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THE EFFECTS OF SUPPLEMENTAL FEEDING ON WINTERING BLACK-CAPPED CHICKADEES (*POECILE ATRICAPILLA*) IN CENTRAL MAINE: POPULATION AND INDIVIDUAL RESPONSES

W. HERBERT WILSON, JR.[1]

ABSTRACT.—In a remote area of central Maine, I established bird feeders stocked with black oil sunflower seeds to supplement the food of wintering Black-capped Chickadees (*Poecile atricapilla*). The chickadees discovered experimental feeders established in late October within two weeks; feeders established in mid-January were discovered more slowly. Weekly censuses showed that chickadee abundance was significantly higher in the presence of the feeders. Mark-recapture analysis revealed that as many as 110 and 70 chickadees were using the feeders at the two most intensively studied sites over 2-day periods. Ambient temperature had no influence on the rate at which banded chickadees visited the feeders. The visitation rate of banded chickadees was higher during the first third of the winter; perhaps competition for feeder access increased as increasing numbers of unbanded chickadees used the feeders as the season progressed. The frequency of feeder use varied markedly among the chickadees at each feeding site; this variation could not be explained by age of the birds (first-winter versus adult birds). Variability in feeder use was also apparent for individual birds over time. *Received 24 July 2000, accepted 2 February 2001.*

Acquiring food is a particularly acute challenge that wintering passerines must meet in cold environments. Winter temperatures may dip beneath the lower critical temperature (Withers 1992) for many passerines, necessitating an increase in the metabolic rate at a time when daylength is short and food abundance is low. It is not surprising that the experimental supplementation of food results in enhanced winter survivorship of Black-capped Chickadees (*Poecile atricapilla*), demonstrating that food can be a limiting resource (Brittingham and Temple 1988, 1992a, b; Desrochers et al. 1988; Egan and Brittingham 1994).

The U.S. Fish and Wildlife Service has estimated that 63 million United States citizens feed birds (Caudill and Laughland 1998). For much of the heavily human-populated eastern seaboard, bird feeders are likely to be encountered by passerines at some time during the year; feeders are now a part of the landscape for birds. The objective of this study was to examine the effects of supplemental feeding on Black-capped Chickadees in a remote region of central Maine with a sparse human population, where no other sources of supplemental food were available for wintering chickadees. I examined both population and individual responses to supplemental food.

[1] Dept. of Biology, Colby College, Waterville, ME 04901; E-mail: whwilson@colby.edu

MATERIALS AND METHODS

This study was conducted along Long Falls Dam Road on the eastern shore of Flagstaff Lake, Maine (45° 10′ N, 70° 01′ W) at altitudes ranging from 350–440 m. Most of the study area was Maine Reserved Land, protected second growth forest. There were no human dwellings along this portion of the road and the closest bird feeders were 15 km distant. The forest was dominated by conifers: red spruce (*Picea rubens*), balsam fir (*Abies balsamea*), eastern white cedar (*Thuja occidentalis*), eastern hemlock (*Tsuga canadensis*) and eastern white pine (*Pinus strobus*). Common deciduous trees were paper birch (*Betula papyrifera*), American beech (*Fagus grandifolia*) and quaking aspen (*Populus tremuloides*).

A National Weather Service station was located at Long Falls Dam, adjacent to Long Falls Dam Road. Mean high and low monthly temperatures for the study period were −4.9 and −13.7° C for December, −5.4 and −17.4° C for January, and −4.2 and −15.7° C for February.

In October 1995, a total of 16 sites was established along 19 km of Long Falls Dam Road. Consecutive sites were at least 1.0 km apart. Each site had similar topography and forest composition (primarily red spruce and balsam fir). The 16 sites were grouped into four blocks of four consecutive sites, with each of four treatments randomly assigned once in each block. These treatments were (1) Continuous, in which sunflower seed was provided *ad libitum* from 25 October 1995 until 12 March 1996; (2) Early, in which sunflower seed was provided *ad libitum* until 11 January 1996 when the feeders were taken down; (3) Late, in which food was provided only between 11 January and 12 March 1996; and (4) Control, where food was never provided. Only three replicates of the Early treatment were conducted because of theft of the feeders at one site.

