DOMINANCE IN WINTER FLOCKS OF CHICKADEES

BY FRANCES HAMERSTROM

THE Black-capped Chickadee (*Penthestes atricapillus*) was chosen for this study * for several reasons: it is common and so tame that it can be baited to feeders near a house, making practicable long hours of winter observation without blinds. It is easily handled and marked, it feeds in flocks in winter, and it fights—sometimes!

Flocks of Chickadees were watched in central Wisconsin from about the first of the year until spring dispersal during three winters, from a different farm house each winter. These houses were surrounded by essentially similar cover types: scrub oak, jack and white pine, and open fields.

The difficulties in gathering dominance data from a wild population were greater than I had anticipated; however, I hardly needed to disturb the birds at all. They were behaving as would any baited or winter-fed flock.

TECHNIQUES

All birds were banded with U. S. Fish and Wildlife Service bands, and some were given additional colored celluloid bands. All birds were also marked with colored tail feathers, one or two to each bird. These were either small white feathers dyed bright shades of pink, green, orange, yellow, etc., with Diamond dyes, or naturally distinctive feathers, such as Mallard speculum, Blue Jay wing, or Prairie Chicken breast feathers.

Most feathers had to be cut down in size, and then were glued and tied to the bird's own tail feathers (Edminster, 1938), or were inserted by a modification of imping. One of the birds own tail feathers was cut off near the body, leaving a hollow stub. The tip of the shaft of a colored feather was dipped in Duco Household cement and inserted in the stub.

To keep birds perfectly still while the feather marking was going on, they were stuffed head first into a woolen sock a trifle larger than a mitten thumb.

For the most part, feather marking proved satisfactory. Birds were easily recognized without the disturbance of frequent trapping and handling. Feathers stayed on an average of at least two weeks and sometimes a month, in one instance as long as 70 days, and could be recognized at 15 or 20 yards with eight-power glasses and about half as far with the naked eye. The major disadvantage was that certain colors could be seen more easily than others.

Colored celluloid leg bands were used (in addition to the colored feathers) only in 1939–40, but I found them hard to distinguish.

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The mechanical disturbance caused by the colored feathers appeared to be very slight, even when a new feather was awry. Bands appeared to annoy the birds more than feathers.

The psychological disturbance is harder to evaluate. That birds can distinguish colors appears to be beyond question (Van Eck, 1939), although I know of no experiments on chickadees or on any closely allied species.

Schjelderup-Ebbe found considerable psychological disturbance in marked domestic chickens. Crawford (1939) summarizes his experience thus: "A very suggestive type of work was begun by Schjelderup-Ebbe on the recognition by group members of individuals belonging to the group. He altered the appearance of hens' heads by covering the comb with a bonnet, or by coloring comb and head feathers with various dyes. In most cases the transformed member of the group was treated as a stranger and was forced to work her way into the closed dominance hierarchy through fighting." Heinroth (1911) suggests that birds recognize each other largely by their faces. It is possible that these hens would have ignored tail markers.

I have imped colored feathers in tails of Chickadees, Blue Jays, White-breasted Nuthatches, House Wrens, and Prairie Chickens, and was unable to notice any change in behavior as a result of wearing a colored feather. These imped passerines never appeared to lose composure for more than a moment. Upon release, Chickadees often gave the *chickadee* call, which seems to express annoyance rather than terror; often they flew straight to a feeder a few feet away and proceeded with their interrupted meal. Dominance in no way appeared to be associated with certain colors: colors used on dominant and on subordinate birds were exchanged without a corresponding change in dominance.

Prairie Chicken (*Tympanuchus cupido americanus*) cocks, on the other hand, when imped on the booming grounds, were often forced to the edge of the ground for two or three days, and showed a loss of prestige and composure. They boomed in a half-hearted way and were easily intimidated by other cocks. I am under the impression, however, that this was due to the shock of recent handling.

