

AGONISTIC AND SOCIAL BEHAVIOR OF CAPTIVE REDPOLLS

BY WILLIAM C. DILGER

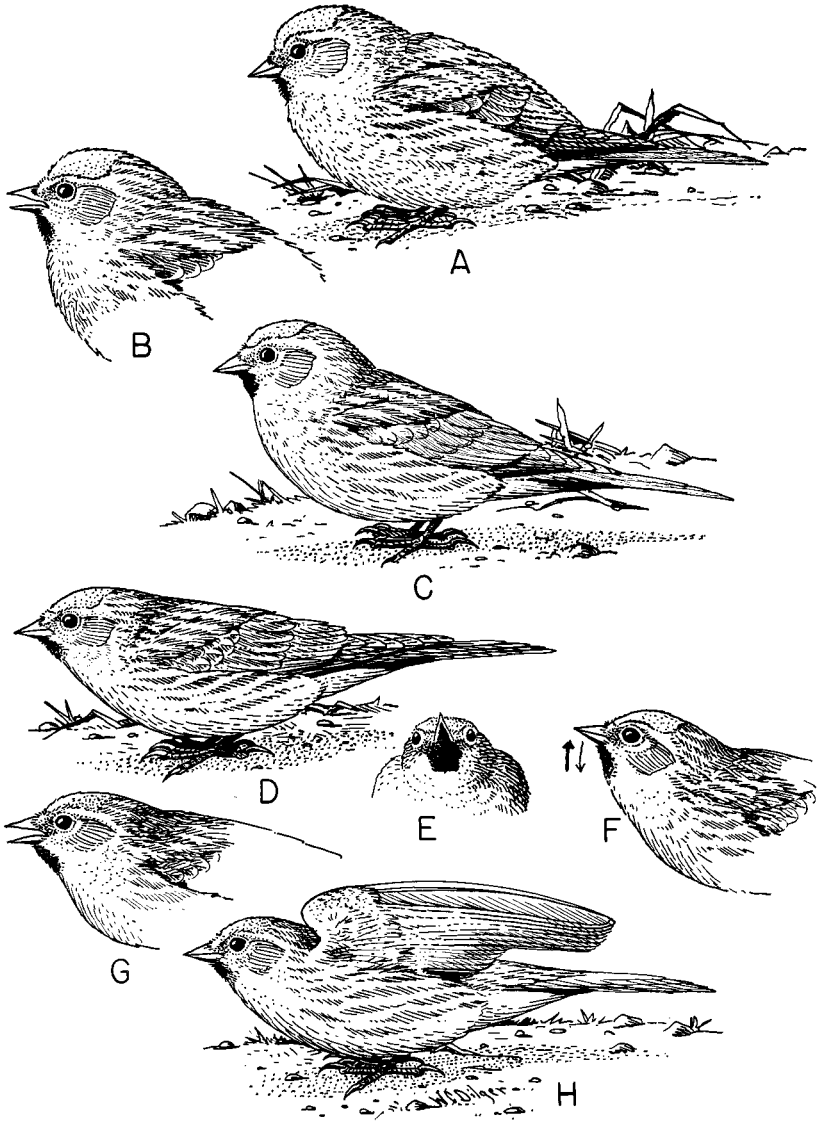
THE birds used in this study were trapped on the campus of St. Lawrence University, Canton, New York, during February and March of 1956. A simple droptrap operated manually by means of a long cord was used, and a mixture of canary and rape seed served as bait. After two or three birds were caught and placed in a small cage next to the trap little difficulty was experienced in quickly obtaining others. Deep snow throughout the trapping period seemed to facilitate the trapping, as food was presumably difficult to procure elsewhere.

The objectives of this study were as follows: (1) to describe and evaluate the agonistic (attack-escape) behavior; (2) to describe and evaluate any social hierarchy that might be established; and (3) to obtain information on the changes in behavior associated with the gradual onset of reproductive condition during the spring.

Thirty-one Common Redpolls (*Acanthis flammea*) were used as a source of observational data, but only eight of these were studied intensively. The others provided subsidiary data as did the wild ones which remained in the vicinity. All captives were color-banded to facilitate the ready recognition of individuals. The group of eight was placed in a semi-box type cage measuring 3 feet by 2 feet by 2 feet high. The back, sides, and bottom were fashioned of plywood. The top was covered with ½-inch mesh screening and the front was constructed of glass in order to increase visibility into the interior. A sliding metal tray on the bottom facilitated cleaning the cage. The substrate consisted of paper over which a thin layer of coarse quartz sand was spread. Two perches running from front to back were fastened to the back of the cage about 6 inches from the floor and about 18 inches apart. A third perch, running parallel to the cage front, was fastened to the cage sides about 18 inches from the bottom and about a foot from the back.

Food consisted of a standard canary mixture (three parts canary and one part rape seed). In addition, small amounts of parakeet conditioning food were supplied. This consisted of a mixture of small seeds and a mash made up of milk proteins, dried egg yolk, ground oyster shells, vitamin supplements, etc. Fresh water and cuttle bone were continually available. Food and water were placed in steep-sided glass dishes about 4 inches in diameter and 1½ inches deep.

