

JUVENILE DISPERSAL AND DEVELOPMENT OF SITE-FIDELITY IN THE BLACK-CAPPED CHICKADEE

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ABSTRACT.—Dispersal of young was studied in a non-migratory population of the Black-capped Chickadee (*Parus atricapillus*) in southeastern Wisconsin. Eighty-eight chickadees were color-banded as nestlings. After fledging, the birds remained with their parents on or near the parental territory for about 3 weeks. In late June or early July family breakup occurred suddenly, with the young moving rapidly away. Most of the birds disappeared completely from the area; 6 were later discovered in the breeding population at distances of 0.4 to ca. 11 km, with a median dispersal distance of 1.1 km. This movement appeared to be an innate dispersal mechanism. In contrast, among 103 chickadees first trapped in July and early August as independent juveniles and later found on their breeding territories, the median distance from point where banded to territory was 204 m (maximum = 1,160 m). As distances up to 2.4 km could have been detected in our study area, we conclude that by late July and August chickadees have virtually finished dispersing and are developing site tenacity in the places where they will subsequently breed. Whether dispersal also occurs in spring was investigated using the monthly patterns of arrivals and disappearances from winter feeders. Adults and summer-banded juveniles inhabiting the parts of the study area nearest the feeders arrived for the first time at the feeders in November and December, but birds from more remote areas continued to arrive through the winter and spring. In previously unbanded juveniles there was an increase in arrivals in March and April. On the basis of an analysis of loss rates by sex and age, we conclude that only about 5% of yearling males and 9% of yearling females undertake some dispersal or spacing movements in spring. Thus, in the Black-capped Chickadee the main dispersal mechanism is an innate, rapid, fairly long-distance movement of the juvenile, taking place in summer just after family breakup. A small fraction of the yearling population undertakes some dispersal movement in the winter or spring. *Received 20 February 1978, accepted 7 September 1978.*

In ecology dispersal is defined as the movement of an organism from site of birth to site of breeding (Howard 1960, Johnston 1961). Many species have evolved specific behavioral adaptations that insure that dispersal movements will take place at a certain time in the ontogeny of the individual. Additional movement may be forced on individuals of any age by environmental influences such as availability of, or competition for, resources. Howard (1960) refers to these modes of dispersal as innate and environmental, respectively, while Johnston (1961) and Berndt and Sternberg (1968) use dispersal for the former and spacing for the latter. Murray (1967) questioned the existence of innate dispersal in vertebrates and formulated a model in which the dispersal distances observed in nature could be explained solely on the spacing type of movement, "dependent only on the relative dominance of individuals in procuring a breeding site."

While the importance of dispersal in such processes as ecological succession, colonization of islands, and speciation has long been recognized, the intrapopulation aspects have been relatively neglected. Gadgil (1971: 253) states: "Dispersal is one of the most important and among the least understood factors of population biology." Many currently active areas of ecological study require thorough elucidation of dispersal mechanisms on an individual basis for full understanding of the phenomena

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under investigation. For example, the origin, development, and areal extent of song dialects in birds must depend heavily on the precise mode of dispersal in the species—how far and in what directions young birds move from their hatching sites, and at what age in reference to the age of song imprinting or song development. Likewise, many of the ideas concerning the evolution of altruistic behavior rest on certain assumptions regarding dispersal. It is of interest to know, for each species, by what mechanism dispersal is accomplished.

The present investigation of dispersal in the Black-capped Chickadee (*Parus atricapillus*) was part of an intensive study of the population dynamics of this species. The specific questions we tried to answer were: (1) do young chickadees drift slowly and haphazardly away from their birth place or parents (spacing movements), or is there a more directed or predictable movement suggestive of an innate dispersal adaptation?; (2) how far on the average do they move?; and (3) do the movements occur throughout the prereproductive parts of the birds' lives or are they restricted to more specific times?