Supplemental food was provided using Magnum® sunflower seed feeders, two feeders per site except as noted, according to treatment (Continuous, Early, Late). The feeders were made of 6-mm hardware cloth, measured 18 cm in diameter and 30 cm tall, and permitted several birds to feed at once. Each feeder was suspended from a wire cable strung between two trees at a height of approximately 2 m. The two feeders were placed within 5 m of each other to facilitate simultaneous observation. Each site was visited weekly (except for two weeks in late December). The feeders were filled each week with black oil sunflower seeds. During my 2-wk absence I placed a third feeder at the two sites that received the heaviest use to ensure that the food would not be depleted. At the end of my 2-wk absence, every feeder had some seed remaining.

Each week I conducted a morning survey along Long Falls Dam road. At each of the 16 sites I stopped my car and spent three min censusing chickadees. At many of the sites, no birds had been banded so no attempt was made to identify banded birds for these counts. For sites with feeders where bird abundance was high, I recorded the maximum number of chickadees that I could see or hear at one time within the 3-min observation period.

As block effects were not evident (one-way ANOVA, $F_{3,281} = 1.112$, $P = 0.344$), the four blocks were pooled to increase the degrees of freedom for the error term. A repeated-measures two-way ANOVA was used to test for differences in numbers of birds in each of the four treatment types, for differences among dates, and for the expected interaction between date and feeder treatment. Scheffé post hoc contrasts were used to identify where significant differences lay.

On 9, 11, 18 and 29 November 1995 I mist netted birds feeding at the four Continuous sites. Each Black-capped Chickadee was banded with a unique combination of an aluminum U.S. Fish and Wildlife Service band and two color bands. Chickadees were aged as either HY (first winter) or AHY (adult) according to the amount of wear on the rectrices (Pyle 1997).

I visited the four Continuous sites repeatedly for 2-d periods every week of the study period except for the 2-wk hiatus in December. I chose two Continuous sites (Sites 1 and 12) for my most intensive observations. During each week's observations I made at least four 30-min observations at each site. I visited once in the early morning (07:00–09:30), once in the late morning (09:30–12:00), once in the early afternoon (12:00–14:00) and once in the late afternoon (14:00–16:30) over the 2-d period.

During each 30-min observation I stood at a point equidistant from the two feeders. The observation distance varied from 5–8 m, determined by optimal viewing location within the vegetation. During those 30 min I recorded the visit of every Black-capped Chickadee that came to the feeder and took a seed. Birds that came to the feeder and were displaced or frightened away before feeding were not counted. I used 7 × 42 binoculars and a hand-held audio tape recorder to observe feeders and record data. I measured the temperature at the beginning and end of each 30-min period, and used the mean of those two measures in subsequent analyses.

Individual Black-capped Chickadees were identified with various degrees of precision. Some birds that came to the feeders did not provide me a sufficient view to determine if bands were present; these chickadees were recorded as C (chickadee). I recorded unbanded birds that visited a feeder as uC (unbanded chickadee). Other birds were obviously banded but viewing angles prevented me from seeing all three bands; these birds were recorded as bC. Finally, some birds that came to the feeder could be identified by their unique combination of color bands.

For each 30-min period I calculated the total number of successful feeder visits made by the chickadees. However, two confounding effects, variable chickadee numbers and variable feeding rates, make such data difficult to interpret. To separate these two effects, I used the mark-recapture analysis program NOREMARK (White 1996) to estimate the total number of chickadees using the feeders each week. This software explicitly allows for resighting of marked but imprecisely identified individuals (bCs in the present analysis). The software also does not assume that the probability of resighting for each marked individual is the same. NOREMARK does incorporate the assumption of a closed geographic population. Before generating population estimates, I had to classify the C chickadees, i.e., those that I could not see well enough to know if they had been banded or not. I classified C chickadees for each 30-min observation period by totaling the number of uC bird visits and the number of banded bird visits (bC birds plus all visits by uniquely identified birds). The proportions of unbanded and banded birds were used to apportion the unclassified chickadees to either the banded or unbanded class.

Because the site fidelity of banded chickadees was very high, I was able to document patterns of feeder use by individuals in the population of banded birds. Using estimates of total feeder visits by all banded birds at each site, I tested for differences in feeder use as a function of time of day using the early and late morning and early and late afternoon criteria defined above. I also tested for seasonal differences, dividing the study period into early (9 December–11 January), middle (11 January–8 February) and late (13 February–12 March) winter periods. In each case, one-way ANOVA was used to test for significant differences overall and pair-wise Scheffé contrasts were used to identify means that were significantly different. Unpaired *t*-tests were used to test for differences in mean number of feeder visits of adult versus first-winter chickadees.

