# CHICKADEES AT ADJACENT FEEDING SITES: THE EFFECTS OF FOOD DEPRIVATION

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ALTHOUGH wintering Black-capped Chickadees (*Parus atricapillus*) have been studied at feeding sites for some time, our understanding of their winter movements and feeding patterns remains limited and imprecise. The primary purpose of the present study was to examine the effects of depriving each of two adjacent feeding sites successively of all food. Secondly the study tested the conclusions of past research regarding the size and stability of chickadee feeding congregations.

Past studies are in agreement that many chickadees remain at a given feeding site for the duration of a winter (Butts 1931, Wallace 1941, Odum 1942). They also find that individuals commonly move from one site to another in the vicinity; three-fourths of a mile is the maximum distance reported. The only previous study of the effects of food deprivation on the movement of a known congregation was conducted by Butts (1931). He found that 11 of 14 chickadees visiting one feeder moved 640 m to another feeder after the original feeding site had been deprived of food for several weeks. The birds did not return to the original feeding site when feeding was resumed, for which a 2-week interruption in feeding at all sites may have been responsible. The results were also complicated by decreased use of feeding sites with the approach of spring.

## METHODS AND SETTING

Our research was conducted near Ithaca, New York, site of the original Butts (1931) study. Ithaca lies in the beech-maple-hemlock sector of the eastern deciduous forest. The Butts study site was by Lake Cayuga at 100 m elevation; the present study was conducted in the nearby uplands at 250 m. Surrounding hills tended to be partly forested, providing a large potential breeding area at distances mostly over 1 mile.

The feeding stations were located on a 20-acre "island" of conifer plantation and deciduous woods in a "sea" of agricultural pasture and cropland (see Figure 1). The study plot was joined on the southwest corner by a 5-acre deciduous woods, itself bounded on all other sides by fields, and a band of woods along a stream adjoined the northwest corner of the plot.

Conifer plantations composed 57% of the study plot. Three-fourths of this plantation consisted of dense 25-m spruces with a few interspersed European larches. Little herbaceous or shrub growth survived under this cover. By contrast, shrubs and herbaceous plants occurred commonly under the 10-m red pine plantings that accounted for the rest of the coniferous area. The remainder of the study plot consisted of brushy field (22%), deciduous woods (14%), and lawn and shade trees (7%).