THE STUDY AREA AND THE CHICKADEE POPULATION

The study was conducted at the University of Wisconsin–Milwaukee (UWM) Field Station, Ozaukee County, Wisconsin, at the edge of the Milwaukee metropolitan area. The Field Station lies in a morainal area of rather rough topography with substantial areas of natural vegetation. The dominating feature is Cedarburg Bog, about 800 ha in size. This has complex patterns of successional vegetation including several bog lakes, sedge marshes, bog shrub zones, large areas of bog conifer forest, and some swamp hardwood forest near the periphery. Several islands in the bog basin support upland forest, while a large interior portion is occupied by string bog, a coniferous forest-edge type of habitat found in many Canadian bogs but unusual this far south (Grittinger 1970). Surrounding the bog are many smaller bogs and swamp forests, extensive patches of upland hardwood forest, old fields in various stages of succession, and cultivated fields. Most of the interior of Cedarburg Bog is a designated Wisconsin State Scientific Area, as are parts of the UWM Field Station located on the west side of the bog.

Figure 1 depicts all the regularly utilized chickadee habitat in the Cedarburg Bog and Field Station region. The blank areas (fields, pastures, marshes) contain hedge rows, patches of trees or shrubs and the like that provide corridors for chickadee movement. There are few substantial barriers to chickadee dispersal. The chickadee population work has been conducted mainly within a 440-ha area referred to hereafter as the basic study area. The boundaries and configuration of this area were established after several years of observation of the movements of color-banded chickadees visiting the Field Station winter feeders (Fig. 1). Few of the color-banded birds range beyond the boundaries of the basic area either in winter or in the breeding season. Likewise, there are few unbanded birds breeding within the basic study area.

The basic study area contains three "intensive study areas" (Fig. 1): a 26-ha gridded plot in upland forest (but including some peripheral wetland forests), an 18-ha gridded plot in bog conifer forest, and a 16-ha ungridded area in string bog where locations could be accurately determined by natural landmarks. In or near these plots seven winter feeders were located. These were in operation from 15 November to 30 April each year. There are also many privately operated winter bird feeders around Cedarburg Bog; those that are known to us are shown in Fig. 1. Most chickadee flocks in this area are within range of winter bird feeders.

The Black-capped Chickadee is the only parid occurring in this area. Most chickadees in the basic study area are color-banded during their first winter of life and study of these birds over 10 yr has shown the population to be stable and non-migratory. We cannot exclude the possibility of an occasional bird migrating, but such birds must certainly form a negligible fraction of the population. Since 1970 breeding season populations within the basic study area have varied from 201 to 284 individuals, including non-territorial birds. There is a regular pattern in population size, high one year and low the next, although there were two low years in succession in 1973 and 1974. Although there are some slight density-dependent effects on reproduction they are not enough to offset the differences in breeding density; thus in years of higher breeding density the overall number of juveniles becoming independent is also higher than in the years of low breeding density. There is a strong inverse relationship between the density of juveniles in

