum of Natural History, University of Kansas, Lawrence, Kansas, May 17, 1954.