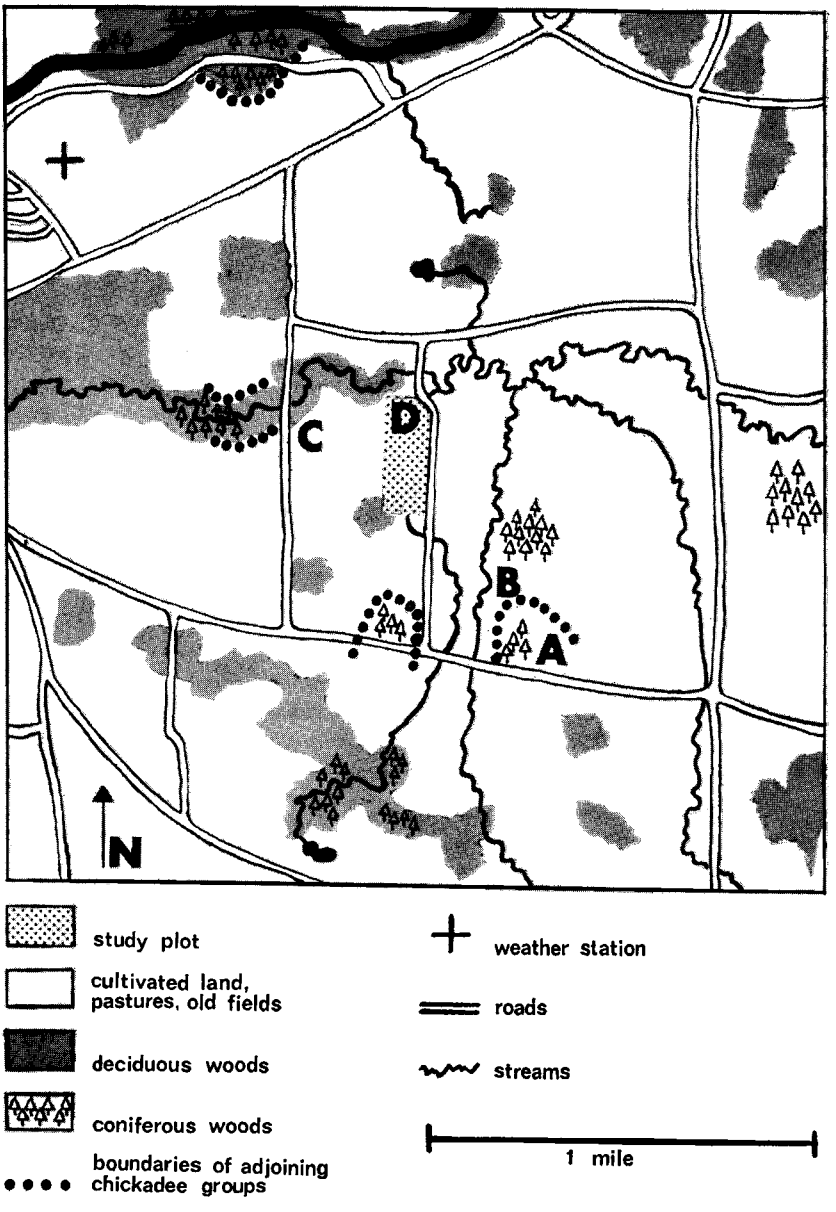



Figure 1. The extent of open land surrounding the study plot. See text for explanation of letters.

The feeding sites were 180 m apart. Site 2 was near the middle of the study plot while site 1 was close to the south end. Each had crushed corn and suet available, in addition to sunflower. The study was conducted during the winter of 1968–69. Weather data indicate a winter of average temperature, precipitation, and wind, except for February, when precipitation and wind were below average.

The first part of the study included banding and collecting descriptive data on feeding site preferences. The second part involved manipulations of food availability ("food deprivations"). During December and January chickadees visiting the feeding sites were caught in mist nets and banded. Both color bands and U. S. Fish and Wildlife bands were applied, weights taken, and the birds immediately released. Banding was continued until 90% of all feeder visits were by banded individuals. This criterion was met at site 2 by 3 January and at site 1 by 27 January; it continued to be met during February without additional banding at either station.

The basic data of the study were records of the time to the nearest minute of every chickadee visit to the feeding sites during continuous observation periods of more than 45 minutes. Any day containing an observation period was called an "observation day." Total observation time averaged 1.3 hours per observation day except during the food deprivation periods when they averaged 2.0 hours per day. Special identical sunflower feeders at each site forced chickadees to peck upward and forward to obtain a seed. This movement invariably exposed both tarsi, providing good views of the color bands. The feeders also made the recording of visits easier as only one chickadee could feed at a time.

Aggressive encounters indicating dominance were noted. An individual was said to dominate another if it chased the other from the feeder before the latter was able to feed. In a few cases when two birds fought for position near the feeder before either fed, the winner was said to dominate the loser.

Various summary measures of chickadee feeding-site visits were derived. The simplest was a "presence" measure, which indicated that a given individual was present at a given feeding site one or more times during a given observation day. Two indices of the frequency with which individuals visited feeding sites during the observation periods were formulated. The first was a simple count of the number of times an individual took a seed from a feeder (feeder visits). The second was a measure of how many times an individual returned to a feeder during the observation period (station returns). To be registered as a return, the bird had to be absent from the station for 20 minutes or more. Finally an index of "preference" between feeding sites was calculated for each individual. The percentage of total observation days that an individual visited each feeding site was determined. Preference was defined as the difference between these percentages. For example, an individual seen at site 1 on 85% of the observation days and at site 2 on 20% of the days would be said to prefer site 1 by 65%. Percentages were used in place of frequencies because the numbers of observation days at the two sites were not equal.

## RESULTS

The winter population of chickadees on the study plot was remarkable for its size, for its stability, and for the pronounced feeder preferences that most individuals exhibited. We captured a total of 47 chickadees during the December-January banding period. One died during banding. Of the 46 individuals released with bands, all but one resumed visiting one or both sites. The single individual, banded 21 December, did not

disappear, but was reported in early January visiting a feeder 0.8 km from the study plot (Figure 1, point A), where it was observed periodically during January and February. Presumably it was a member of an adjacent chickadee population, a group that was seen regularly there and which most closely adjoined the study group at point B.

