

INDIVIDUALITY AND TERRITORIALITY AS DISPLAYED IN WINTER BY THREE PASSERINE SPECIES

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During the winter of 1931-1932 I carried on a detailed study of the everyday behavior of four individuals of each of the following three species: Golden-crowned Sparrow (*Zonotrichia coronata*), Nuttall White-crowned Sparrow (*Zonotrichia leucophrys nuttalli*), and San Francisco Spotted Towhee (*Pipilo maculatus falcifer*). The individuals studied were wild birds captured by means of bird banding traps in the vicinity of the University of California, Berkeley, California, and these birds were placed in large observation cages (sparrow cage, 10 x 3 x 6 feet; towhee cage, 12 x 2½ x 9 feet) in my room at the Museum of Vertebrate Zoology, Life Sciences Building. The cages were furnished with numerous bushes and suspended branches for perches, and a floor of earth and leaf mold.

One species was studied at a time, the Golden-crown from September 25 to November 4, 1931, approximately six weeks; the White-crown from November 4 to December 12, about the same length of time; and the Towhee from January 28 to April 6, 1932, about ten weeks. My general method was to place one individual of a species, distinguished by a numbered metal government band and a colored celluloid band, into the cage; a week later to add a second; then the third, and finally the fourth bird, at weekly intervals. After the observations the birds were released. Their subsequent histories are being followed whenever possible. For further details concerning this study, see my manuscript, "Individual and Specific Differences in the Behavior of Birds," a Master's thesis on file in the University of California Library.

INTERRELATIONSHIPS OF INDIVIDUALS AND TERRITORIALITY

It might be supposed that outside of the breeding season members of any one of the species studied, either in the field or caged, would exist peaceably side by side, with no appreciable difference in the action of one bird toward another; but such proved not to be the case. Not only was there constant activity and dispute in the business of eating, drinking and resting, but the competition of the Golden-crown over a given bit of territory, that is, feeding or resting place, was of a very different sort and intensity from that of either the White-crown or the Spotted Towhee. Putting aside for the moment the question of individuality, I shall try to explain these differences in the interrelationships of the members of a species, and their importance in the territory of the species.

With the Golden-crown, a flocking bird, the relationships of the individuals were fluid, that is, first one bird and then another gained temporary control of a position or a morsel of food. Thus, when a strange food, such as a small bunch of grapes, was put in the cage, each bird gave the typical "curiosity" reaction—it slowly approached the food with neck craned and head cocked, and with little hesitating forward jerks of the body. But any bird might be first, and any other bird might follow and drive it away. Later the first bird often returned and forced off the bird who happened to be in possession. When the birds were especially hungry and seed had been scattered about the cage, all scratched busily for a time. Under such conditions two birds might remain in the same vicinity for a moment, both feeding, before one or the other gave way. I did not see the first birds put in; the last one was greeted mildly, with a peck or two, but soon took its place on equal footing with its fellows.

Age, as indicated by the colors of the crowns, seemed to have no influence in the relationship. None of the birds had had previous experience with banding traps. All were of approximately the same size. Sex was indistinguishable. The birds occasionally rested in proximity to each other, but otherwise never moved in concerted action except under the stimulus of sudden movement or loud noise near the cage, when all fluttered against the wire, or except when, as noted above, all scratched busily.

This fluid relationship of the Golden-crown, in which any approaching bird could successfully usurp the position of any possessing bird, and in which all lived together fairly peaceably, I have called for convenience *supersedence*. (See accompanying table.)

With the White-crown and Spotted Towhee, a different relationship held, which I have described by the word *dominance*. A dominant bird, in my meaning, was a bird which over a definite period of time could successfully usurp the position of another bird, while at the same time successfully defending its own position.

With the White-crown (like the Golden-crown a flocking bird), dominance held, but the degree of dominance of any one individual was subject to change. Thus while the first bird put in, for a time assumed dominance over the second, after several days, the second bird gradually refused to give way and itself successfully took the offensive. When strange food was put in, the birds gave the curiosity reaction of craned neck and raised crest, much as did the Golden-crowns, but the bird that was dominant at the time was usually first. All birds might feed for a while, then the bird that was dominant at the time would drive away the others. A new bird was attacked with more vigor and for a longer period of time than in the case of the Golden-crown. Age, as indicated by crowns, and previous experience with banding traps, seemed to have no influence on dominance. Sex was indistinguishable. All birds were approximately the same size. There was no concerted action except under stimulus of sudden movement, loud noise, or hunger.