Flock Composition

No individual Chickadee appeared to show a preference for feeding with any other individual, and no sign of friendships or the formation of cliques was noticed. One can simply say that birds using the feeder were apt to arrive at the feeder in groups. The members of a group took turns feeding, and left the feeder together. Groups were in no way fixed, varying in size and composition from day to day, sometimes from hour to hour. Wallace (1941), on the other hand found a definite association between certain individuals in his Chickadee flocks.

For convenience sake, I am calling a "flock" all the Chickadees which visited the feeding station during a given winter.

The flocks were not constant; newcomers appeared from time to time and regular feeders disappeared from the stations, sometimes for a week or so and sometimes permanently. It was clear from the scarcity of unmarked birds by the end of the first week of trapping that the regular visitors to the feeders were caught by that time. Thereafter, again judging by the scarcity of unmarked individuals, it was clear that the new birds were being caught and marked within a day or two of their arrival at the feeder. (There was one exception: in 1940 two trap-shy unmarked birds were seen almost daily from February 5 to February 17. On February 17, two unmarked birds were caught and thereafter there were no sight records of unmarked birds until March 2, when No. 8, a new bird, came to the feeder and was marked straightway.)

Size of Flock

I was at first led to the conclusion that size of flock was definitely correlated with severity of winter; the winter of 1936–37 shows the largest flock, the most severe cold, and the deepest snow. However, I now believe that, given reasonably suitable cover, it is the food supply over a number of years which largely determines the size of the flock. At Lenox, Massachusetts, Wallace (1941) sometimes found 40 or more Chickadees coming to one feeder at the Pleasant Valley Bird and Wild Flower Sanctuary in a day. The Sanctuary has had a decade of winter feeding.

Easily obtainable food may, in rural communities, be supplied by deliberate feeding, or by ordinary farm and household practice. The combination of dishwater dumped in the snow and feed scattered for

TABLE 1

Chickadee Flock Size at Rural Stations

Observer, locality	Winter of	Total number banded	Estimated population	Number of years station was occupied by humans		Number of years previously unoccupied by humans	Distance to nearest farm or feeder
				With winter feeding	Without winter feeding		
Leopold, Baraboo	1937–8	7	7	1		4?	2/3 mi.
	1938–9	11	11	2			2/3 mi.
	1939–40	21	21	3			2/3 mi.
Hamerstrom, Hancock	1939–40	8	8	1		9	1/3 mi.
Hamerstrom, Plainfield	1938–9	7	7	1		12?	1/3 mi.
Hamerstrom, Necedah	1936–7	24	24	2	5		1/2 mi.
Ruskowsky, Necedah	1939–40	18 (1 day)	25–30	14+			1/2 mi.

chickens may serve the birds as well as a feeder.

Table 1 gives the total winter Chickadee flocks at a number of rural banding stations in different years. The population figures vary considerably. This seemed astonishing until I noticed that, with the exception of the Necedah stations, they were *growing* populations in territories unoccupied by man during the preceding several winters. The flock size was 7 or 8 the first winter of occupancy, 11 the second, 21 the third, and of the two still older flocks observed, one was known to be larger (24 birds), and the other was estimated at 25-30 birds. It would seem that it takes at least 3 or 4 years to build a flock up to carrying capacity starting from a previously unfed flock.

In other words, increase in size of a winter flock is determined not only by conditions at the moment, but also by what food was available in the preceding few winters. This deals only with upper limits: flocks may be rapidly reduced in size by cutting off the food supply, causing a shift to other feeding places (Butts, 1930).

I do not agree with Butts' conclusions: "It is thought that the feeding stations did not increase the number of birds in the area." However, his work was done where previous feeding and the proximity of human habitations had doubtless already raised the Chickadee population well above unfed levels.

The mechanism by which a flock is built up leaves much room for speculation. Why does it take more than one year to fill up good winter territories near feeders? Chickadees come into a new territory slowly—too slowly to fill it in one year. Individuals may move rather far (I know of one band return of over 50 miles; Maxon, *in litt.*), so it might appear that moving birds should be able to fill new winter territories fairly quickly. However, during winter, when good winter territories would be recognizable as such, the cruising radius is small—usually less than a half mile (Butts, 1930; Aldo Leopold, unpubl.); thus the chances of finding a new territory would be correspondingly few. Furthermore, of the birds which did come in during winter, not all stayed. Plainly, this sort of random movement into a territory could not explain the steady building up in succeeding years.