Other neighboring groups of chickadees were observed repeatedly at locations indicated on Figure 1. Commonly it could be ascertained that five or six different individuals were present and that none were banded. Despite approximately 20 field hours of checking these locations outside the study plot, only one color-banded individual was seen (Figure 1, point C). It was not identified and could have been one of two individuals that disappeared after a short period of regular feeder presence. In other words, it may have switched its feeding range rather than having such a large range. The suggestion is, then, that the population of banded chickadees restricted its winter range almost totally to the 20-acre conifer-rich study plot. When reentering the plot from trips farther afield, we were impressed by the likelihood of encountering fully banded groups of chickadees, even at point D (Figure 1). Outside the plot chickadee groups were scarcer, appeared smaller in number, and were composed of unbanded individuals. In addition to indicating the small range of the banded individuals, these observations also showed the study plot contained no large group of chickadees that never visited the stations and thus remained unbanded.

Virtually all the chickadees could be found either at one feeding site or the other during observation periods conducted at widely varied times of the day. For example, at site 1, 1-hour periods began at 15:30, 10:30, and 12:30 on 27 January, 1 February, and 2 February respectively. Despite these varied times, all but one or two of the 18 individuals known to prefer site 1 came to its feeders during each observation hour. These data suggest that each individual returned to its feeding site many times each day and thus probably did not engage in long foraging trips away from the study plot.

While the chickadees centered their winter lives about the study plot and visited the feeders regularly, individuals differed in their frequency of appearance. Spearman rank correlations on site 1 data found the two measures of frequency to be somewhat correlated ($r_s$ = 0.57). In other words, there is a small association between how many separate visits an individual made to a feeding site and how often it visited the feeder while it was there. Comparing the frequency ranking, summed over a 4-day period in January, with ranking from a similar period in February, we found rank correlations of 0.61 for feeder visit data and 0.64 for station returns.

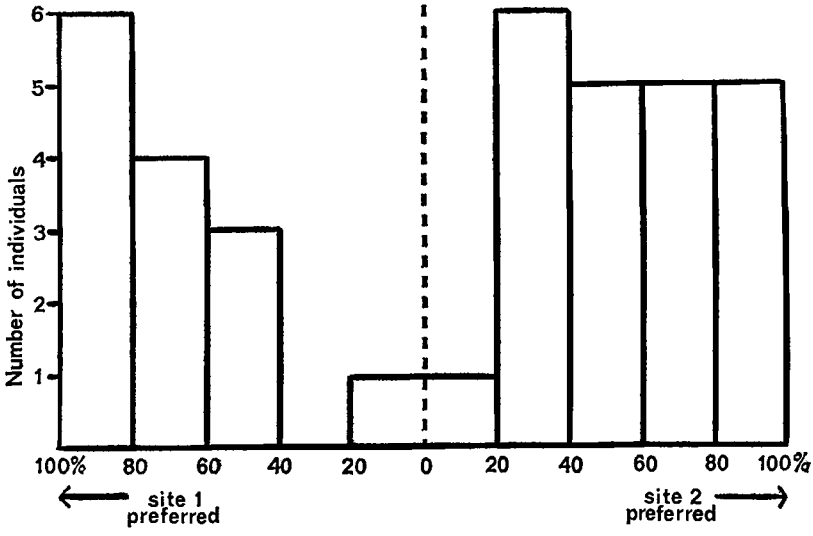



Figure 2. Histogram of feeding site preferences. Preferences are defined as the difference between the percentage of observation days an individual visited the two feeding sites.

The tendency for individuals to go occasionally on sunflower seed "rampages" contributed to the instability of the frequency data. One individual would have consumed 11.1 g of sunflower had it eaten all those taken between 11:00 and 16:00 one day. This bird weighed 12.0 g when captured a few weeks before. A whole pile of uneaten sunflower seeds was found beneath this bird's regular perch late that afternoon. Butts (1931) reported even higher rates of feeder visiting, but his individual hid seed kernels rather than just dropping many of them.