Close observation was made easier by the quickness with which they became habituated (a learning process characterized by a waning of a response despite repeated stimulation but not associated with any reinforcement . . . see Thorpe (1951) for a thorough discussion) to the cages and to human pres-



Postures of Redpolls: (A) Submissive display, (B) Defensive Threat, (C) normal relaxed posture, (D) basic Head Forward Threat display, (E) Head Forward Threat with Chin-lifting (front), (F) Head Forward Threat with Chin-lifting (side), (G) Head Forward Threat with Gaping, and (H) Head Forward Threat with Wings-raised (high intensity).

ence. As a matter of fact, it was not unusual for freshly caught birds to feed in the gathering cages as they were being carried from the trap to the laboratory! Once established in the observation cages they soon permitted observations to be made at a distance of 3 or 4 feet without the slightest apparent alarm.

The methods used to determine the function ("meaning" to other individual(s)) and stimulus strength of each of the displays discussed are those ordinarily used by ethologists and frequently discussed in the literature; for instance, Moynihan (1955*a*) and Hinde (1955-56). In brief, four types of evidence are utilized: (1) the circumstance in which the display occurs; (2) the behavior demonstrated by both participants immediately before and after the display is given; (3) the behavior accompanying the display; and (4) the components of the display.

As might be expected, these birds proved to be highly social and their various activities tended to be performed in concert. This included eating, drinking, bathing, preening, stretching, etc. Periods of such activities alternated throughout the day with periods of resting. No sexual behavior was noted during the first weeks after capture, nor in the wild birds which remained in the vicinity. The captives were subjected to normal day lengths.

AGONISTIC BEHAVIOR

Agonistic behavior in redpolls, as in other animals, consists in part of a number of displays which serve to reduce the attack tendency and/or to increase the escape tendency of opponents or potential opponents (see Hinde, 1956, for a discussion of the use of the term "tendency"). As in other types of displays, these agonistic displays were most pronounced when the tendencies were in greatest conflict. In the case of agonistic displays the conflicting tendencies were usually the attack and escape tendencies. Sometimes other tendencies were also present and contributed additional variables.

It is thought, as a result of the findings of many investigators working with many kinds of animals, that the attack and escape tendencies are usually, if not always, simultaneously present in any animal demonstrating agonistic behavior (Moynihan, 1955*a* and *b*). Either may be so preponderant that the animal either simply flees (escape) or attempts to supplant or fight (attack) the opponent. Commonly, however, the two tendencies are in some degree of conflict resulting in various displays depending upon the actual and relative strengths of the conflicting tendencies. In such displays, it is usually possible to recognize the presence of both tendencies by the expression of motor elements associated with the attack and the escape behavior. The relative proportion of these motor patterns may be, but are not necessarily, associated with the relative strengths of the two conflicting tendencies. Thus, between

the acts of simply fleeing and of simply attacking, there is a rather elaborate series of displays expressing varying proportions of actual and relative strengths of attack and escape tendencies. The type of display forthcoming is dependent both upon the internal state of the animal (specific action potential) and upon the nature of the external stimulus(i).

There are obviously an infinite number of actual and relative strengths of both the attack and escape tendencies between simple fleeing and simple attack. It is equally obvious that there are not an infinite number of displays which occur between these two extremes. Ordinarily only a few such displays exist, which means that each display functions within a rather broad spectrum of actual and relative strengths of tendency conflicts. This stabilization of display types within a certain amount of variability of tendency strengths has been termed "typical intensity." Morris (1957) presents a thorough discussion of this phenomenon. It might be mentioned here that the establishment of a typical intensity for a display is the result of conflicting selective pressures acting in a manner to insure maximum "understanding" of what the displayer may do next while at the same time minimizing any possible ambiguity.

It may be of value to mention here the fact that the amount of attack or escape valence cannot always be determined by the proportion of attack and escape motor elements incorporated in a given agonistic display. Once such a display has evolved and become at least partly ritualized (see Blest, in press) its threshold of response may have become shifted somewhat from its original source. Hence, a display made up of (and originally caused by) a preponderance of escape tendency may have its threshold of response shifted, through selective pressures operating until the display comes to have a high attack valence. The Spread Display of the Wood Thrush (*Hylocichla mustelina*) (Dilger, 1956) for instance, seems to have incorporated a great amount of escape motor patterns (much plumage fluffing and ruffling) but the display itself has a high attack valence. Thresholds, of course, can shift the other way and motor patterns originally associated with attack can come to have a greater escape valence. It must be remembered that any shifts in the form and/or "meaning" of displays must be coincident with the innate and/or learned "understanding" of the recipients.

Motor patterns associated with the attack tendency in redpolls consist of orientation toward another individual, locomotion toward another individual, and/or associated intention movements (see Daanje, 1950, for a discussion of intention movements). The acts of pecking, biting, holding, etc., are also, of course, associated with the attack tendency.

Motor patterns associated with the escape tendency in redpolls are orienting

away, or moving away, from other individuals as well as the intention movements for doing so.

The various plumage adjustments such as sleeking, ruffling, and fluffing, which are incorporated are all probably intention movements to locomote and/or temperature adjustment mechanisms. The discussion by Morris (1956) of these phenomena is useful in this regard. The fluffing of the plumage associated with the escape tendency (submissive display) serves an appeasement function (Front. A). This posture is similar in many ways to the posture adopted by sick, cold, or resting birds. Its use as an appeasement signal may have been facilitated by its previous association with an inactive and therefore non-aggressive state, as well as by its difference from the Head Forward Threat (Hinde, 1955-56).