RESULTS

Fig. 1 presents the data for the 3-min censuses of Black-capped Chickadees at the 16 sites along Long Falls Dam Road. Two standard errors (95% confidence interval) are

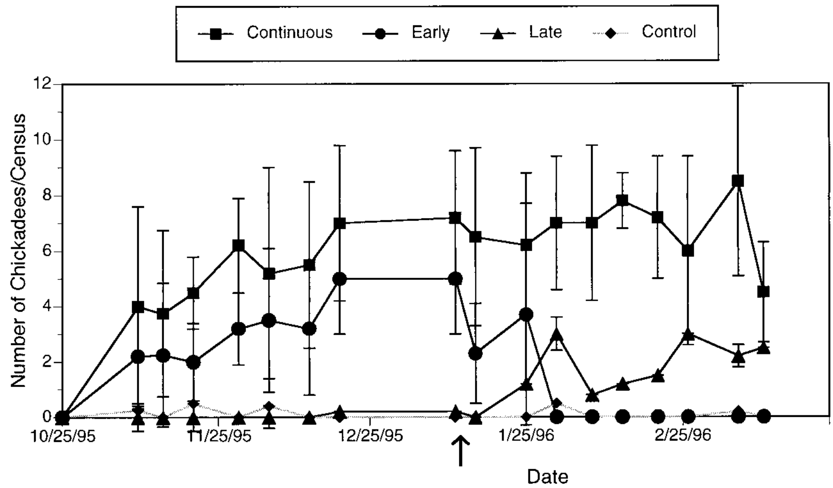

FIG. 1. Mean (± 2 SE) abundance of Black-capped Chickadees counted during 3-min observation periods at sites in central Maine during the winter of 1995–1996. Supplemental food was provided continuously (Continuous), during the first half of the winter (Early), the second half of the winter (Late) or not at all (Control). Means for the four treatments are from four replicates, except for three replicates for the Early treatment. The vertical arrow below the x-axis indicates the point at which feeding was terminated in the Early treatment and begun in the Late treatment.

shown for each mean. The two-way ANOVA for the entire dataset revealed that treatment ($F_{3,217}$ = 154.007), date ($F_{18,217}$ = 4.007), and the treatment × date interaction ($F_{54,217}$ = 3.121) were all highly significant ($P < 0.001$ in all cases). Grand means (number of chickadees/census) for each treatment were 5.5 ± 0.37 SE for Continuous, 1.8 ± 0.28 for Early, 0.8 ± 0.18 for Late, and 0.1 ± 0.05 for Control treatments. Scheffé post hoc contrasts indicated that each pair-wise combination of the four treatments was significantly different ($P < 0.01$ in all cases). These data demonstrate the obvious attraction of chickadees to bird feeders.

After the feeders were removed from the Early sites and placed at the Late sites, chickadee abundance at the Early sites declined. An increase on 25 January at the early sites is explained by a January thaw that occurred on 21–22 January and resulted in the melting of 50 cm of snow, exposing seeds previously fallen from feeders which were found by the chickadees. Subsequent snowstorms covered the fallen seeds again and the chickadee abundance at the Early sites fell to zero.

The rate at which chickadees discovered feeders with seeds varied between the early and late periods of the study (Fig. 1). The feeders at the Continuous and Early sites were established on 25 October and were discovered by chickadees by 9 November, my next visit to the sites. Chickadee density at the Early sites increased slowly until 11 January. Feeders established at the Late sites on 11 January were discovered more slowly than feeders established in October. Chickadee counts at the Late sites never reached the levels of those at the Early sites. One Late site was not found by chickadees until 13 February. Chickadee abundance at the Control sites was nearly constant and close to zero between 5 December and 14 March.

Re-encounter rates of banded chickadees at the four Continuous sites were high (Table 1), especially at Site 1 where only one chickadee

TABLE 1. Re-encounters of color-banded Black-capped Chickadees at each of the Continuous sites in central Maine on 11–12 March 1996. The birds had been banded 9–29 November 1995.