With the Spotted Towhee, an ordinarily solitary bird, dominance held sway rigidly. The first bird put in, a male, maintained his authority over all the rest during the entire period of captivity. The second, also a male, was next in the point of dominance; the third, a female, next; and the fourth and last bird, a female, remained the "underdog," chased by the other three. It is an interesting point here that when No. 2 was put in, No. 1 attacked him vigorously, pecking him and pursuing him all over the cage, and only gradually diminishing the force of his attacks as the days passed. But when No. 3 was put in, No. 2 and not No. 1 immediately attacked the newcomer. No. 1 continued to maintain his authority, chasing any bird that got in his path, but did not go out of his way to pursue No. 3; while No. 2 used exactly the same tactics that had been used on himself. Similarly, when No. 4 was put in, No. 3, and not No. 2 or No. 1, gave chase and harried the newcomer without pause or provocation. In each case, almost a week passed before this special pursuit of a newcomer died down.

I could detect only one difference in the attitude of the sexes toward each other—only the two males actually fought. On several occasions early in the morning as the birds were actively feeding, No. 1 approached No. 2 in the typical attacking posture, crown flat and bill outthrust with a menacing jab, but No. 2, instead of giving way, assumed a defensive posture, his head held back close to his body, but his bill facing his rival. They stood thus a second, and then sprang into the air with a flurry of feathers. In an instant they had separated again, with No. 2 in retreat and No. 1 pursuing. No. 1 always seemed to be victor in these encounters.

When strange food was put in the cage, No. 1 was always first. He would approach unhurriedly with his eye on the food, and his crown feathers often slicked down and glossy so that his head looked snake-like. If the food was something much prized, such as wood beetles, all the birds might approach and eat for a moment, the two females daring the threatening gestures of the males until they were actually turned on and driven sharply away.

All birds were mature and of approximately the same size. Previous banding experience seemed to have no effect on dominance. The birds never acted in unison except under the stimulus of sudden movement, loud noise, or hunger.

CONCLUSIONS AS TO DOMINANCE AND TERRITORIAL POSSESSION

My observations on such a small number of birds of course warrant no dogmatic conclusions. However, I can suggest a theory to explain the relationships found in various species.

To summarize: in the Golden-crown Sparrow no one bird was continually dominant; supersedence was the general rule. With the White-crown, although dominance was shown, it was constantly changing. In the Spotted Towhee, dominance was distinct and rigid.

Here is a possible solution of the differences: The two species of sparrows studied are both flocking birds, the flocks feeding, each, over a large general area. In the large group comprising a flock, each individual sparrow is accustomed to having many others feeding close by (two to three feet apart is the usual feeding distance), and it is very unlikely that any one bird could enforce its will on the whole group. Instead, there must be a constant give and take, with many small conflicts over the possession of a given bit of territory or food, but seldom a quarrel which is actually injurious to the combatants, in the main the members of the groups associating together fairly peaceably. In the Golden-crown, this situation would be represented in its extreme form. In the small conflicts over any exact bit of foraging territory, any suddenly approaching bird would have the advantage of attack over the feeding possessor. Indeed, the very fact of quick movement near-by would probably encourage the instinct to retreat. At any rate, in the majority of cases, except when all the birds were very hungry or quarrelsome, the attacker would gain the right of way undisputed, the retreating bird merely hopping off a few feet and then foraging once more. It would not even be necessary to attack, often the mere approach of another bird would be the signal for a bird to hop on, the approximately two to three foot spacing being thus maintained. This certainly seems to hold true in large flocks in the field; and with my caged Golden-crowns it definitely did hold.

It may be noted that this principle of supersedence is the exact opposite of Howard's theory of territorial possession in the breeding season. In supersedence, the intruder has the right of way; in the other the possessor has the right of way. However, the two theories are perfectly compatible. In the breeding season flocking birds have separated out, preparatory to mating and nesting, and each male chooses a particular clump of bushes or tract of shrubs in which to reside, and defends his property vigorously from all male invaders. On the other hand, out of the breeding season, all—males and females—are foraging over the same general territory and none is claiming any particular location. In the latter case, it does not seem illogical that the rights of the individual should be reversed, so that no one bird has exclusive right to a bit of territory, but must give way and share with its fellows.