Visual Displays.—The displays dependent upon conflicts caused by the presence of attack and escape tendencies are mostly variants of the Head Forward Threat posture (Front. D). This posture is characterized by the bird's crouching slightly by bending its legs at the hip, knee, and "heel"; the plumage is sleeked to varying degrees (these are all probably originally intention movements to fly); and the head is carried in line with the body and pointed toward the opponent. When the escape tendency is relatively strong the feathers of the crown are somewhat fluffed. The various fluffings associated with the escape tendency occur in situations where the escape tendency is thwarted either by an incompatible tendency such as attack (intrinsic thwarting) or by a combination of intrinsic thwarting and some external prevention of overt escape such as being confined in a cage or the near presence of a number of dominant individuals (extrinsic thwarting). If the escape tendency is not strongly thwarted the bird may merely orient away from the external source of escape stimulation or locomote away in various speeds and manners depending upon the strength of its actual or relative escape tendency. In situations characterized by strong extrinsic escape thwarting, but subjected to persistent attack by an opponent, the bird may exhibit strong fluffing of the entire plumage as well as strong "defensive threatening" (Front. B). The same sort of motor patterns may be evinced also by birds prevented from overt fleeing because of strong intrinsic thwarting (such as a strong incubation tendency, etc.) while subjected to persistent attack.

"Defensive Threat" in redpolls consists of the bird's fluffing the entire plumage, retracting the neck (both manifestations of escape) and at the same time orienting toward, and gaping at, the opponent (both manifestations of attack).

In the opposite situation (where strong attack is thwarted either intrinsically or extrinsically) there seems to be no particular associated display but merely ambivalent intention movements, expressed alternately, characteristic of the

two incompatible tendencies which have been simultaneously activated. For instance, a dominant bird with a strong tendency to feed may be approached by another individual. The dominant bird, although obviously exhibiting a very aggressive tendency and also very "hungry," often does not adopt a display but alternately demonstrates intention movements to eat and to attack.

The fact that thwarted escape is more often associated with a display than is thwarted attack probably is indicative of the fact that it is more of an advantage to an animal with thwarted escape to make its position clear to an opponent. The animal with thwarted escape is essentially indicating fear but a willingness to attack if further molested. An animal not able to flee is quite likely to avoid further attack if such information is communicated to an aggressor; hence, considerable biological advantage is gained. On the other hand, an animal with a thwarted attack usually has little if anything to lose if the actual attack has to be put off temporarily; hence, there probably is not as much selective pressure brought to bear which would tend to cause the evolution of a display in these circumstances.

Aside from the above special cases of thwarting of strong escape or attack tendencies there are several displays given by redpolls which are indicative of varying readiness to attack. Progressing from a simple orientation of the head toward the opponent (lowest indication of attack) we next find the Head Forward Threat (Front. D). This basic threat posture has been described above. Ordinarily the whole bird is oriented toward the opponent, but at low intensities only the head may be so oriented. In general, the head in any case makes the finer adjustments; the body sometimes being only roughly oriented. For instance, if the opponent is above the displaying bird, the body will remain roughly horizontal but the head will be pointed directly at the opponent. The same is true if the opponent is below the displaying bird but here the head would be lowered toward the opponent rather than raised. If it is possible for the whole bird to be oriented toward the opponent but only the head is so oriented, then the attack tendency is actually and/or relatively weak. The display with the next highest attack valence is the Head Forward with Chin-lifting (Front. E and F). Here the head is lifted in a quick perfunctory manner, sometimes several times. This action exposes the black chin and the pattern of the gonys to the opponent's view. The movement is repeated if the opponent does not, by its actions, signal some change in its mood. Other black-chinned carduelines such as the Hawfinch (*Coccothraustes coccothraustes*) and the Bullfinch (*Pyrrhula pyrrhula*) adopt a similar course of action (Hinde, 1955-56).

If the actual or relative strengths of the attack tendency continue to rise, then the Head Forward Threat is associated with Gaping (Front. G). The plumage is also more sleeked here than with the Chin-lifting, and even more so

than with simple Head Forward Threat. Gaping is quite likely to have been derived from the intention movement for biting. Sometimes Gaping and Chin-lifting occur together, but this is not as common as either is alone. Apparently the exact relative and/or actual strength limits of the attack and escape tendencies responsible for Chin-lifting plus Gaping are more restricted than they are for either of these patterns alone.

Further rise in the actual and/or relative attack tendency is characterized by various strengths of intention movements to fly at the opponent. The display here is still essentially a Head Forward Threat but the plumage is very sleeked and the wings are raised to varying extents but remain closed. The wings may merely be raised a bit from their supporting feathers, thus exposing the carpal joints or they may, in extreme cases, be raised over the back (Front. H). Raised-wing displays, particularly the higher intensity forms, are not particularly common in the redpoll, and most attacks are either effective somewhere short of Wing-raising or they become supplanting attacks in which case the Wing-raising is such a quick transitory action that it can scarcely be perceived. In extreme cases the attacker may actually peck at or bite the opponent but this is rare even in captivity where escape is difficult. I have never seen it among individuals in the wild.

Auditory Displays.—Bill Snapping, presumably another intention movement to bite, which incorporates an auditory component, was not observed in these birds although it is common in many other passerines including some other carduelines (Hinde, 1955–56).

Redpolls, however, use vocal signals in agonistic situations. The commonest is a rather harsh, sharp *cheh, cheh, cheh* sound and seems to serve an intimidatory function. It was heard usually while the birds were in the higher attack displays and was uttered by dominant individuals as a warning. A similar utterance, only higher pitched, more musical, and slower in cadence, seemed to serve as a location call among members of the flock. Interspersed among bouts of these latter vocalizations are frequent utterances of a *sweeeeeeeeee* note. This is very similar to a vocalization heard from American Goldfinches (*Spinus tristis*) and Pine Siskins (*S. pinus*). It has a rising inflection, is rather high in pitch, and is quite musical.

