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Population Dynamics of the Black-capped Chickadee

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must be at hand if the lesson is to be repeated often enough to be absorbed. Nature centers and field stations serve a vital purpose in education of man for his place as the major animal of the natural world. Yet, at best, such facilities can only supplement and illuminate that evidence which child or man find in their everyday environment. Without question, urban botany has been neglected. This neglect must cease if man and city are to survive.

Plants are as essential to city living as they are to the family isolated on the back forty. The responsibility of the professional botanist is clear. No longer is it enough that he serve merely as a source of information on poison ivy, sick trees and deadly berries. He must function actively in the city to encourage the use of plants to ameliorate the urban environment for man and thus to make possible realization of man's full potential.

The botanist will not make the grade alone. The herb grower, the landscaper, the amateur gardener and the teacher, especially at the elementary level, must join with him to improve the urban environment and to give its inhabitants opportunity to develop skills and understanding of the uses and needs of plants, and thus of the basis for life on earth.

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POPULATION DYNAMICS OF THE BLACK-CAPPED CHICKADEE

SCOPE OF STUDY

The Black-capped Chickadee is an abundant, familiar bird in Wisconsin, known to almost everyone. In summer it is widespread in nearly all kinds of woods, although it is more numerous in younger second-growth forests, swamp forests or along forest-edges than in mature climax types. In winter, it becomes more restricted to dense thickets, bogs or swamps, especially where conifers like cedars or hemlocks occur; however, it also congregates in large numbers in towns or suburban areas wherever it can find artificially provided food at bird-feeding tables.

I and a number of UWM students have been investigating the Chickadee at the UWM Field Station since 1965. At first, we were mainly interested in the annual fat and weight cycle but as time went on, it became apparent that this species provided an ideal opportunity for investigating some of the major unsolved problems of population ecology. Since 1968 we have been concentrating our efforts more and more on a year-round study of Chickadee population dynamics.

Among the ultimate questions we are trying to answer are these:

1. Is the Chickadee population regulated, in the sense that mechanisms come into play which tend to keep the populations at a constant level, preventing extremely high or low levels from developing? Or does the population simply fluctuate at random, with no regulation?

2. What part does social behavior, especially territoriality, play in population dynamics? Wynne-Edwards, (*Animal Dispersion in Relation to Social Behaviour,* 1962) has developed an elaborate theory in which such behavior is claimed to be vitally important in regulating population levels. Other ecologists dispute this and it is at present one of the most controversial of ecological questions.

In our attempts to find some answers to these questions, our study has evolved along these lines. First, we attempt to have all the birds in our area banded and color-banded according to a code by which we can recognize each bird individually when seen with binoculars in the woods. We use a U.S. Fish and Wildlife Service numbered aluminum band plus two color-bands on the legs of each Chickadee. The abbreviations of the colors are used to form names such as BAGO, RAGO, WOAT, etc. By varying the arrangement of the bands, we can distinguish several hundred birds as individuals in the field.

Second, when we band the birds we determine the age and sex, the precise location where trapped, and, whenever possible, the parentage (in the case of young birds in the summer) and associates. Thus we know fairly accurately the age and sex composition of our population; we know in many cases the individual histories of the birds, who their parents were, who they mated with, who they were associated with in the fall or winter flocks, and other such information.

Third, during the nesting season we attempt to locate and identify all the breeding pairs not only on the Field Station itself but also in adjacent parts of Cedarburg Bog and other nearby woods. Since Chickadees become rather secretive at this season (many casual bird-watchers are unaware that Chickadees are present in the summer as well as in winter), our technique is to traverse the woods systematically and at uniform distances stop and play a tape recording of the Chickadee song or one of its calls. This usually brings about a quick response from the male territory-holder who can be identified easily when he comes to attack the recorder. We can then attempt to find its mate and in many cases we are successful also in finding its nest cavity. In certain parts of the area we take the time to try to identify the territory boundaries as precisely as possible. The tape recorder in conjunction with a mist net is also used to trap and band family groups in mid-summer or groups of young birds in late summer and fall.

As the end result of these efforts, we can prepare a map of the Field Station area showing the location of all of the Chickadee territories, the code names of the territory-holders, and in some cases the exact size and extent of the territories. From this we can determine the total population size of breeding Chickadees in the area, as well as the density in different kinds of habitat.

Fourth, in the late summer and fall we attempt to follow the dispersal movements of young Chickadees after they leave their family groups. At this time there is a general reshuffling of the population with many new associations being formed which continue into the winter flocks. Some young birds leave our area, others which have been raised elsewhere immigrate into it, and some substantial fraction undoubtedly suffers natural mortality. All of this is important to the understanding of population dynamics, but unfortunately we have not yet had sufficient time or money to do a proper job of studying these dispersal phenomena.