I suspect that the key lies in tradition. Instead of repeating this random building up from a fresh start, the territory begins its second winter with a nucleus of old-timers,[1] which is added to by the slow accretion just described. It seems likely that this accretion may be made up largely of juveniles. A saturation point is probably reached in time, but I do not know how soon nor at what density.

Thus, Chickadees do not move into a new territory fast enough to fill it in one year, but individuals live long enough (3 to 8 years: Butts, 1930; Wallace, 1941), and return consistently enough to maintain its

[1] A high proportion of banded old-timers have been recovered by banders, Butts (1930). Wallace (1941) recovered 9 out of 10 banded Chickadees at the same station the following winter.

continuity. It seems likely that the habits of old, experienced birds play a strong part in determining the number wintering in a desirable location. Errington (1941) has suggested that a similar mechanism may be effective in determining covey size of Bob-whites from year to year.

Fighting

Chickadees fight, but not under all circumstances. In 1936–37 there were 66 fights (4 between unidentified birds); the flock was large (12 birds, often seen daily), and weather was severe. In 1938–39 not a single fight was observed during the entire season; the flock was small (3 or 4 birds seen daily) and weather was considerably milder. In 1939–40 the weather was again mild for the most part, though not as mild as in the preceding year. The flock was small—more than 3 birds were seen on only one day. Ten fights were seen during the season.

From my own data it would seem that the amount of fighting was proportional to the severity of the weather; however Mary Ruskowsky told me that she saw many fights in her large flock in 1939–40, the same winter in which I saw only 10 in a small flock. The behavior of the Ruskowsky flock would lead one to suspect that the size of the flock has more influence on the amount of fighting than does the weather.

Year	Max. no. birds seen per day	Severity of winter	No. of fights	No. fights per bird per day	Observer
1936–37	12	Very severe	66	.24	F.H.
1938–39	4	Mild	0	0	F.H.
1939–40	4	Moderately mild	10	.13	F.H.
1939–40	19+	Moderately mild	many	?	M.R.

Dominance

The order of dominance for any two birds was clear, but for the flock as a whole it was so complex that attempts to arrange the birds in precise order of dominance failed. As can be seen from Figure 1, dominance is largely uni-lateral. Schjelderup-Ebbe describes this type of dominance for domestic chickens as follows: "The 'peck right' was found to be uni-lateral, i.e., in 1,900 observed instances of pecking, if animal A once succeeded in worsting B, B thereafter was never observed to peck A, except on the rare occasion of a general revolt against the despot" (Crawford, 1939).

Of 76 observed fights in Chickadees in two winters, only one reversal was noticed. In 1937, No. 8 vanquished No. 10 once and was vanquished by No. 10 once; both these birds stood high in dominance. They usually won fights and were very pugnacious.

All the observed fights were about food.[2] About 1,051 feedings were noted during the winter of 1936–37, and of these, 66 involved fights.