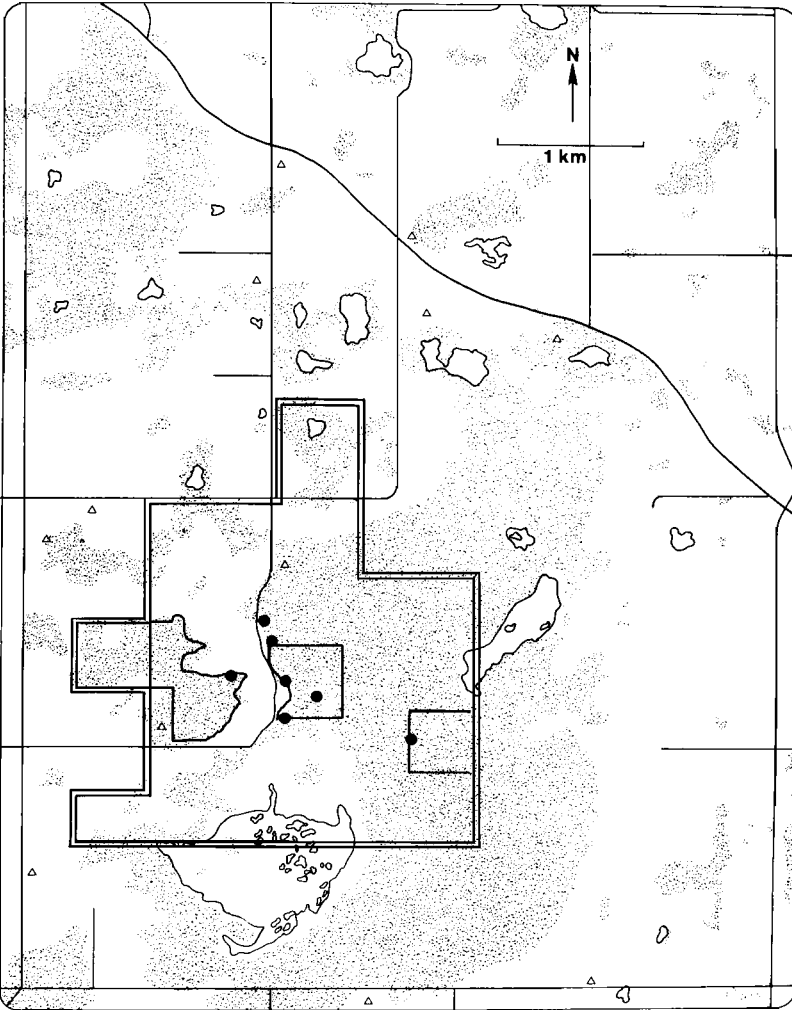


Fig. 1. Cedarburg Bog area showing all suitable chickadee habitat (stippled). Double boundaries enclose the basic study area. Single boundaries enclose the intensive study plots: from left, upland deciduous forest, bog coniferous forest, string bog. ● = UWM winter feeders. △ = privately-owned feeders.

July and August and the number of juveniles banded at that time that are recovered in the study area in winter. For reasons explained beyond we believe that this represents differences in survival rather than dispersal. Since 1970 winter populations have varied between 238 and 324, depending largely on the survival of juveniles. Details of the population dynamics will be reported elsewhere.

METHODS

Movements of birds color-banded as nestlings.—In 1970, 1971, and 1972 a total of 88 nestlings were banded from 19 nests in the intensive study areas. All of these were natural nests and most were 3–16 m above ground. Considerable effort was involved in climbing to the nests (often with the aid of a forester's swing), cutting into the nest cavity, extracting and banding the nestlings, and replacing them in the cavity after repairing it with wire and tape. Each family was given a distinctive color code. All of the banded families successfully fledged with one possible exception, a low nest with 5 nestlings that may have suffered predation, although the evidence was equivocal.

After the birds fledged in late June or early July, the color-banded families were followed and studied until the time of family breakup. Meyer continued to search for the young birds in the intensive study areas throughout July and August. Meanwhile in July and early August of each year we were systematically netting independent juveniles throughout the basic study area (see below), and we especially watched for the birds color-banded as nestlings.

In the winters following banding of the nestlings, the intensive study areas and our winter feeders were under close surveillance for these birds. In addition, Meyer conducted extensive special searches not only throughout the basic study area but through all chickadee habitat within 3 km of the banding areas, i.e. essentially all of the chickadee habitat shown in Fig. 1. Notices were placed in local newspapers asking for notification of the occurrence of color-banded birds at private feeders.

In each breeding season, a total count census of all chickadees in the basic study area was conducted, and those birds banded as nestlings that survived and entered the breeding population were then detected. The locations of such birds were plotted on large scale maps so that straight line distances from hatching site to wintering or breeding location could be measured. For precise determination of the breeding location the nest-site was used where known; however in the majority of cases the center of the pair's activity during the population's main period of incubation (8 May–5 June) had to be used. Stefanski (1967) showed that during incubation chickadees restrict their movements to small areas near the nest site.

Movements of birds banded as independent juveniles in summer.—Between 1 July and 20 August each year since 1969 we have trapped samples of independent juvenile chickadees from all parts of the basic study area except near the periphery, using portable mist nets into which birds were lured by playback of tape-recorded songs or calls. It should be stressed that in our summer trapping we caught only a fraction (perhaps 25–50%) of the juvenile chickadees present in the area.