There were some color differences among the males, chiefly in the amount of pinkish suffusion on the breast and the presence or absence of this suffusion on the cheeks. There was no correlation between color and social position. The most dominant male (The Green ♂) was less highly colored than the least dominant male (The Red ♂). The females also exhibited some variation and one, the Green ♀, had a very faint pinkish tinge to the sides of her breast, but she was the least dominant female (sex confirmed by autopsy).

SOCIAL HIERARCHY AND SEXUAL BEHAVIOR

As an outcome of rather intense agonistic activity from the time of capture, these birds soon established a very rigid social hierarchy. This hierarchy remained with no change until certain shiftings gradually took place coincident with the slow development of sexual activities later in the season. The hierarchy was established as far as I could determine, within three days from the time the birds were placed together. The establishment of such a rigid social order implies, of course, that the facility for individual recognition is well developed.

About 600 encounters were recorded and evaluated. An encounter was recorded whenever one individual avoided another as a result of an oriented action. Actual physical contact was very rare. Hereafter, individuals are designated by their band color and sex.

The males were all dominant over the females in the non-reproductive hierarchy. Moreover, the hierarchy was a linear one running from the most dominant male, through the males to the most dominant female, and thence to the least dominant female. Very few reversals of expected outcomes of encounters were noted, and most of these were clearly "mistakes" on the part of the birds involved. In most of these cases a dominant bird would be approached rapidly and from the rear by a less dominant individual which apparently did not "recognize" the individual it was approaching (most of the individual recognition features seemed to be associated with the head). The dominant bird would flee from this "pseudo attack," evidently before it recognized the identity of the "attacker."

The order which was established, starting with the most dominant bird, was as follows: Green ♂, Yellow ♂, Blue ♂, Red ♂, Blue ♀, Yellow ♀, Red ♀, and Green ♀. A graphic representation of this hierarchy can be seen in Fig. 1A. The circles represent the individual birds. The widths of the solid bars and lines are proportional to the number of "wins" over the bird to which they are connected on the right. The shaded bars and broken lines represent "reversals" in the straight-line hierarchy. Again, the widths are proportional to the number of encounters. This method of graphically representing data was adapted from one utilized by Baerends *et al.* (1955) for demonstrating the interrelationships of sexual behavior patterns in Guppies (*Lebistes reticulatus*).

Redirected Aggression.—It can be noted that birds adjacent in the hierarchy tended to be involved in more encounters with each other than with those which were not adjacent. This is to be expected, as such birds are more nearly alike in dominance value. When it became apparent that the Red ♂ was being particularly aggressive toward females, I suspected redirection on his part. A careful note was then made of what the Red ♂ did immediately

after each losing encounter with another male, and in almost every case he immediately attacked a female, thus clearly demonstrating the redirection nature of these attacks. Not only did he typically redirect to the females but these attacks were especially vigorous and commonly involved feather-pulling and other physical contact. For a discussion of the phenomenon of redirection see Moynihan (1955*b*). The other three males were never observed to indulge in redirection activities of this sort but each of them, during the normal course of events, found themselves defeating other males. Not being able to defeat a male seems to be a source of rather strong thwarting in a male.

The relationship between position in the hierarchy and aggression is not clear. For instance, the Green ♂, the dominant bird, was not particularly aggressive in the sense that he most often initiated encounters which he won. On the contrary, encounters involving him were commonly initiated by other birds which violated his individual distance. If we think of this hierarchy as a straight line from the most dominant bird to the least dominant bird, it is more accurate perhaps to say that the hierarchy is due to an increasing tendency to recognize dominance rather than a decrease of aggressiveness through the same series.

There are many possible reasons why one bird should be more or less dominant than another. Possible factors tending to permit animals to be successful in agonistic encounters include such things as: physical superiority because of size, agility, good health, etc.; "psychological" superiority because of having won initial encounters; and being on some sort of territory or even in a more familiar location as opposed to the opponent. All of these could work in varying combinations to cause one individual to be more dominant than another. The reverse of the above conditions, on the other hand, tends to cause animals to be less dominant.

It must be remembered that the attack and escape tendencies have not evolved as a means to an end nearly to the extent other tendencies have, such as the sexual, feeding, and drinking tendencies, for instance. Attack and escape are almost always associated with gaining some advantage relative to other tendencies, and as such may be thought of as "service tendencies." Their expression allows an animal to gain food, water, space, mates, and escape from enemies or other undesirable or dangerous features of the environment. The use of attack and escape tendencies may, upon occasion, even be somewhat interchangeable. For instance, a bird may learn that it can approach a more dominant individual more closely if it adopts a submissive posture than it could otherwise. This might well allow this individual to feed, drink, or bathe in situations where it otherwise could not. In a case like this, the animal has profited by learned use of the escape motor patterns whereas it might

have employed motor patterns associated with aggression in the presence of a less dominant individual.

A less dominant individual near a more dominant one conducts itself in such a way as to minimize the possibility of provoking an attack. The greater the disparity between the social positions involved, the greater the care taken by the less dominant bird not to provoke an attack. Less dominant birds do not move quickly in the presence of dominant individuals. They do not approach directly and from the front, but approach indirectly and from the rear or obliquely. They avoid orienting the head toward a superior, and frequently have the plumage fluffed to some degree indicating their submissive tendency. The Green ♀, the lowest bird in the hierarchy, was almost perpetually in the Fluffed Submissive posture.