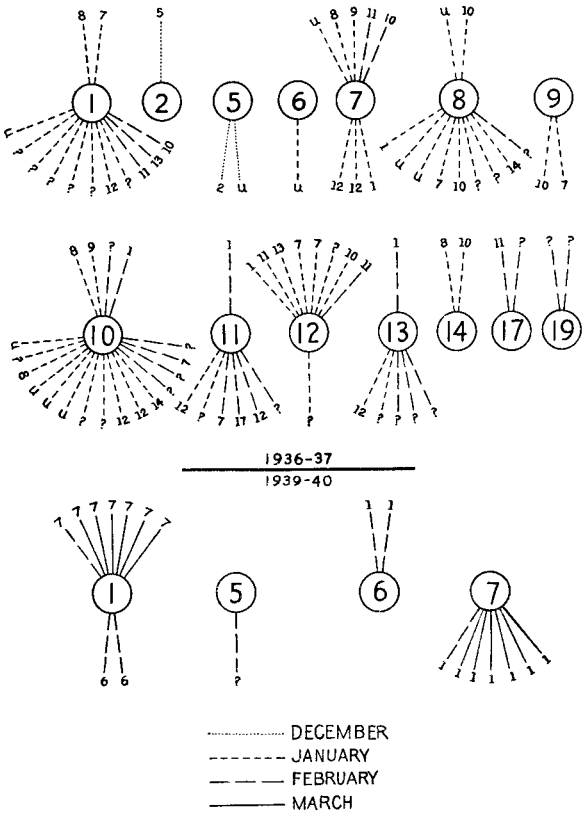

Figure 1. Fighting record.

Each diagram gives the fighting record of the individual within the small circle. Each line extending from the circle represents a fight in which the encircled bird vanquished another if the line extends below, and lost to another if the line extends above.

For example, bird No. 7 in 1936–37 vanquished No. 12 twice and No. 1 once. He was vanquished by No. 8, No. 9, No. 10, and No. 11, and by an unbanded bird new to the station. Unidentified birds are indicated by question marks.

[2] In addition to the fights listed, I saw four contacts of a very different nature: one bird flew at another. These flurries looked like Nice's (1934) description of the nuptial pounce of the Song Sparrow. These occurred on January 17, February 6, and twice on February 7, in 1937. Some of the spring fighting in 1940, though indistinguishable from earlier fighting at the feeder, may have had to do with mating behavior.

In 1939–40, 10 of 417 observed feedings involved fights. Care was taken to distinguish between fights and half-hearted encounters in which the birds did not actually touch each other. The latter were not recorded as fights.

It is reasonable to suppose that subordinate birds would often give way before a fight was precipitated. In fact Odum (1941a) uses this as a criterion of dominance in Chickadees at Rensselaerville, New York. I was unable to distinguish between giving way and peaceable exchange of position at the feeder when one bird was through and another came to take its place, so included only actual fights. Simple feeder replacements without fighting did not appear to be correlated with dominance, perhaps because I was unable to recognize the milder forms of hostility and to separate them from peaceable exchange.

Although all fighting occurred at the feeders, no significant relationship between fighting ability and *number* of feedings was found. The birds that fought most often fed most often, whether they won or lost. In 1936–37,[3] dominant birds fed slightly more often than subordinate birds, and subordinate birds fed slightly more often than the neutrals. In 1939–40, however, of the two birds using the feeder most often, the subordinate No. 1 averaged 5.6 feedings per day to the dominant No. 7's 5.2 feedings per day. There may be an advantage in being a fighter, whether a winner or a loser; on the other hand, the fact that losers fed almost as often as winners may be explainable otherwise:

(1) Birds concentrating near the feeder would tend to feed under crowded conditions and therefore be apt to fight more.

(2) The losers, having had their meals interrupted, may have had to come to the feeder more often than if they had been allowed to feed uninterrupted. Actually, vanquished birds were just as apt to feed immediately after battle as not. Nine times losers left the feeder after fighting and did not return straightway, but in 14 instances losers waited nearby and fed immediately after the winner ceased eating.

There may be a relationship between fighting ability and *amount* eaten at the feeders. In order to get as much to eat as winners, losers should have had to feed more often than winners. This was the case in the small flock in 1939–40. No. 1 at the bottom of the peck order fed more often than No. 7 at the top. In 1936–37, when the flock was large, losers did not feed as often as winners. I suspect that the influence of dominance on opportunities for feeding is negligible in small flocks but increases as flocks become large or the food supply becomes inadequate.

Behavior Toward Newcomers

Intolerance toward newcomers was demonstrated in 1936–37, although only by certain individuals, particularly by No's 10, 8, and 1. Of 66 battles, only 22 were between old-timers (banded birds). After

[3] No. 5 bird and the neutrals, with two exceptions, were in the territory less than five days each, so the data for them are very scant. "Neutrals" are birds which were never seen to fight.

the first week of trapping there was always a great preponderance of banded birds near the feeders, so chance encounters would be more apt to result in fights between old-timers. However, it appears that new birds were more apt to be involved in fights. Moreover, after the first week of trapping, no banded bird ever won a fight until he had been in the territory at least three days.