Birds banded as independent juveniles were retrapped at the winter feeders and individually color-banded and then detected during the annual breeding season censuses, as described above. Straight line distances were measured between the sites where captured in July or August and the places where located the next breeding season.

Movements in the fall, winter and spring.—A general bird-netting operation in the intensive study areas in the fall of each year provided much information on the locations and movements of both juvenile and adult birds. In winter and early spring the feeders were under observation at least 1 day a week and usually more frequently. Detailed records were kept of the locations, dates, and times of occurrence of color-banded birds at the feeders.

Age and sex determination.—Because this population has been color-banded since 1967 the ages of most birds in the population since 1970 have been accurately known. Birds first trapped after early November could not be aged by the standard methods of plumage features or skull ossification. However, as the study area was initially set up to encompass the flock ranges of all birds likely to visit the winter feeders, and as most adults in the area at the beginning of each winter are already banded, we believe that a high proportion, perhaps 90%, of the unbanded birds trapped in winter and spring are first-year birds.

Sex was determined provisionally at the time of first capture by wing chord measurements and later verified by behavioral characteristics during the breeding season.

RESULTS

Onset of post-fledging dispersal.—Observations of six families in the upland woods showed that after the young fledged the families stayed together for about 20 days (Holleback 1974). Generally they remained within or close to the parents' original territories, but occasionally families were seen up to 300 m outside the parent's nearest observed boundary. Family dissolution was abrupt, i.e. on one day the parents and young were observed together, while on the next only the parents could be located. Again, a few exceptions were noted, when parents were seen still feeding and caring for some of their offspring while others were seen in distant places. We had 19 observations of at least 12 different color-banded juveniles from the 6 families in the 3 weeks following attainment of independence. These varied from 180 to 760 m from their nest sites, and from 50 to 590 m from the nearest locations where they had been seen with their parents. However these birds were not subsequently seen