Less dominant birds in general behave as if they had a very keen awareness of the presence of superior individuals. Dominant individuals, on the other hand, essentially behave as if their inferiors existed hardly at all.

"Unprovoked" attacks were made only by the Red ♂ and then only on females to which he was redirecting. These attacks were unprovoked in the sense that the recipient did nothing to warrant them. Such attacks are provoked, however, in the sense that these females were the only available individuals to which the redirecting Red ♂ could find a safe outlet for his otherwise thwarted aggression. These females had apparently learned to leave him alone even when they became aggressive with the onset of the reproductive season.

Straight line hierarchies were also found in Red Crossbills (*Loxia curvirostra*) (Tordoff, 1954) and in the Chaffinch (*Fringilla coelebs*) (Marler, 1955). No mention of redirection being evinced by the least dominant male is made by either of these two authors. However, Tordoff does mention that the least dominant male crossbills were particularly aggressive toward females and that this "provides an outlet for aggressive drives in the males ranked low in the male peck order." Marler does not emphasize any particularly great amount of aggression of low ranking males toward females, but both of his tables on page 111 indicate that in each case the low ranking male was involved in an inordinately great number of encounters with females. This seems to be enough evidence to suggest that low-ranking male Red Crossbills and Chaffinches may also redirect to females.

Marler (1957) came to the conclusion that Chaffinches have no innate, spontaneous appetitive behavior for fighting when in non-reproductive condition. This conclusion is in accord with my findings with redpolls. Fighting (usually only displays) only occurred in response to some external situation. This was ordinarily a situation where the attacker had to violate individual distance in order to feed, perch, bathe, drink, etc. Marler expresses

his findings in this regard thusly: "When they seek fights, it can be related either to an aggressive mood aroused by external stimuli in the immediate past, or to a learned association between fighting and other activities."

After the hierarchy had been established for a few days the amount of overt aggression was markedly reduced. It was as if each bird had learned its place and the slightest reminder was all that was necessary to maintain the order. A dominant bird would merely have briefly to orient its head toward a lower ranking individual in order to cause it to retreat or stop. Often relatively very dominant birds would continue whatever activity they were engaged in at the time (husking seeds, preening, stretching, etc.) while orienting the head briefly at the opponent—with complete effect. Most of the displays occurred between individuals close in the rank order. This is to be expected as these individuals were closest in dominance and thus the attack and escape tendencies typically involved in each case tended to be closest in strengths.

Reversal of Dominance.—As the birds demonstrated gradually increasing tendencies to behave sexually, the females gradually assumed an increasing amount of aggressiveness directed toward the males. Fig. 1A shows the Red ♀, the first to demonstrate this, having increasing success against the Yellow ♂. Fig. 1B was computed from data accumulated immediately after those for Fig. 1A and shows the reversal of dominance at a further stage. It is curious to note that the females did not become dominant over the males in general but that each female tended to select a particular male upon which to bestow her attentions. The male thus singled out behaved gradually less aggressively to "his" female as well as to other females. The Red ♂, however, continued his disproportionate aggressions against females and hence was not "chosen" by any of them as the recipient of their attentions. This, in effect, made the flock one male short and both the Red ♀ and the Green ♀ concentrated on the Yellow ♂. Aggression between these two females did not increase, however.

Hinde (1955) found the same shift in dominance in several other cardueline species, for example: Canary (*Serinus canarius*), Greenfinch (*Chloris chloris*), Bullfinch, Hawfinch, and the European Goldfinch (*Carduelis carduelis*). This situation is also found in the Chaffinch (Marler, 1955). These data and those of Hinde, Marler, etc., show that males, when in non-sexual condition, are dominant over females.

The suggestion is made that if this mechanism of female avoidance of the least dominant male, because of his redirected aggression, is working in the wild then it might serve to reduce the possibility of such "weak" males from contributing to the gene pool. There is at present no evidence from the