With the White-crown, the principle of supersedence does not hold with the same force. Here dominance is shown, the aggressiveness of the various birds of

a group differing, some individuals being able to usurp successfully the territory of others, while defending their own against attack. But dominance thus in evidence is not fixed. During my observations on the captive birds, no one White-crown was all-important throughout the period. The relationship was constantly changing, first one individual and then another gaining dominance over its fellows. As with the Golden-crown, the argument is always over a small section of forage or roosting ground, and once the dominant bird has acquired the territory, he is usually satisfied, feeding in his new possession and warning other birds away from the vicinity, by making little rushes at them, or demonstrating with head thrust out and a vigorous *cheep*.

Here, then, is a flocking bird which, while each individual is distinct at any given time in its degree of dominance over its fellows, nevertheless forages in the same general territory with a large number of its kind, and which attacks its neighbor only when it particularly desires, and is able to usurp, a bit of territory. The aggressiveness of the individuals differs, but no one bird is constantly dominant over the whole territory.

In these two species of flocking sparrows, the treatment of a newcomer of the same species differs to about the degree that the manifestation of dominance differs. With the Golden-crown, a strange bird is received peaceably. The rule seems to be that where there are many, and no bird master, there is room for one more. The newcomer may be pecked at a few times, probably because it is a strange object; but after a few hours, or a day or two at the most, it is accepted as one of the flock, taking the same part in the supersedence of feeding as the others.

In the White-crown, the newcomer has a more hostile reception. He is attacked almost at once and subjected to considerable persecution before he is finally accepted as one of the group. An aggressive individual, however, may soon defend itself and in a day or so may even be taking the initiative in attacks.

The Spotted Towhee is a solitary bird. In the field, except for the breeding season, only one towhee is ever found, save momentarily, in any particular location. Thus it is not hard to understand the actions of the captive towhees. The first bird put in the cage evidently took possession of the whole territory. The second bird that entered was immediately attacked and chased, not from any particular foraging ground, but from anywhere in the cage, with the obvious desire of forcing it to leave the vicinity entirely. The attacks were repeated, and often consisted of actual blows given the newcomer, who made little attempt to defend himself, but constantly fled from the bill of his persecutor. As the days passed, the force of these attacks diminished, but there was never any doubt as to which was dominant. The second bird never, throughout the observations, attacked the first, although occasionally, when attacked, he defended himself with some vigor. In the short fights that ensued, however, he eventually always retreated.

With the third bird, and the fourth, the condition was the same; obviously each newcomer was considered as an intruder to be at once driven away. There can be no doubt that in the field the first bird would have quickly forced away all of the others, just as each of them in turn would have driven away intruders on his own property.

Here, in the case of a solitary bird, we have Howard's theory of territorial possession by isolation in force the year round, except, of course, that both sexes have territorial possessions and a male drives away an invading female with exactly the same promptness that is used on an invading male. But the point is, the possessor is in the right, and enforces his rights without hesitation. There is no tolerance

of a newcomer, except, as in the cage, where necessity demands, and then the dominance of the possessor is rigorously enforced. Where the birds are spread out so that each has a sufficient territory for maintenance of its food supply, such a system is highly desirable. Invasion by another bird of the same species might mean a shortage of food and hence death for both. Thus the unsociability of the Spotted Towhee, his constant hostility toward all others of his kind (perhaps even his fierce appearing eye, which is red!), is explained. It is a necessary expedient in the struggle for existence and for the survival of the species.

INDIVIDUAL DIFFERENCES AMONG BIRDS

During my study of the three species of birds, I was much interested to note a number of individual differences both in appearance and behavior among the members of the same species. Of course there were also the strictly specific characteristics of plumage—the immature and mature crowns of the sparrows, and the more brilliant coloring of the male towhees. But there were besides these, evident small variations among individuals in the way the feathers were carried and in the posture of each bird. Thus individual D among the Golden-crowns had a habit, not shared by his fellows, of frequently raising his crest. No. 1 towhee, after he had been in the cage a week or so, unlike his fellows kept his body feathers almost constantly fluffed out, so that he looked like an animated puff ball. To see this round ball of feathers, with red eye glaring, fiercely enforce its dominance over the other birds was most impressive to the observer.