How much in-and-out movement from the study plot occurred? The absence of any major increase in the percentage of unbanded chickadee visits to the feeder suggested no important influx of new birds during the winter. The opposite was also true. Few banded individuals departed or died. Of the 46 released with bands, all but five, or a total of 89%, were still visiting the feeding sites in early March. Of these five, the fate of three was indeterminate. Two disappeared in early January, and the third never returned after its preferred feeder was emptied during the food depreviation study. Of the two known losses, one moved 0.8 km away, as indicated above, and the other was found dead near a feeder, perhaps having hit a nearby window.

The chickadees showed substantial preferences for either one feeding site or the other, despite the small distance between them. The preference

results are shown in Figure 2. If most individuals visited both feeding sites equally often, the histogram of differences would cluster about 0. The data strongly contradict this hypothesis. Most individuals preferred one feeding site to the other and the differences were often pronounced; 29% of the chickadees were never seen at their nonpreferred feeders prior to the site 1 deprivation. The birds' strong site preferences are also shown by the extremely low rate at which individuals visited both stations during periods of simultaneous observation. An average of only 2.3 individuals were seen at both sites per hour of observation. Times of movement between stations ranged from 2 to 25 minutes.

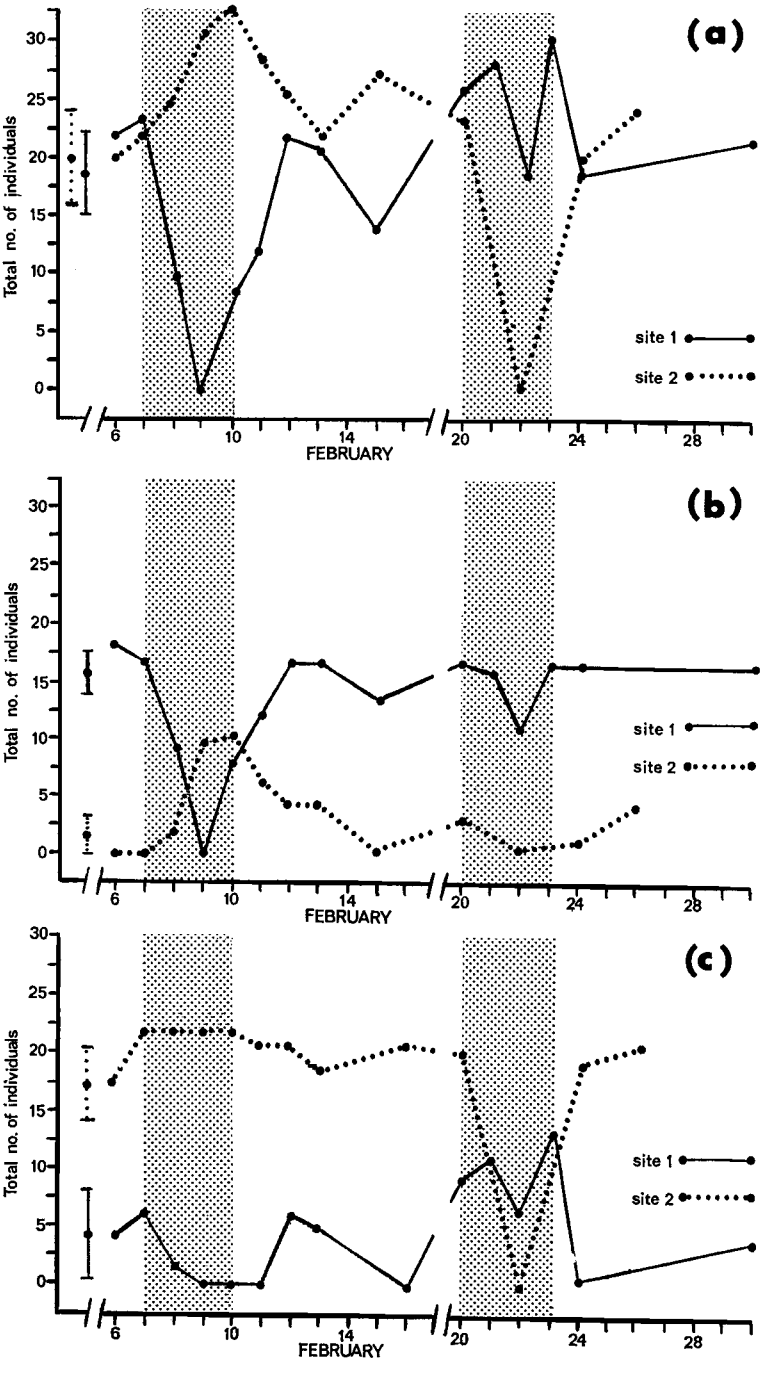
Based on the distribution in Figure 2, it was decided to consider a 20% difference as the criterion for considering an individual as showing a preference between stations. This resulted in recognizing 18 individuals preferring site 1 and 22 birds preferring site 2. By this criterion only two individuals showed no preference; both were among the three individuals uncommon at both feeding sites.