Site	Number of chickadees banded	Number of chickadees re-encountered	Re-encounter rate
1	18	17	0.94
5	23	17	0.74
12	14	9	0.64
16	14	10	0.71

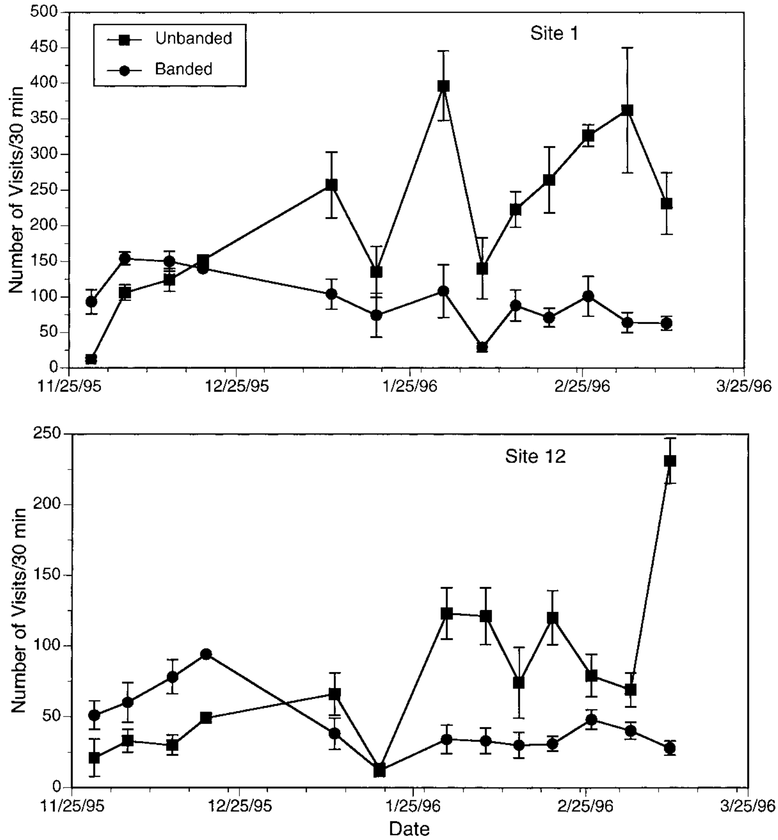

FIG. 2. Mean (± 2SE) number of feeder visits by banded and unbanded Black-capped Chickadees at Sites 1 and 12 (Continuous treatments) in central Maine during the winter of 1995–1996.

was not re-encountered on the final 2 days of the study. That chickadee had been observed only once after banding, on 11 January. Fidelity to the banding site was high; over the course of the study I recorded 3976 visits to feeders by individually identified birds, and only 19 (0.48%) of those visits were at sites other than the site where a particular bird was banded.

In Fig. 2, the mean number of visits by banded and unbanded chickadees at Sites 1 and 12 (Continuous treatment) is shown for the duration of the study period. At Site 1, the total number of visits by the 17 banded chickadees remained nearly constant over the duration of the study. The number of visits by unbanded chickadees varied greatly from week to week but showed a net increase throughout the study. At Site 12, visits by banded chickadees peaked in late December, then remained infrequent throughout the remainder of the study. Unbanded chickadee visits increased through time with a maximum during the last observation period in March.

Using NOREMARK, I generated population estimates of the chickadees visiting Sites 1 and 12 throughout the study (Fig. 3). At Site 1, the estimated number of chickadees, including the 17 banded chickadees, increased nearly linearly throughout the study, peaking at 110 birds. At Site 12, the number of chickadees present showed a general pattern of increase, peaking at 70 birds in late February.

Mean air temperature for each observation period varied from −18–11° C. However, feeding visitations were not negatively correlated with ambient temperature as expected at either Site 1 ($r^2 = 0.021$, $P > 0.50$, $n = 51$) or Site 12 ($r^2 = 0.008$, $P > 0.50$, $n = 47$).