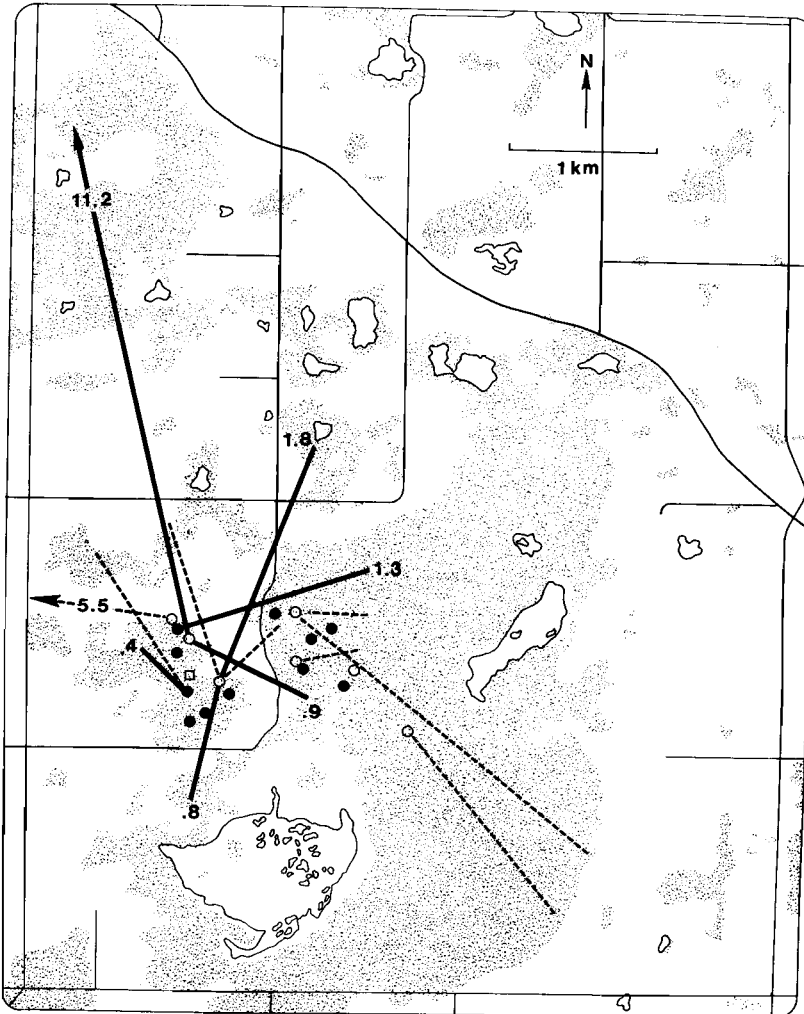


Fig. 2. Dispersal of chickadees banded as nestlings. □ = 1970 nest; ○ = 1971; ● = 1972. Broken lines connect birthplace and winter location. Solid lines connect birthplace and breeding location. Numbers at ends of solid lines are distances in km. All birds found breeding were also located in winter but their winter locations are not shown.

in these same places and were evidently in transit at the times of observation. Most of the 88 birds banded as nestlings disappeared completely from the intensive study area immediately after family breakup.

Only a few attempts were made to track individual juvenile birds during this period and these were usually unsuccessful. On 3 July 1976 Weise followed one unbanded independent juvenile at a distance without disturbing it. In about 30 min, flitting from tree to tree and pausing now and then for foraging, it moved 500 m in a generally southerly direction, passing unaccosted through three adult territories. It was then approached by two other juveniles, and there was a brief chase and some dominance or aggressive calls. The bird under observation then moved 200 m farther south at which point it was lost to view while still continuing in the same direction. We believe this exemplifies the sort of movement involved.

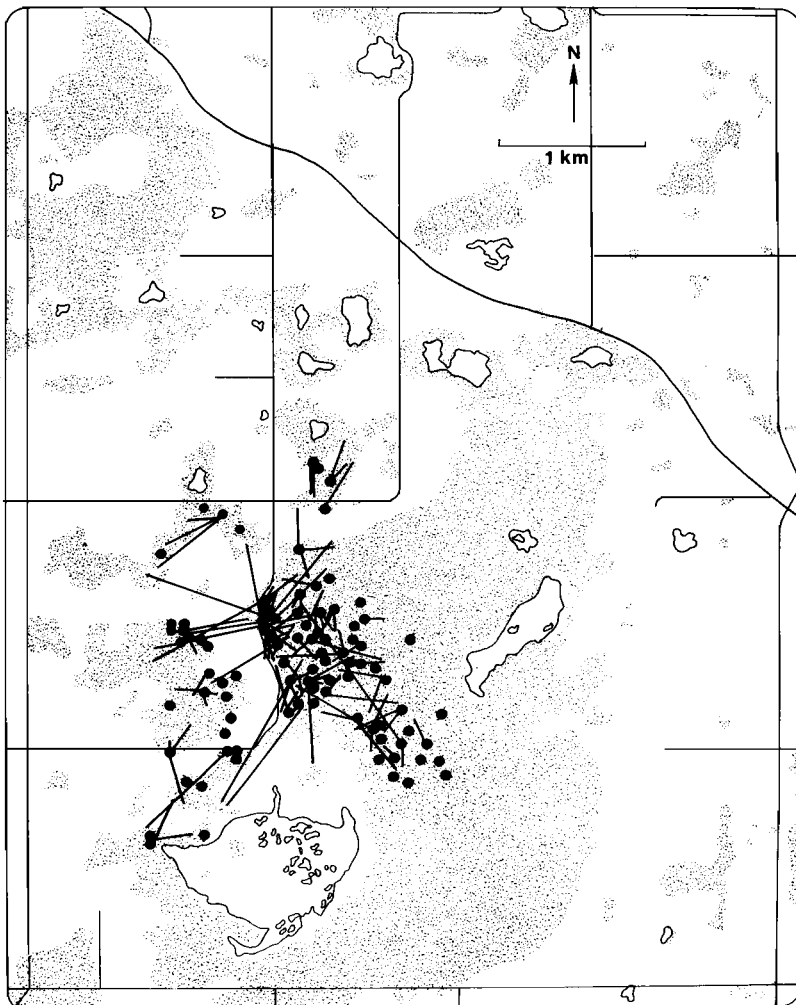


Fig. 3. Movements from place where individuals were banded as independent juveniles in July–August to their breeding sites in subsequent years. Composite of 6 yr. ● = point where juvenile chickadees were banded (regardless of whether any were subsequently found breeding).