The frequency of aggressive encounters was low. The number of encounters per hour of observation ranged from 0 to 4 with a mean of 1.0 prior to the food deprivations. Data to construct a dominance hierarchy were sufficient only for site 1 preference individuals. It showed no "loops" (A→B→C→A), but one "reversal" (A→B→A). Of the encounters at site 1 prior to the site 1 food deprivation 16% were between birds preferring site 1 and those preferring site 2. As about 20% of the individuals present on an average observation day were of site 2 preference, the results do not suggest higher rates of aggressive encounter with visitors.

## Results of Food Deprivation Studies

By the end of January it was clear that the groups of chickadees at the adjacent feeding sites overlapped only partially. Most individuals visited one site much more regularly than the other, and many had never been seen at their nonpreferred site. We became increasingly interested in what effect food deprivation would have on this pattern. All food was removed from site 1 on 7 February at noon. It was restored 72 hours later on 10 February at noon. The same procedure was followed at site 2 from 20 to 23 February. Mean temperatures per day during the first and second deprivation respectively were −6° C and −1° C, mean wind velocities (at 1 m) were 7.4 km/hour and 5.4 km/hour; precipitation totaled 0.25 cm and 0.75 cm.

Figure 3 shows the general effect of the food deprivations on the presence measure. At the left side of each graph, the data from observation days prior to the site 1 deprivation are summarized to show the mean and variability in number of individuals present on an average day.


(a)
Total no. of individuals
site 1
site 2
6
10
14
FEBRUARY
20
24
28
(b)
Total no. of individuals
site 1
site 2
6
10
14
FEBRUARY
20
24
28
(c)
Total no. of individuals
site 1
site 2
6
10
14
FEBRUARY
20
24
28

The empty feeders were watched each day during the site 1 deprivation. On 8 February, some individuals continued to "check" the empty feeders but by 9 February no chickadees appeared. At site 2 the influx of individuals from site 1 increased the total number of individuals present to 76% of the total banded population, the highest percentage recorded at one site on a single day all winter (Figure 3). After food was restored at site 1, it took several days to regain the prestudy pattern.

Examining the data more closely revealed that one and only one individual showed essentially nonelastic feeder behavior, visiting only one site until it was deprived of food and then visiting only the other site, and so on. This individual was also peculiar in being the lone chickadee that fed almost exclusively from the ground under the feeders. All other individuals used the ground infrequently, if at all. While this exception is interesting, the central result is that January preference patterns remained stable into early March, despite the temporarily disruptive feeding pauses.

The rate of aggressive encounters during the influx of visitors from the other site was 0.5 encounters per hour of observation at the active site. This rate is within the range of these obtained before the food deprivation studies.

During the site 1 deprivation eight individuals, almost half of the site 1 preference group, were never seen at site 2, only 180 m away. Between the feeding deprivations, we searched for factors that could account for this pattern of selective visiting and nonvisiting, hoping to predict in advance which individuals would and would not be recorded at site 1 during the site 2 deprivation. The possibility of a relation between position in the dominance hierarchy and the visiting pattern received no support from the site 1 deprivation data. As no dominance hierarchy could be constructed for site 2 preference birds, the idea was rejected at this point.