Further, old-timers appeared to have the advantage in their early encounters with newcomers: banded birds vanquished unbanded birds (newcomers) 9 times and unidentified birds (probably newcomers) 22 times, but were vanquished by unbanded birds only twice, by unidentified birds 5 times. It is likely that many of the unidentified birds were also newcomers, as the presence of colored feathers and bands was easy to detect; still, the fights were so quick that it was sometimes difficult to identify both participants.

Although Odum's (1941b) criteria of dominance differed from mine, he noted a similar attitude toward newcomers. Having moved birds from one flock to another, he observed that the new birds were subordinate to the resident birds the first day; however, they were not driven away. A few of the introduced birds stayed in the new range, displacing some of the resident birds and apparently finding their proper level in the flock.

In 1939–40 practically no intolerance toward newcomers was noticed. Of 10 fights only one was between a banded bird and an unidentified bird, a probable newcomer. This, together with the fact that no fights were seen during the winter of 1938–39, makes it seem likely that intolerance toward newcomers appears only in the larger flocks.

Behavior of Newcomers

Newcomers appeared to be at home in the territory within a few hours and were as apt to win as to lose fights from the second day on, depending upon their individual prowess. However, in 1936–37 no bird arriving after January 21, and in 1939–40 no bird arriving after February 3, ever won a fight. This may have been because the newcomers were subordinate birds which had been forced out of other territories, or it may have been an early spring movement of females into the territory.

At the very first, the behavior of newcomers in the territory was strikingly different from that of the regular visitors, but the difference is difficult to describe. New birds flew to the feeders uncertainly, and showed even more uncertainty in selecting perches and "paths" to and from feeders. I could almost always detect a new bird before I saw that it had not been banded. This uncertainty of behavior may have caused the others to pick on him.

Idiosyncrasies in Feeding

I had wondered whether subordinate birds would be forced to feed earlier or later, i.e., at "inconvenient" times. There were no favorite

feeding hours for any of the birds nor for the flock as a whole. Any bird was apt to feed at any hour of the day, regardless of his position in the hierarchy.

Birds that had been in the territory for some time formed habits which were extraordinarily persistent. For example, it was the custom of No. 1 (1940) to rotate around a piece of suet when feeding, while No. 7 (1940) faced southwest, squatted well down on his tail, and hammered awkwardly away. Upon leaving, No. 7 usually perched on the edge of the tray for a moment, but if he left in a hurry, he touched with his feet the spot where he usually perched and then flew on. I never saw him fly away without either sitting on or touching this spot.

Behavior of a Cripple

No. 8, a crippled bird, appeared on January 5, 1937. One tarsometatarsus had been recently broken near the foot and was badly swollen. He was plainly much handicapped, and was obliged to hang from the feeder (a hanging bag of suet) by one foot and to flutter while feeding. By January 19 the swelling had almost disappeared but he still fed awkwardly. A glance at Figure 1 shows that he stood high in order of dominance and indulged in a more than average number of battles, of which he won 9 of 11. He lost one fight to an unbanded bird and one to No. 10, the best fighter of the whole flock.

The cripple did not appear to be particularly dependent on the feeders, but used them about as often as the average good fighter.

Speculation on the Role of Dominance in the Wild [4]

It is not inconceivable that dominance looms progressively more important as more primitive conditions are reached. Suburban Chickadees, if forced away from the feeder, stand a very good chance of finding a new food supply within a block or two, rural Chickadees, within a mile or two; but Chickadees entirely dependent upon wild food might well be at a grave disadvantage if severe weather not only taxed their strength but also cut off part of their food supply.