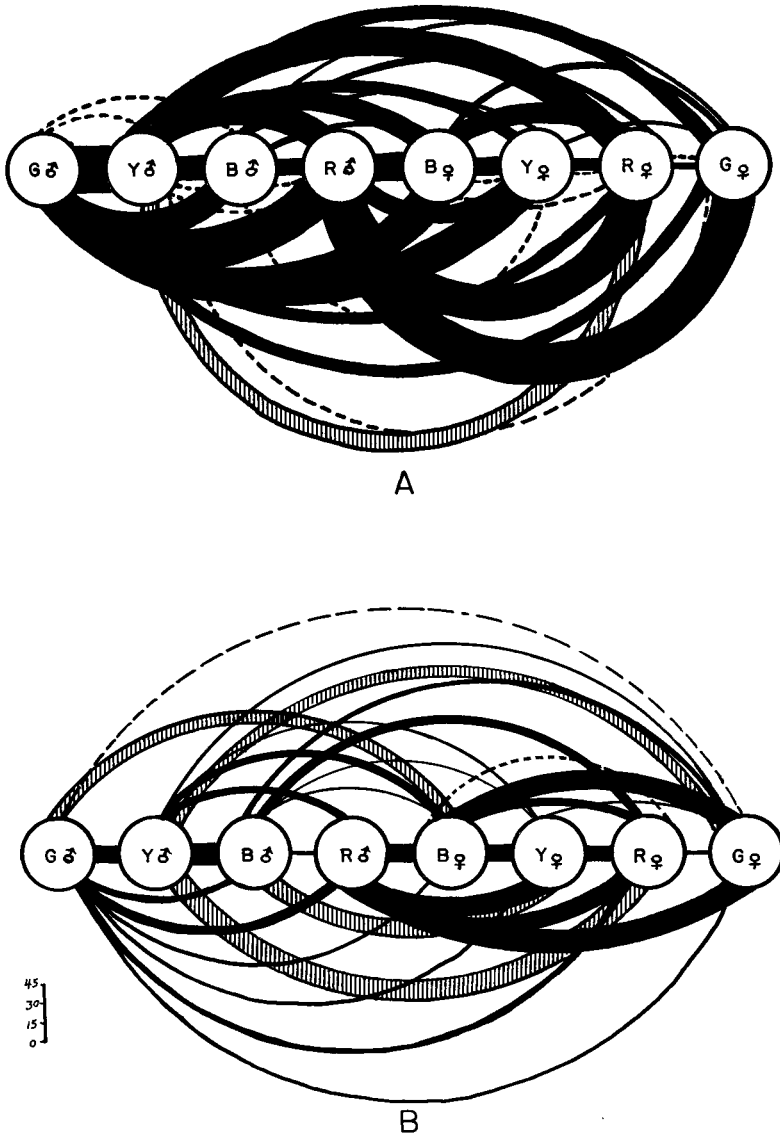


FIG. 1. Diagrams of encounters among individuals: (A) April 9 to April 22 (28 hours of observation), (B) April 23 to May 11 (38 hours of observation). Black bars and continuous lines should be read from left to right, shaded bars and dotted lines from right to left. The thickness of the bands are proportional to the number of encounters which the individual at the beginning of the bar won over the one connected to it at the end.

wild to indicate this. For a number of reasons it would seem unlikely, although the possibility remains.

The Green, Yellow and Blue males also began to sing more often and finally established territories in the small cage. Each chose a spot as far from the others as possible. The Red ♂ did not choose a territory and although he sang upon occasion, he maintained his dominance over females to the end of the investigations in early May. Actual encounters between males decreased during this early reproductive period. The songs apparently served to discourage encroachment upon the tiny territories. The males continued to feed, drink, and bathe side by side with no indication of increasing aggression among them. The fall in the amount of aggression among the males is probably due to the fact that they spent so much more time "on territory" that violations of individual distances decreased in frequency. An ordinary amount of aggression continued at feeding and watering places.

A new vocalization, other than advertising song, became apparent with the onset of this reproductive period. This was a harsh, rather high-pitched dry buzz with a speeded up ending; somewhat like the sound made by tearing a piece of coarse cloth. The function of this was not determined. This was largely because it was usually impossible to ascertain which bird uttered it at any given time. What little information I could gather seemed to indicate that it was indicative of a thwarted sexual tendency. Males were heard to give this vocalization if a female refused to be fed or if one moved away from this or other advances by the male. The advertising song, like the advertising song of many carduelines, was mainly composed of a conglomeration of the usual social and agonistic vocalizations.

The Green ♀, the lowest ranking bird, kept herself in almost perpetual fluffed posture during the non-reproductive period but changed greatly later on, during the reproductive phase, and became quite active, especially in showing aggression to the Yellow ♂. As the reproductive season progressed the females began to spend more and more time in the company of the male to which they displayed most of their aggression. The birds in the cage were now most commonly seen sitting in pairs although considerable social coherence in the entire flock was still apparent.

Another manifestation of increasing reproductive condition in these birds was the advent of "courtship feeding." This normally consisted of the male passing food to the female. The food itself was always partly digested and never whole seeds. The tendency to courtship-feed gradually increased over a period of weeks. The increase in tendency was manifested by an increase in the completeness of the motor patterns involved until finally the complete act was typically performed. This act may either be initiated by the male or by the female. The male may gently peck at the corner of the female's

mouth and she, if so inclined, will then open her mouth. The female may initiate courtship feeding by soliciting with open mouth. During courtship feeding the male stands rather erect and high on his legs, and then reaches down with his bill toward the squatting and somewhat fluffed female. Associated with the actual regurgitation of food by the male is a small amplitude, laterally-rolling vibration of the head which lasts for about a half second for each regurgitation. If the female, amenable to being fed, does not proffer her bill promptly when the male is ready with a beakful, he rapidly vibrates his mandible and tongue up and down with the bill slightly opened. This usually suffices to induce the female to permit a feeding contact. If it does not suffice, the male will then gently peck at the corner of the female's mouth. Feeding contacts ordinarily last for several seconds and sometimes as long as a minute or two. The food is rapidly pushed into the female's mouth with quick piston-like motions of the male's tongue. A bout of bill wiping by both individuals immediately follows the feeding bout. Sometimes the bills become rather generously daubed with the pasty white food.

Indications of courtship feeding began in early April. At first these were little more than repetitive gentle pecking by the males at the sides of the bills of the females. The postures of the two birds were always as described above even though the tendency to perform the feeding act was typically very low. A little later the motor patterns of the actual food regurgitation and transfer appeared but no food was actually passed. The complete act was ordinarily performed by a little past the middle of April. The frequency of occurrence of "normal" courtship feeding increased until the end of April. At this time the tendency for the males to perform this act waned markedly. The females, however, retained a strong tendency for being fed. After the first week in May courtship feeding remained a common activity but usually involved two females. It seems likely that this condition was an artifact of the conditions of captivity. It may be that because the birds were not able to perform the normal reproductive cycle, including the holding of adequate territories with the associated privacy of the pairs, the males were caused to cease their courtship feeding activities abnormally early, thus causing the females to resolve their still strong courtship feeding tendencies among themselves.