Time of day had different relationships with visitation rate at the two sites as determined by contingency analysis ($\chi^2 = 12.06$, $P =$

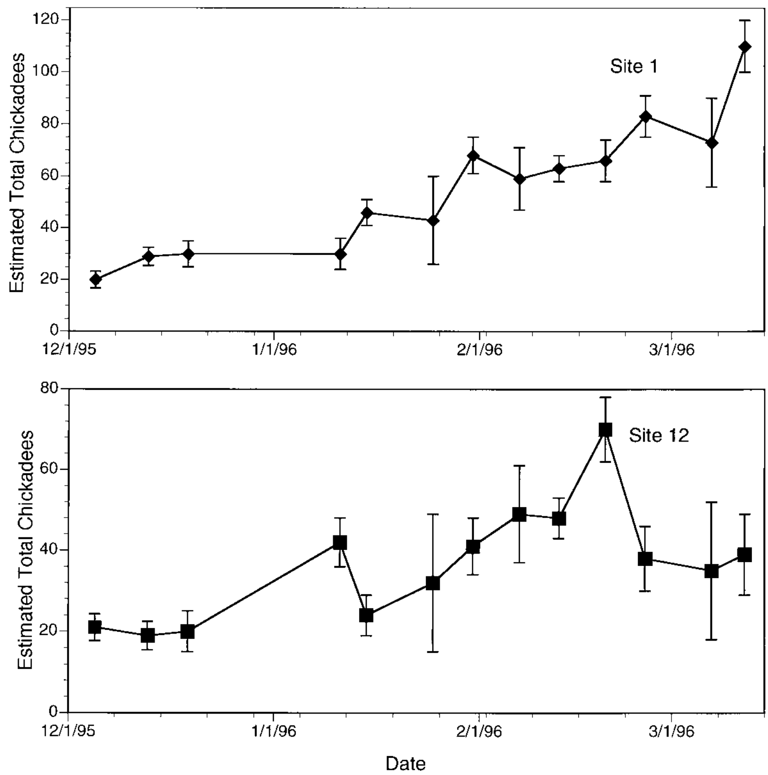

FIG. 3. Estimated number of Black-capped Chickadees at Sites 1 and 12 (Continuous treatments) in central Maine during the winter of 1995–1996. Estimates (± 2SE) are based on mark-recapture analysis using NOREMARK (White 1996).

0.007; Table 2). At Site 1 there was a trend of increasing feeder visitations during the day with the late afternoon mean significantly greater than the two morning means ($F_{3,49} = 3.256$, $P = 0.029$). At Site 12, however, there was no significant association with time of day ($F_{3,44} = 1.476$, $P = 0.234$).

Feeder visitation by the banded chickadees varied across season at Site 1 ($F_{2,50} = 8.240$, $P = 0.0008$) and Site 12 ($F_{2,45} = 13.537$, $P < 0.0001$; Table 3). At both sites, significantly more visits occurred during the first third of the study period than either the middle or last third (Scheffé contrasts, $P < 0.001$). The mean number of feeder visits during the middle and late portion of the study period were

TABLE 2. Relationship of time of day and feeder visitation by banded Black-capped Chickadees in central Maine during winter, 1995–1996. Values are means (± SE). Means which share the same letter are not significantly different (Scheffé post hoc contrasts, $P > 0.05$).

Site	Early morning (07:00–09:30)	Late morning (09:30–12:00)	Early afternoon (12:00–14:30)	Late afternoon (14:00–16:30)
1	78 AB	69 A	107 BC	119 C
	(12.9)	(13.2)	(12.2)	(13.3)
2	30 D	48 D	45 D	33 D
	(5.1)	(8.8)	(6.1)	(5.0)

TABLE 3. Relationship of stage of winter and feeder visitation by banded Black-capped Chickadees in central Maine during winter, 1995–1996. Values are means (± SE). Means which share the same letter are not significantly different (Scheffé post hoc contrasts, $P > 0.05$).

Site	Early winter (5 Dec.–11 Jan.)	Mid winter (11 Jan.–13 Feb.)	Late winter (13 Feb.–12 Mar.)
1	138 A	78 B	74 B
	(9.0)	(13.3)	(9.2)
12	62 C	26 D	37 D
	(7.2)	(4.3)	(3.4)