The largest flock of Chickadees I ever saw far from human habitation was in the vicinity of a dead skunk which had been partly scavenged by some fairly large animal. The skunk was presumably an easy food supply. In the case of a prolonged ice storm, the small wild foods on which Chickadees usually subsist might be unavailable, but the fairly large animal might continue to scavenge on the carcass, thereby exposing it again to the Chickadees. As long as the carcass lasted, it would serve as a feeding station, and dominant and subordinate birds alike could eat. Once it was gone, all alike would starve.

In such a case dominance would have no survival value. Suppose, however, that by the time the carcass had been finished, a very small

[4] The idea that dominance may have survival value is not a new one. Noble (1939) states: "It is to a fish's advantage to be at the top of the peck order because the dominant fish in the long run secures more food and more mates."

amount of food could be gleaned through cracks in the ice-coated trees—but so little that each "find" was food enough for only a bird or two. The dominants would clearly have the advantage, to the extent that the subordinates might die of starvation and cold.

So dominance might result in forcing vanquished birds away from a limited food supply to their death. Moreover, the resulting mortality might be selective in favor of one sex. Allee (1938) has found that, when the breeding season is not in progress, in some species the males dominate over females, in others the females over the males. The two birds I succeeded in sexing did most of their fighting toward spring, when the male was dominant over the female, however, this female was the winner of two encounters with another bird. I did not determine the sex of any of the regular winter fighters. However, a high proportion of one sex might die, upsetting the sex ratio and thereby slowing up the population recovery for a few breeding seasons. A sex differential in winter-killing of Bob-whites has, in fact, been observed (Hawkins, unpubl.), although its mechanism is unknown.

Conclusions

Chickadees are only momentarily disturbed by banding and imping of tail feathers.

Winter feeding, whether deliberate or not, is apt to increase the size of the flock. At rural feeders the upper limit was not reached until at least the third year after feeding started—possibly not even by then.

Less fighting was observed in small flocks than in large.

Dominance is not linear, but is practically uni-lateral (one reversal in 76 fights).

Poor fighters did not appear to be at a disadvantage in using the feeders; they ate almost as often as good fighters. They may have been forced to come back more often, having had less at each feeding.

A cripple was high in dominance.

Newcomers can be detected by their behavior.

There appears to be some tendency for other birds to pick on newcomers, particularly in large flocks.

Survival value: I found no evidence that the individual's chance for survival is affected by his rank, at least as far as feeding is concerned. Survival value might be influenced by dominance when the flock is very large or food scarce.

References Cited

Allee, W. C.
1938 The social life of animals. W. W. Norton & Co., N.Y.

Butts, Wilbur K.
1930—1931 A study of the Chickadee and White-breasted Nuthatch by means of marked individuals. *Bird Banding,* 1:149–168; 2:1–26, 59–76.

CRAWFORD, MEREDITH P.
1939 The social psychology of the vertebrates. *Psychological Bull.*, 36:407–446.

EDMINSTER, FRANK C.
1938 The marking of Ruffed Grouse for field identification. *J. Wildlife Management*, 2:55–57.

ERRINGTON, PAUL L.
1941 An eight-winter study of central Iowa Bob-whites. *Wilson Bull.*, 53: 85–102.

HEINROTH, O.
1911 Beiträge zur biologie, namentlich ethologie und psychologie der Anatiden. *Verhandl. V. Internat. Ornith.-Kongresses, Berlin*, 1910:598–702.

NICE, MARGARET M.
1934 Song Sparrows and territory. *Condor*, 36:49–57.

NOBLE, G. K.
1939 Neural basis of social behavior in vertebrates. *Collecting Net*, 14: No. 6 (unpaged reprint).

ODUM, EUGENE P.
1941a Annual cycle of the Black-capped Chickadee. *Auk*, 58:314–333.
1941b Winter homing behavior of the Chickadee. *Bird Banding*, 12:113–119.

VAN ECK, P. J.
1939 Farbensehen und Zapfenfunction bei der Singdrossel, Turdus e. ericetorum Turton. Aus dem Zoologischen Laboratorium der Reichsuniversität Leiden: 1–50.

WALLACE, GEORGE J.
1941 Winter studies of color-banded Chickadees. *Bird Banding*, 12:49–67.

PINCKNEY, MICHIGAN