Two other hypotheses received some support from the site 1 deprivation. The first postulated that the more an individual depends on a feeder for its winter food, the more likely it would be to change feeders under deprivation. This hypothesis arose from the fact that the first two site 1 birds to be recorded regularly at site 2 during the site 1 deprivation

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Figure 3. Number of individuals present one or more times at the feeding sites during observation days in February. The food deprivation periods are shaded. Average number of individuals (± 1 SD) present in January is shown at the left. (a) Total individuals present at each site. (b) Site 1 preference individuals. (c) Site 2 preference individuals.

TABLE 1
PREDICTED AND OBSERVED RESULTS OF THE SITE 2 FOOD DEPRIVATION

| | Hypothesis I (feeder dependency) | | Hypothesis II (bounded feeding range) | |
|---|---|---|---|---|
| | Based on feeder visits frequency | Based on site returns frequency | Based on field sightings | Based on prior presence at nonpreferred feeder |
| Number predicted to visit site 1 | 12 | 12 | —[1] | 14 |
| Number behaving as predicted | 7 | 6 | —[1] | 13 |
| Percent behaving as predicted | 58 | 50 | —[1] | 93 |
| Number predicted not to visit site 1 | 10 | 10 | 5 | 8 |
| Number behaving as predicted | 1 | 2 | 5 | 7 |
| Percent behaving as predicted | 10 | 20 | 100 | 87 |
| Total | 22 | 22 | 5 | 22 |
| Percent behaving as predicted | 36 | 36 | 100 | 91 |

[1] No predictions.

were individuals that visited site 1 with considerable frequency. The second proposed that wintering chickadees occupy bounded feeding ranges and will not cross their edges even after a 3-day food deprivation at the feeding site within their feeding range. This hypothesis emerged from an extremely small amount of field data collected prior to the site 1 deprivation. It appeared to show that site 1 chickadees not recorded at site 2 were seen in the field at the extreme south end of the plot, the location farthest from site 2.

To generate predictions under the second hypothesis for the site 2 deprivation, we gathered field data at the extreme north end of the plot. Identifying color bands, often on both legs, of chickadees active in conifers in February proved most difficult, but we found five individuals, all site 2 preference birds. All five were among the eight site 2 birds never seen at site 1 up to that time. A check showed that one or more visits to site 2 prior to the site 1 deprivation was an accurate predictor of visiting site 2 during the deprivation in 83% of the site 1 group. These factors led us to treat previous presence at the nonpreferred feeder as a second source of data potentially supporting the second hypothesis.

Table 1 shows the predictions formulated for the site 2 deprivation and the observed outcomes. To generate the predictions we assumed that the proportion of the congregation visiting site 1 would be equal to the proportion visiting site 2 during the prior deprivation. The result

was clear without statistical tests. Hypothesis I was a chance or worse-than-chance predictor of chickadee behavior. By contrast, hypothesis II was an excellent predictor of individual behavior. While we could only make five predictions on the basis of the field sightings, every one was correct. No individual ever sighted on the part of the study plot farthest from site 1 was seen there during the second deprivation.

## Discussion

The density of individuals on the study plot was about ten times greater than that found by Odum (1942) or by the other studies he summarizes. As some individuals never visited their nonpreferred station, their ranges were probably no larger than 3–6 acres, or about ten times smaller than those reported in the past (Butts 1931, Odum 1942). A number of factors no doubt contributed to this atypical concentration. First Hamerstrom's (1942) data indicated that populations build up across winters and do not peak until at least the third winter. At our site feeding had been continuous during the preceding three winters. Second the great bulk of previous research was done in deciduous rather than coniferous habitats, yet Odum (1942) found larger concentrations in coniferous than in deciduous woods. Third the coniferous study plot in the present study was separated from other wooded areas by large open fields, perhaps limiting the chickadee's accessible feeding range.

The results show more fully than past work the remarkable degree to which chickadee feeder congregations can maintain bounded winter ranges. Not only did most chickadees remain on the study plot throughout the winter, they also continued to visit one of the two feeding sites much more regularly than the other. Each visited its preferred feeding site many times each day, a finding also reported by Butts (1931), and even showed a limited degree of stability in the relative frequency of its visits. Finally birds did not visit an adjacent feeding site only 180 m outside their feeding range, even when their own feeder was empty for 3 days in midwinter.