Fifth, we study intensively the winter flocks: their structure and social organization, their movements, and in particular their dominance hierarchies or "peck orders". That is, we attempt to determine the status in the flock of each individual bird—how aggressive it is in relation to its companions. This is crucial to evaluating Wynne-Edwards' theory since he believes that the more aggressive birds have first choice of mates and territories, are more successful in reproduction, and effectively exclude the less aggressive birds from suitable breeding areas, thus providing a homeostatic population-regulating mechanism. The rest of this article will be devoted to our methods of determining the dominance hierarchy.

DOMINANCE HIERARCHY AT A8NW IN WINTER 1970-71

In planning our population study of Chickadees, some difficult questions arose. Dominance relationships are practically impossible to study in free-living birds except at feeders, but this introduces an unnatural element into the study since winter survival patterns would be altered by the presence of an artificial food supply. Nevertheless, we felt that this could be an advantage in solving one of the main questions, that of the role of territory. If winter survival were increased artificially, then one of two things would happen: either the territories would become smaller and the breeding population more dense, indicating a minor role for territorial behavior; or the territories would remain large and some of the birds from the large winter flocks would be unable to breed, indicating a major role.

Therefore, we did establish winter feeding stations for Chickadees, in fact, we "saturated" the area with feeders in the belief that this would prevent all the birds from the whole area concentrating in one place. Each winter flock would remain within its own natural range and would not be tempted out of it by a distant feeder.

Since 1967, from November through April, we have had six feeding stations spaced within the Field Station to provide for all the winter flocks, Some flocks have ranges of movements which include only one station, while a few flocks include two stations in their range. In the winter of 1970-71, there has been one small unique group of birds which has consistently moved about over a range that includes four of the feeders.

The feeders are designed so that only one bird can feed at a time and near each feeder is a canvas blind from which an observer can watch the birds as they come to feed. During the last three winters, our plan of observation has been as follows: one day of each week we try to get six observers together for observation sessions at the six feeders. Ideally we have four one-hour sessions spaced through the day, all of the feeders being observed simultaneously. In these sessions, each Chickadee visit is recorded in relation to time, each bird is identified, and aggressive interactions or encounters between birds are noted and recorded by suitable symbols. Without going into all the details, generally each interaction takes the form of a displacement, in which one bird is driven away from the feeder by another. This ordinarily involves merely threat displays and postures, although in intense encounters vocalizations or an actual chase or attack (pecking) may take place. In any case, a decision can usually be made as to which bird is the winner and which the loser.

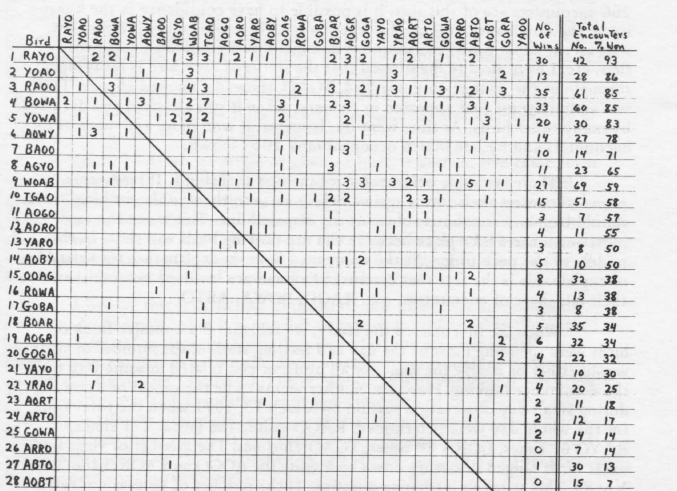

Table 1 Aggressive encounters at feeder A8NW in winter 1970-71. Wins read across, losses read down. Total encounters include some in which one participant was unidentified.

Table 1 illustrates the results of this technique for one of the feeders (designated by location A8NW) for one winter (1970-71). The results were first organized month-by-month and when this revealed that only a very few birds changed status during the winter, all of the results were combined into this one table. There were 30 birds that consistently used this feeder. These are designated by their color-code names. Reading across the table for each bird, we can see the number of encounters won over each other bird. For example, RAYO had no encounters with YOAO, won twice against BOWA, once against YOWA, and so on. Reading down the vertical column for the same bird, we see that it lost twice in encounters with BOWA, but had no other losses. The birds are listed according to their ranks in the peck-order, and this in turn is based on the win percentage. Thus, RAYO is the top-ranked bird, having won 93% of 42 encounters (including some in which the opponent was unidentified).

The figures to the right of the diagonal line indicate encounters compatible with the linear arrangement of dominance ranks. Those to the left indicate apparent inconsistencies, i.e., low-ranking birds winning encounters with others of higher rank. From our observations, it seems that most such reversals occur when the dominant bird is off balance, in an awkward position in the feeder, or taken by surprise. In any case, since only 38 (14%) of the 266 encounters are of this sort, it is possible to have confidence in the linearity of the dominance ranking. In other words, the top member is dominant over all the other birds, the second is dominant over all others except the first, etc. I have already mentioned that the status of each bird is fairly rigid throughout the winter; only one bird, TGAO, showed a marked change. This was an immigrant that appeared in January, when it was attacked and defeated by many other birds. As time went on, however, it won more and more of its encounters and by late March occupied rank 10 as shown.