However, these individual variations in physical appearance could not be trusted to distinguish the birds *without* the aid of bands or some age or sex indication. This I proved to my combined satisfaction and sorrow with the first two Golden-crowns studied. They were put into the cage the same day and without any mark of identification. Both were young, immature crowned, and as like in appearance as two peas. From the first their behavior was very different. While I had them both under constant observation during any particular day I could distinguish them by some small thing such as a ruffled crown or drooped wing, which served readily enough. But unfortunately when I returned the next morning, as likely as not the drooped wing or ruffled crown would have disappeared, and instead one bird would have a misplaced tail feather. So although they still behaved very differently, how could I be certain which was which?

Consequently, I could never be sure of the exact relationship between these two birds (A and B), and hence the question mark on the chart. However, when all four birds chased each other indiscriminately away from a prized bit of cuttlebone, with the attacker in every case displacing the bird in possession and himself being displaced, the general trend of supersedence was plain enough.

Far more important, then, than any physical variation of the individuals, were the small differences in behavior. Such differences were apparent in every activity of the birds. Thus as regards eating, Golden-crowns A and B ate small wood beetles readily, but C and D refused to touch them. Among the towhees, No. 4 was the only one to touch berries of *Berberis darwinii*, yet *she* ate them with seemingly great relish.

In perching, Golden-crown D had a special lookout upon which it almost invariably rested and from which it drove the other birds if they happened to perch there. Moreover, it had a special route to this perch which it alone used.

As regards sleeping roosts, I could not make certain whether the sparrows used the same ones every night, but the towhees did. Towhee No. 1, the dominant bird, slept on the ground in one corner behind some thick brush. Every night he retreated

there and hollowed out the leaves with his breast, appearing suddenly, to drive away with a rush, any other bird that approached. No. 2 slept in the brush in the opposite corner. No. 3 retired early to the very tip of a dead tree, where she perched in plain sight. No. 4 roosted last, in the brush as near to No. 1's corner as No. 1 would let her.

Even in drinking, all the birds were not alike. When the water dish was freshly filled and put in the cage, a few drops often clung to the outside. Although no other bird was ever seen to notice them, White-crown No. 4 was often observed hopping up and pecking off these drops. When they had disappeared it drank as usual from the water in the pan.

As regards the inter-relationships of the birds of a species, their behavior seemed to a certain degree entirely the result of specific characteristics. Thus the super-sequence of the Golden-crowns and the strict dominance order of the towhees was difficult to explain in any other manner. On the other hand, with the White-crowns, although a changing dominance apparently was the specific rule, just which bird was dominant seemed more of an individual matter. I will give one illustration.

On November 19, 1931, the last two White-crowns, Pink (marked by pink band) and No. 4, were trapped and brought to my room. At noon I banded Pink and put it into the observation cage. At first the bird lay limp in my hand. When I put it down it flew quickly to the far end of the cage and sat quietly in the bushes. For several moments the birds already in the cage, Red and Green, fed about without paying any attention to Pink. Then Green flew over, looked at Pink, and hopped away. Shortly after, Red flew up and perched near Pink. Red leaned over and with the head thrust out horizontally stared at the newcomer. Then suddenly Red pecked Pink sharply. Pink tumbled from the perch and fluttered to the ground to escape the attack. Red followed and pursued Pink about the cage. When Red desisted in order to eat, Pink hovered in the background, moving its body continuously in nervous jerks. Green in the meantime bothered neither Red or Pink unless they got in the way, in which case Green drove both from its path.

After an hour had passed, and the vigor of Red's attacks on Pink had somewhat diminished, I put the other new bird, No. 4, into the cage. No. 4 flew into the bushes and sat quietly. Both Red and Green hopped up and looked at No. 4, but did not attempt an attack. All three hopped off and began scratching. Pink still hovered in the background. After about ten minutes, No. 4 hopped down and fed with Red and Green. Red paid no attention to No. 4. Green approached until its bill touched that of No. 4. Neither bird would give way. Then Green thrust out its bill with a sharp peck. No. 4 uttered a *cheep* and kept its bill toward the attacker, but did give ground ever so slightly. Presently Green left No. 4 to scratch, and did not approach again. All the birds then fed.

By the next morning No. 4 had already gained dominance. No. 4 was the most active, the most alert, and the most pugnacious of the group. It usurped the food of the others at will except for Green, who occasionally disputed its authority. Pink remained for two weeks the underdog, forced to relinquish its position whenever it was desired by any of its companions. However, after the first day Red no longer singled Pink out for special persecution.