This "pseudomale" behavior on the part of the females which fed other females might be expected to be performed by females relatively higher in the dominance order than those being fed (see the excellent review paper by Morris (1955) on this subject). This was typically not the case. All of the females participated in this behavior but in the vast majority of cases the Yellow ♀ was the recipient and the Red ♀ the one assuming the "pseudomale" behavior. There were but four cases observed involving a dominant

female feeding a less dominant one, (Blue ♀ feeding Yellow ♀). The Red ♀ was observed to feed the Yellow ♀ 35 times. The reason for this is not clear to me. It may be tied up with the fact that females are normally dominant to males during the sexual phase of their behavior and/or it may be because the Yellow ♀ had an abnormally low threshold for being fed. Even when the males were feeding the females, the Yellow ♀ was the commonest recipient of food. Even though the Yellow ♀ was the usual partner it was the Blue ♂ with which she finally paired, but he was never seen to feed her! The Blue ♂ did not feed any female very much although he sang more persistently than did any of the other males. The Red ♀ was seen to be fed by males only twice; once by the Green ♂ and once by the Blue ♂. A very fleeting feeding contact was once observed in which the Red ♀ fed the Yellow ♂ (the only case of a female feeding a male observed). The Yellow ♂ was once seen briefly to feed the Red ♂ (the only male-male feeding observed). In this latter case the male demonstrating the "pseudofemale" behavior was the less dominant individual.

Unfortunately, I was forced to terminate my observations on these birds early in May and was unable to follow this behavior any further. cursory observations past early May were enough to reveal the fact that the females finally became totally dominant over their males and that Red ♂ never gave up his redirected attacks.

The following spring at Cornell University I liberated two pairs of these birds into a large (16 feet by 22 feet by 8 feet high) outside flight cage adjacent to my office. The remainder of the original birds had been liberated with the exception of a few kept in cages in the laboratory. The flight cage was densely planted in places with *Viburnum* bushes or small hemlocks. Nevertheless, the birds never successfully nested, although further sexual behavior was observed. This included further male sexual displays, copulations, and low intensity nest building.

The male displays mentioned above consisted of a posture oriented at the female and looking very much like a Wings-raised Horizontal Threat, except that the wings (held out horizontally from the body) were spread and quivered. This would be shown for many seconds at a time. The head was often tipped up slightly and the mouth held open. Males in this posture would make tiny, quick hops along a perch or on the ground toward the female. No associated vocalizations were noted although they may have been very faint. The males also performed another display which seemed to be derived from inhibited mounting of the female. This consisted of a "moth-flight" (rapid wing beats of small amplitude) while hovering just above a perched female. If the female responded by crouching, slightly spreading and quivering her wings, and raising her head and tail, the male would immediately land

on her back and attempt copulation. The duration of copulations were usually about three seconds. The female would immediately afterward ruffle and shake her plumage and engage in a bout of preening. The male usually flew off some distance and began advertising song from one of his song perches. Males also occasionally were seen to preen after copulations.

The low intensity nest building observed consisted of females gathering fine pieces of grass, rootlets, etc., and carrying one or more bits of the material about the aviary for some time. Her male would ordinarily follow her about while she was so engaged and, more frequently, would engage in both the Head Forward Threat type display or the "moth flight" display.

EXPERIMENTS ON THE EFFECTS OF STARVATION AND PROXIMITY

Shortly after the 31 redpolls were captured, experiments were conducted to investigate the effects of starvation and proximity on agonistic behavior. All birds were in the non-reproductive condition during the course of these studies.

Since food and water were continually available, hunger and/or thirst had little or no effect on the social order. Most of the encounters, as mentioned above were caused by violations of individual distances. The only effect of hunger shown by birds that were equally deprived of food for a short period (three or four hours) and then presented with food, was to prompt less dominant birds to be more "reckless" about violating the individual distances of more dominant birds. This, of course, increased the number of encounters but their outcomes did not even temporarily upset the established hierarchy. The effects of differential starving on dominance have not as yet been studied. The starvation experiments were repeated a number of times and longer periods of starvation prompted greater numbers of encounters than did shorter ones.

I have noticed that during the winter ordinarily inferior Tree Sparrows (*Spizella arborea*) in possession of a food source became temporarily higher in dominance until their tendency to eat had markedly waned. These birds dug little pits in the snow in order to expose seeds which had been placed out for them. Such birds would often dig themselves nearly out of sight. Less dominant birds would vigorously defend their pits against ordinarily more dominant birds and would be successful until they had eaten for some time; after which they could be driven off by these dominant individuals. The relationships among hunger, thirst, aggression, and dominance are not at all clear as the evidence so far is somewhat conflicting. Marler (1955) studied the effects of starvation on the social order of Chaffinches and had results similar to mine for redpolls, and the same may be said in regard to Andrew's (1957) study on *Emberiza*.

In order to study the relationship between proximity and aggression in redpolls I constructed two identical food hoppers which were placed side by side and fashioned in a manner which allowed them to be slid along a horizontal rod calibrated in centimeters. The feeding apertures of the hopper could thus be placed at various distances from one another. This set-up was essentially similar to one used by Marler (1955) in order to investigate the same phenomena in Chaffinches. His results were similar to mine. Unfortunately, I was obliged to discontinue the investigations before an adequate amount of quantitative data became available. The females tolerated each other at much closer distances than did the males. The distances involved were about 4 cm. between females and about 10 cm. between males. Heterosexual combinations were intermediate at about 7 cm. The equivalent distances for Chaffinches (Marler, 1955) were 7 to 12 cm. for females, 18 to 25 cm. for males, and 8 to 12 cm. for heterosexual combinations. Marler found that there were some differences among various flocks in this regard. Some individuals were also more tolerant than others regardless of their positions in the hierarchy. Thus the most dominant male was not necessarily the least tolerant individual. These findings were also in agreement with my observations on redpolls except I had no measure of flock differences since I worked mostly with but one flock.