There are some other points of interest to Table 1. If birds were prone to contest their status against others close to them in the ranking, there should be many encounters close to the diagonal line. This is not the case: most encounters take place between the top-ranking birds and those in the middle of the peck order. At the moment, I have no explanation for this. Also unexplainable is the fact that certain individuals are involved in more than their fair share of encounters, e.g., RAOO, BOWA, ABTO.

When we first started the study, we felt that if a cohesive flock of birds were spending most of the day at a feeding station, the number of visits would either be nearly the same for all birds, or else related in some way to the dominance ranking. However, neither seems to be the case. For example, during an all-day observation session on March 13, 1971 when the total visits for the whole day were determined, RAOO visited the feeder 111 times, RAYO 61 times, GORA 88 times, TGAO 86 times. The number of visits by other birds ranged smoothly down to 6 visits for AOGO and AORO and 2 for YAOO. This raises an intriguing question. If the number of visits is not related to dominance, what is it related to? That it is not strictly chance or random is shown by the fact that in different observation sessions on different dates, the birds are quite consistent in this respect, certain individuals coming often and others seldom, to the feeder.

Without attempting to show all the data on which they are based, some additional comments can be made about the A8NW group of birds. Twenty-four of the birds are of known sex, 14 males and 10 females. This departure from an equal ratio is not significant and judging from all our data, a 1:1 sex ratio is probably the rule in Chickadee populations.

Of the 30 birds, 14 or 47% are immature birds in their first year of age, i.e., they were hatched in 1970. Ten (33%) are 2 years old, three (10%) are 3, two (7%) are 4, and one (3%) is 5 years old. The ratio of immatures to adults is 47:53, as compared with 73:27 in 1969-70. This variation from year to year is extremely important in population dynamics. It apparently depends largely on the survival of young in summer and fall. As pointed out above, we have been unable to study this in detail; what data we have indicates that in 1969 over 80% of the young produced in the May-June nesting season were still alive in December and entered the winter flock of 1969-70. Last year, on the other hand, only about 20% survived, accounting for the prevalence of adults in this winter's flocks. The reasons for these year-to-year differences in survival are not known.

The dominance ranking is not closely correlated with age: YOAO and RAOO are both immature birds, for example, while YAOO at the bottom of the order is 3 years old. However, there is a good correlation with sex: all of the top 11 birds are males and the five lowest birds are females.

Of 10 adult birds whose 1970 territories were known, their locations varied from 0 to over .5 mile from the A8NW winter feeder. In 1969-70, one bird at this feeder came from a territory two miles away (banded by Donald Beimborn in an unrelated banding project). It is interesting to note that the top-ranking male RAYO held a territory which probably included the location of the A8NW feeder. Its mate was never discovered. The top-ranking female AOGO occupied a territory just to the southeast of the feeder. Its mate ARGO was not in the winter flock, having disappeared, presumably dying of some natural cause, in the fall of 1970.

Of 12 birds whose origin or place of birth is known, five came from territories within 0.1 mile of the feeder and others from distances up to 0.5 mile. It is obvious that this winter congregation is not a discrete year-round flock. From other sources of information, we are able to identify sub-groups that are more discrete and cohesive, but this subject is too lengthy to describe here. At any rate, the Chickadee has a complex social organization, many facets of which remain to be explored and understood.

I believe this is sufficient to illustrate our objectives and methods and to make the point that it is possible to rate each individual in the population in terms of its aggressiveness. By the end of the summer of 1971 we hope to have enough data to make some meaningful correlations between dominance status and 1) survival, 2) size, weight and physiological condition, 3) choice of mate, and 4) location, size and suitability of breeding territory. This information should provide at least partial or preliminary answers to the basic questions listed earlier in this paper. It should also suggest certain field experiments which might be designed to test these hypotheses and eventually lead to some conclusive answers.

ACKNOWLEDGMENTS

A study of this sort would be impossible without a number of colleagues. A considerable number of UWM students have worked on this project. Some are using certain aspects of it for graduate thesis subjects, others for undergraduate independent study topics. Most, however, have contributed their efforts for no tangible reward, finding this sort of research to be not only an exciting educational experience, but also a lot of fun. My co-workers have included: John Barker, Kemper Will, Thomas Pleyte, Mark Pleyte, Donald Morzenti, Wallace MacBriar, Christine Fredrich, Jeff Fredrich, John Meyer, Cindy Feil Meyer, Kate Katcher. Paul Matthiae and Drs. Robert Ficken and Millicent S. Ficken have also helped on many occasions.

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