During the winters of 1971–72 and 1972–73 Meyer, in his searches of the entire vicinity around the Field Station, located 12 of the 88 birds banded as nestlings (Fig. 2). Straight line distances from hatching point to winter locations varied from 0.5 to 2.4 km. In addition, one bird was reported and verified at a winter feeder 11.2 km from its birthplace, and another was killed by a cat at a residence 5.5 km away. The directions taken by the birds appeared to be random. The median distance for the 14 birds was 0.8 km.

Since daily foraging ranges of chickadees in winter may exceed 1 km, these winter records shed little light on the crucial question of distance from birth place to breeding place. In the routine breeding season censuses in the basic study area, five of the birds banded as nestlings were located as breeding birds. In addition the bird at the distant (11.2 km) feeder was observed there in subsequent winters and can

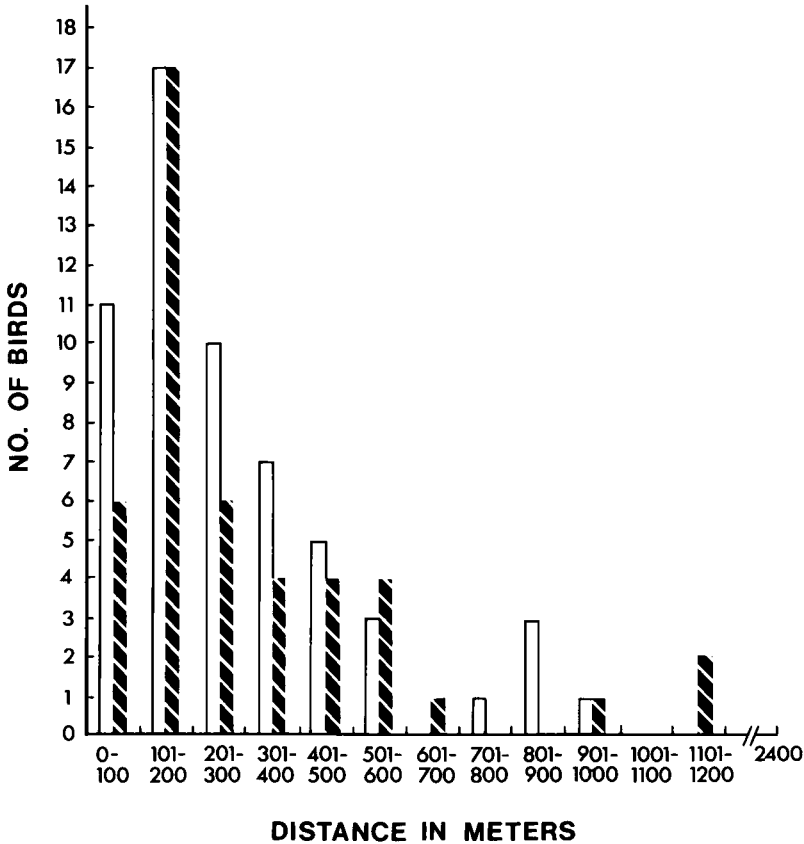


Fig. 4. Distances from point where individuals were banded as independent juveniles in July–August to their breeding sites in subsequent years. Composite of 6 yr. Open bars = males, $N = 58$, median = 211 m; solid bars = females, $N = 45$, median = 198 m.

be presumed to have nested within a km or so of that site. Thus, the distances from birth places to breeding sites for six birds were: 0.4, 0.8, 0.9, 1.3, 1.8 and ca. 11 km, with a median of 1.1 km. This median is probably a minimum estimate since, while we know for certain that there were no others of these birds within our study area, it is quite likely that there were a few undetected survivors that bred outside the study area at distances greater than 1 or 2 km.