The distance measurements stated are indicative of a zone, rather than an abrupt threshold distance. This zone is measured as the distance at which approximately half of the time individuals would be tolerated and half of the time not tolerated. Birds showing some indication of submissive behavior (plumage fluffing) were tolerated at closer distances than those demonstrating some intensity of aggression. Again these findings agree with those of Marler (1955).

The initial vigor demonstrated by the various birds of the flock in their agonistic encounters may have played a role in the eventual determination of the social hierarchy. All birds were placed together at the same time so that prior residence did not have a bearing on social position. It may have been that at least some of these birds "knew" each other in the wild and this may have had a bearing on the eventual social structure in the cage.

I am indebted to the R. T. French Company of Rochester, New York, for financial aid enabling me to pursue this study, and also to Dr. Edward Warner of St. Lawrence University for his friendly cooperation and for making the facilities of the Department of Biology available.

SUMMARY

Thirty-one captive redpolls were studied in the laboratory but only eight of them (four males and four females) were studied intensively. Their agonistic behavior was described and evaluated, and the Head Forward

Threat display and its variants were found to be the chief displays indicative of varying readiness to attack. They have the usual passerine fluffed submissive posture and employ a defensive-threat display involving simultaneous submissive patterns and attack patterns.

This flock of eight birds quickly developed a linear hierarchy beginning with the most dominant male and running to the least dominant female. This is similar to hierarchies found in captive Red Crossbills and Chaffinches. The least dominant male showed an unusual amount of aggression to females and this was demonstrated to be caused by redirection.

Each female eventually, as the birds gradually began to behave sexually, became dominant over a particular male. This reversal of sexual dominance is known for several other species. The least dominant male was never "chosen" by a female, presumably because of his continuing history of re-directed aggression.

Mild starvation of a few hours increased the number of encounters but did not affect the social hierarchy. It was found that females tolerate each other at smaller distances than males tolerate each other. Heterosexual combinations were intermediate in this regard.

LITERATURE CITED

ANDREW, R. J.

- 1957 Influence of hunger on aggressive behaviour in certain buntings of the genus *Emberiza*. *Phys. Zool.*, 30:177-185.

BAERENDS, G. P., R. BROUWER, AND J. Tj. WATERBOLK

- 1955 Ethological studies on *Lebistes reticulatus* (Peters). I. An analysis of the male courting pattern. *Behaviour*, 8:249-334.

BLEST, A.

- In Press The concept of ritualization. In current problems of the behaviour of animals and man (W. H. Thorpe and O. L. Zangwill). Cambridge.

DAANJE, A.

- 1950 On locomotory movements in birds and the intention movements derived from them. *Behaviour*, 3:48-98.

DILGER, W. C.

- 1956 Hostile behavior and reproductive isolating mechanisms in the avian genera *Catharus* and *Hylocichla*. *Auk*, 73:313-353.

HINDE, R. A.

- 1955-56 A comparative study of the courtship of certain finches. *Ibis*, 97:706-745; 98:1-23.

- 1956 Ethological models and the concept of "drive." *Brit. Jour. Phil. Sci.*, 6:321-331.

MARLER, P.

- 1955 Studies of fighting in Chaffinches (1) Behaviour in relation to the social hierarchy. *Brit. Jour. Anim. Behav.*, 3:111-117.

- 1957 Studies of fighting in Chaffinches (4) Appetitive and consummatory behaviour. *Brit. Jour. Anim. Behav.*, 5:29-37.

MORRIS, D.

- 1955 The causation of pseudofemale and pseudomale behaviour: a further comment. *Behaviour*, 8:46-56.
- 1956 The feather postures of birds and the problem of the origin of social signals. *Behaviour*, 9:75-113.
- 1957 "Typical Intensity" and its relation to the problem of ritualization. *Behaviour*, 11:1-12.

MOYNIHAN, M.

- 1955a Some aspects of reproductive behavior in the Black-headed Gull (*Larus ridibundus ridibundus* L.) and related species. *Behaviour Supp.*, 4:x + 201 pp.
- 1955b Types of hostile display. *Auk*, 72:247-259.

THORPE, W. H.

- 1951 The definition of some terms used in animal behaviour studies. *Bull. Anim. Behav.*, 9:34-40.

TORDOFF, H. B.

- 1954 Social organization and behavior in a flock of captive, nonbreeding Red Crossbills. *Condor*, 56:346-358.

LABORATORY OF ORNITHOLOGY, CORNELL UNIVERSITY, ITHACA, NEW YORK,
APRIL 9, 1959

 NEW LIFE MEMBER


Mrs. G. Hampton (Elizabeth Taylor) McGaw, a graduate of Mount Holyoke College (B.A.), has been interested in birds for many years, strictly as an amateur. Forty years ago Mrs. McGaw taught bird and other nature study to her Camp Fire Girls, then began speaking before women's clubs and granges on the economic value of birds, and now is an active and generous supporter of conservation organizations. She is a life member of the American Forestry Association, the New Hampshire Audubon Society, and is becoming a life member of the A. O. U.