Past research on the genus *Parus* has usually shown the winter feeding range to be the property of the wintering flock. For example Odum (1942) found that three Black-capped Chickadee flocks were almost totally segregated from each other at three closely adjacent feeders. Apparently either the feeders were placed by chance on essentially non-overlapping ranges, or the flocks somehow divided up the feeding sites in a way that achieved minimal overlap. Hinde (1952) reported that the feeding ranges of individual *Parus major* usually corresponded to the flock territory of the flock to which they belonged; he also found that *Parus caeruleus* and *Parus palustris* exhibited the same pattern.

In contrast to these previous findings, all the evidence in this study indicated that the relations between birds and space was at the individual level. First, if stable flocks arrive at a feeding site together, the presence of some individuals should predict the presence of certain others, but like Hamerstrom (1942), we could find no regular associations between individuals. Secondly individuals varied with some consistency in the number of times they returned to the feeding site each day, suggesting that the distances they traveled to and from the site varied among individuals. Third, the preference data seemed to be best interpreted on an individual rather than a group level. Instead of finding groups of birds preferring a given site, we observed virtually every possible pattern (Figure 2). Fourth, individuals gradually began feeding at the active feeding site over a period of days during the food deprivations. We never noted a sudden influx of many outsiders, as though a flock of visitors had acted in unison in abandoning its regular range. It appears then that the groups of chickadees we saw moving together in the woods represented temporary associations of individuals on the common ground of overlapping ranges rather than a semipermanent group all occupying the same range.

There remains the question of how each individual chickadee determined the position and size of its feeding range. Of particular relevance here is the fact that when both feeding sites were within an individual's range, birds still showed large differences in the relative frequency they visited the sites. No previous study of wintering chickadees has suggested that such preferences exist, yet their existence was established beyond doubt when individuals discontinued visiting their nonpreferred feeder after feeding was restored at their preferred feeder.

The chickadee seems to prefer to remain as near as possible to a given point rather than moving at random in a range. Odum (1942) found that Black-capped Chickadees use the same roost night after night. Thus the roost site is a likely focal point within the range as each day's feeding must begin and end there. In this case the size of the total feeding range might be at least partially a function of the distance between the roost and the closest feeder. There were no conifer stands near the three feeders Odum's (1942) village flocks utilized. Nevertheless each group had its regular roost in conifers and had to travel some distance to reach it. Perhaps this was why the roosts and feeders formed the most distant points of elongated ellipse-shaped feeding ranges. On our plot conifers for roosting were right next to the feeding sites so that ranges could be very small.

Loehrl (1950), reporting on *Parus palustris*, also stressed the importance of the roosting site in determining the winter range. This re-

search indicated that the 2- or 3-member wintering groups remained together for days, suggesting a common feeding range for each group. Butts (1927) found that nuthatches (*Sitta carolinensis*) had a frequently visited "headquarters" within their larger winter range. Thus at least some evidence from a related family suggests birds may prefer certain portions of the feeding range.

In summary, the location of an individual's winter feeding range apparently depends first on the location of adequate food sources and second on the location of a permanent roost site. If these conclusions are valid, we suspect that the separation of wintering chickadees from each other is not due to any repulsive forces existing between individuals or flocks. Instead the opposite situation appears to hold. Selection has favored dense concentrations at food supplies rather than dispersal across the winter woods. Even the unexpected separation between individuals on the present densely populated plot could reflect the location of roost sites and not imply the existence of repulsive forces keeping individuals apart.

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## SUMMARY

Color-banded Black-capped Chickadees were studied at adjacent feeding sites near Ithaca, New York during the winter of 1968–69. The density of individuals on the study plot was much larger than those studied in the past. The group's membership was remarkably stable during the period of study. Stability extended beyond simple membership and characterized both the preferences individuals exhibited between sites and, to a lesser extent, the frequency with which they visited the sites.

In February, after feeder population characteristics were noted, several brief food deprivations were conducted at the feeding sites. Both preference data and field sightings proved excellent predictors of which nonregular individuals would visit the site still in operation. The results strongly support the hypothesis that chickadees maintain bounded winter ranges. Contrary to previous work, they indicate that the bounded feeding range is the property of an individual chickadee rather than of a semipermanent flock. The results also show that feeding sites at different points within a feeding range are preferred differentially. An explanation of this pattern is proposed.

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