Even in the strict dominance of the towhees, some differences in behavior were evident. Although No. 4 towhee, a female, was fourth in dominance, she was much more rapid and alert in her reactions than No. 3. It was she, after No. 1, who rushed in to seize food when this was first put in the cage. Although chased by the other three, she always managed to get her full share.

INDIVIDUALITY IN BIRDS

The word *individuality* has been a source of much confusion in ornithology. It may be well to state at once that whenever I use the word to explain my own views I mean by it the expression, through behavior, of the slight innate physiological variations which occur in each individual of a species. This is true individuality.

Julian Huxley in his recent book on "Bird Watching and Bird Behaviour" (1930) points out that when we speak of the individuality of birds we are usually referring to the characteristics of the species and not to those of a single bird. Thus, when we say "a Robin does so and so," what we mean is that "robins do so and so." This, of course, is not a surprising way of looking at things, considering the striking similarity in both physical appearance and behavior among the various members of any one species. However, Huxley himself later points out that true individual differences are present in birds, and are worthy of study.

Howard in his two books, "Territory in Bird Life" (1920) and "Introduction to the Study of Bird Behaviour" (1929), has this same bewildering double meaning in his use of the word individuality. He comments several times in both books on the distinct variations in behavior shown by members of a given species. Indeed, the second book is devoted entirely to the consideration of the behavior during the breeding season of particular pairs of birds of certain species; and the particular pairs are frequently contrasted with other pairs and individuals of the same species to show difference in behavior. Yet in his conclusions in "Territory in Bird Life," Howard makes the following statement (p. 269),

"In winter, then, the individual loses its individuality and is subordinated to the welfare of the community, whilst in spring it regains its individuality, and all its inherited instincts which then come into operation lead to its isolation from the flock."

I must confess when I read this statement I was puzzled as to just how much Howard did mean. Interpreting the word individuality solely from the point of view of the species, the statement is of course, an extremely significant one, explaining the life cycle of a flocking bird. But was this the only sense which Howard intended? Or was he implying also that with the waning of the reproductive impulse, the bird became more of an automaton—that with gregariousness the birds not only acted together but acted alike?

In case this additional meaning may have occurred to other readers and have been accepted by them, I would like to object to it here. It is true that in the field individual variations are usually detected only in the isolation period. because then a particular bird can be recognized and studied in the particular location which it inhabits. On the other hand, in the flock, variation seems to be submerged because the individual cannot be distinguished from the group. But when this difficulty is overcome by means of bands or other devices for identification, as in my observations, individual variations become as apparent in winter as during the height of the breeding season.

Undoubtedly the awakening of the sexual impulse in spring gives stimulus to new variations of the strictly individual sort. But the mere fact that the males separate out and begin fighting for their chosen territory is no proof of true individuality. For this attribute, as Howard himself has so convincingly proved, is a species, one almost might say an avian, characteristic. The individuality of any one bird in the breeding season is evidenced in the particular locality, out of many available localities, which he chooses; in the degree of vigor and alertness with which he discovers and drives out intruding males; in the special timbre of his voice; and in

the relative rapidity of his reaction to danger. In precisely the same way, the individuality of the same bird is indicated in winter by the degree of his quickness in obtaining food; in his relative ability to perceive a menace to the group; in his degree of vigor in defending himself according to the code of the group; and in his own special habits in regard to preference for perches.

With solitary birds the constant individuality of the bird can be most clearly seen. Such birds, after the successful fulfillment of the sexual impulse, nest building, and rearing of young, continue to remain in isolation and to defend their territories. Does a solitary bird immediately lose its individuality with the wane of the reproductive impulse? And has the young bird no individuality until the maturation of the sex organs?

The obvious answer would seem to be *no*.

In conclusion, then, I have used the term individuality in birds to mean the expression, through behavior, of slight innate physiological variations. This individuality I found to be manifested in two ways.

First, in the degree of reaction to the environment. Only rarely did individuals differ in kind of reaction; this is usually a constant specific characteristic. Under this heading come differences in pugnacity, in curiosity, in alertness.

Secondly, I found birds to differ individually in the formation of minor habits, one might almost say idiosyncracies, of behavior. Under this heading come such differences as choice of a special perch and food preferences.

All these differences are admittedly slight, but the fact that they definitely occur, that they are existent and definable, deserves to be heeded.

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