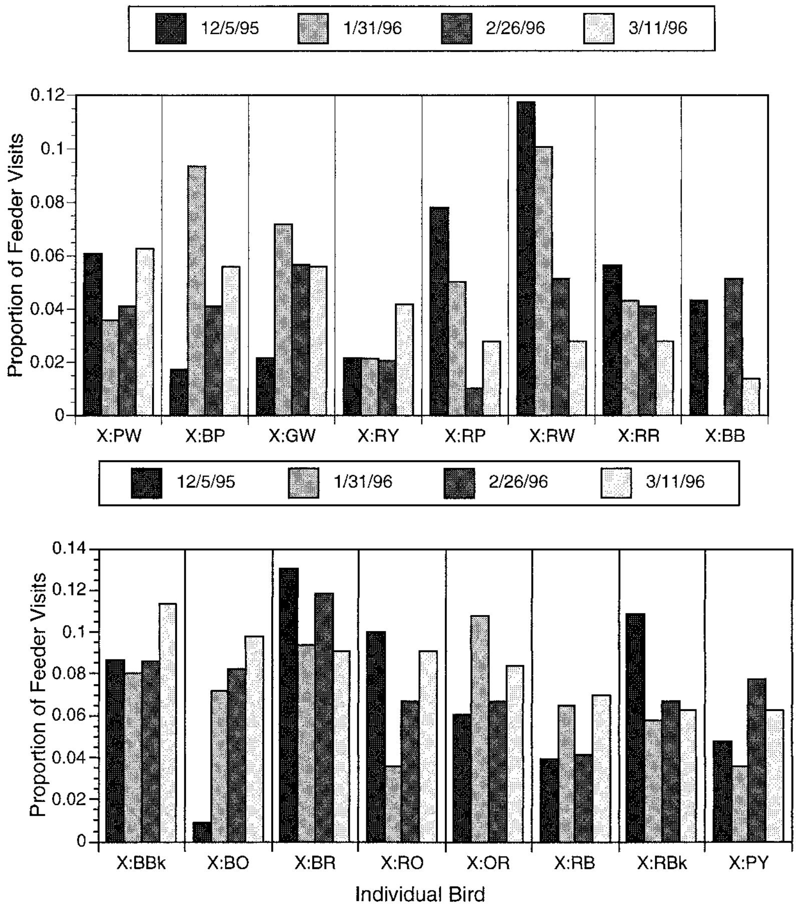

FIG. 4. Temporal variability in feeder use by color-banded Black-capped Chickadees at Site 1 (Continuous treatment) in central Maine on four different dates during the winter of 1995–1996. Values for each chickadee are the proportion of all visits by all chickadees. Band colors are B—blue, Bk—black, G—green, O—orange, P—purple, R—red, W—white, and Y—yellow.

not significantly different at either site (Scheffé contrasts, $P > 0.15$ in both cases).

Individual chickadees showed great variation in the frequency of feeder visitation. At Site 1, the most frequent visitor removed a seed from a feeder 175 times during my observations and the least frequent chickadee removed only two seeds. No relationship was detected between feeder visitations and age of the banded chickadee (first-winter versus older birds) at the four Continuous sites. The mean number of visits by adults and first-winter birds, respectively, was 101.8 ± 12.69 SE and 85.4 ± 19.06 at Site 1 ($t_{16} = 0.690$, $P = 0.500$), 35.7 ± 2.80 and 44.0 ± 6.69 at Site 5 ($t_{17} = 1.179$, $P = 0.255$), and 33.0 ± 7.48 and 31.6 ± 3.00 at Site 16 ($t_{14} = 0.067$, $P = 0.947$). At Site 12, all of the banded chickadees were first-winter birds.

As a measure of variability of feeder use, I randomly chose four weeks during the study to compare relative use of the feeders by the banded birds ($n = 17$) at Site 1 (Fig. 4). Some birds showed erratic use of the feeder (e.g., RP, BP), some increased use (e.g., BO), some decreased use (e.g., RW) and others showed relatively constant use (e.g., PW, BBk).

DISCUSSION

The experimental supplementation of food in this study had strong effects on Black-capped Chickadees at both the population and individual level. At the population level, the expected attraction of Black-capped Chickadees was clearly evident (Fig. 1). The ability of chickadees to locate the feeders more quickly early in the winter compared to later was unexpected. Perhaps chickadees had not yet established winter territories by December. More likely, chickadees may be less likely to wander widely in the coldest part of the winter because of the prohibitive energetic costs of exploring for uncertain food resources. At sites without feeders, the low occurrence of birds was striking. At lower altitudes in Maine, chickadees are often found away from feeders. The density of chickadees around Flagstaff Lake appears to be much lower (Wilson 1994).

The magnet effect of bird feeders on chickadee abundance is greater than one would expect based on point counts (Fig. 1). Mark-recapture analysis indicated that over 100 birds visited Site 1 on a single day (Fig. 3). There were rarely more than 10 chickadees visible at a site at one time but turnover was extremely rapid. On several occasions, I identified all 17 of the banded chickadees at Site 1 within 30 min.

The remarkably large number of chickadees visiting the feeders seems to be at odds with the social system typical of Black-capped Chickadees wintering in the absence of supplemental food. Winter flocks of this species normally consist of a resident mated pair and 6–10 first-winter birds not related to the resident pair (Odum 1941; Glase 1973; Smith 1976, 1994). The winter flock defends a territory against other chickadee flocks, although Desrochers and Hannon (1989) demonstrated that some undisturbed areas in Alberta without feeders may have been used by more than one flock. Territory size varied from 9.8–22.6 ha (mean of 14.6 ha) in eastern New York (Odum 1942) and 8–11 ha (mean of 9.5 ha) in central New York (Glase 1973).

Smith (1991), however, indicated that isolated feeders may regularly attract seven or more flocks, some of which travel from across the territories of four or more other flocks to reach the feeder. In western Massachusetts during the winter of 1995–1996, Black-capped Chickadees underwent a large irruption (S. Smith, pers. comm.). Although I do not have earlier banding data on the Flagstaff Lake populations, these irruptions likely occurred in central Maine as well, augmenting the number of chickadees in the area.

The benefits of territoriality must exceed the costs if territorial behavior is to remain adaptive. In areas where bird feeders are prevalent, Smith (1991) found that chickadees engaged in territorial behavior in the fall when flocks were forming but that interflock aggression decreased through time and territorial boundaries broke down. A similar pattern occurred in the present study with over 100 birds visiting the feeders in a 2-day period at Site 1 and over 70 at Site 12 (Fig. 3). Given that a typical flock size of chickadees is 10, Site 1 may have attracted several nonresident flocks, or irruptive wanderers may have accounted for some of the chickadees observed.

Chickadees from adjacent flocks appeared to continue to discover the feeders throughout the study, especially at Site 12 (Fig. 2). Visits by the banded birds, presumably mostly from the resident flock, showed a 50% decrease after the first third of the study at this site (Fig. 2, Table 3), while there was a concomitant increase in feeder visits by unbanded chickadees. Increased competition for feeder access could explain this pattern; however, agonistic interactions at the feeders were relatively infrequent. Other less subtle competitive interactions (e.g., waiting for a chickadee to leave the feeder before coming to the feeder) may have been occurring more regularly, but it was impossible for me to monitor such interactions accurately.

Ambient temperature was a poor predictor of feeder use in my study, contrasting strikingly with data for Alaskan Black-capped Chickadees. In Alaska Kessel (1976) found a highly significant negative relationship between ambient temperature and feeding rate. The difference between the two studies may be explained by the more extreme temperatures in Fairbanks, where the daily average low reached $-38°$ C, compared to $-20°$ C for the lowest daily average in my study.

One explanation for the lack of a negative relationship between air temperature and feeding rate in Maine could be differential rates of hoarding. Chickadees might hoard more seeds when the air temperature is higher and energetic demands are not as severe; such behavior would result in high feeder visitation rates at warm temperatures. However, over the course of the study I watched 99 chickadees after they had removed a seed from the feeder. In every case the chickadees flew <20 m away and opened the seed. Hoarding at greater distances may have occurred but I have no evidence that cached items represent a significant source of food for this chickadee population.

I expected that chickadees would feed most rapidly during the early morning after a night of fasting, and shortly before going to roost in the afternoon to prepare for the night's fast. At Site 12 there was no differential use of the feeders throughout the day (Table 2). At Site 1 the highest feeding rate did occur in the late afternoon but morning feeding rates were relatively low (Table 2). Chickadees may have used natural food sources in the early morning and late afternoon to gather enough food to last the 14 or more hours of darkness.

Although the literature is rich with studies on the effect of supplemental food on parid populations, virtually no information is available on individual variability in responses to supplemental food. I found a large degree (tenfold) of variation in the number of feeder visits (Fig. 4). Variability might be related to the age of the birds interacting at the feeders, e.g., dominant adults might constrain use of the feeders by first-winter birds. Alternatively, adult birds might have better foraging abilities and therefore depend less on the supplemental food at the feeders. However, neither of these factors adequately explains the variation observed in this study. For Sites 1, 5 and 16, there was no obvious relationship between rate of feeder visitation and age of the birds.

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