Eleven of the 14 winter records and 4 of the 6 breeding records were of nestlings banded in 1971. This we attribute to the difference in survival rate in juveniles in low versus high density years. In 1972, the number of juveniles becoming independent was about one-third higher than in 1971, with consequent higher mortality and fewer birds entering the wintering or breeding population of the next year. We cannot determine from our data whether these differences in juvenile density have effects on the speed or distance of dispersal as well as on survival.

Most of the winter records and all of the six breeding records were of birds originating in the upland forest habitat. Of 40 birds from nests in bog forest or string bog, only 4 (10%) were subsequently recorded in winter or the next breeding season, compared with 10 of 48 (21%) from upland forest nests. On the other hand, in birds

TABLE 1. Distance from point where chickadees were banded as independent juveniles in July–August to their breeding territories in the subsequent year. The comparison is with a Poisson distribution.

	Distance (m)										
	1– 100	101– 200	201– 300	301– 400	401– 500	501– 600	601– 700	701– 800	801– 900	901– 1000	over 1000
Observed	17	34	16	11	9	7	1	1	3	2	2
Expected	2	13	24	26	19	11	5	2	1		

banded as independent juveniles in July or August (after the initial dispersal period, see below), 35% of those settling in bog forest survived to winter, compared with 37% of those settling in upland forest (data from 6 yr). This suggests that bog forest birds suffered greater mortality than upland forest birds while still in the family group stage, but from what cause we do not know.

Cessation of dispersal and development of site-attachment.—From 1969 to 1975, 481 chickadees were banded in July and early August as independent juveniles and 185 of these were recovered at the winter feeders and given individual color codes. Ninety-seven were located on their breeding territories in the first year after banding. Six others were non-territorial the first breeding season after banding, but restricted their activities to small areas in which they had territories in subsequent years. Figure 3 shows for this sample of 103 birds the straight lines from the points where initially banded as independent juveniles to the territories or nest sites in the next breeding seasons. The main point to observe is that these distances are very much shorter than those in Fig. 2. A frequency diagram of these distances (Fig. 4) shows that the longest distance we recorded was 1,160 m, although we could have detected distances up to 2,400 m. The median distance was 211 m for males, 198 m for females, 204 m for sexes combined. The small sex differences were not statistically significant ($\chi^2 = 0.124$, $P > 0.50$, Median test, Siegel, 1956). Ninety percent of the birds had territories within 600 m of the point where banded. This distribution was compared with a Poisson distribution, following the procedures of Kluijver (1951) and Johnston (1956). Appropriate adjustments were made for differences in the areas of the concentric rings around the points of banding and also for the proportion of suitable habitat in each ring. The observed distribution departs significantly from the Poisson ($\chi^2 = 100.8$, $P < 0.005$), with much higher values than expected in the shorter distance classes and somewhat higher (but not significant) values in the longest classes (Table 1).

We also examined the possibility that birds trapped early in July might still be dispersing while those trapped later in the summer were not. In this population,

TABLE 2. Effect of the date when trapped on the distance between the place where individuals were trapped as independent juveniles and their breeding territories in the subsequent year.

Period of trapping	Distance (m)											Median
	1– 100	101– 200	201– 300	301– 400	401– 500	501– 600	601– 700	701– 800	801– 900	901– 1000	over 1000	
July 1–20	3	8	5	2	0	1	0	1	0	0	1	195
July 21–31	6	9	6	6	3	2	1	0	0	0	0	195
August 1–20	8	17	5	3	6	4	0	0	3	2	1	198

families begin to break up and independent juveniles become noticeable about the first of July each year. By 15 July nearly all families have dissolved. Thus, during much of July there must be many juveniles moving relatively rapidly and for long distances as described in the previous section, and one could hypothesize that distances from banding site to subsequent breeding territory would be longer at that time than later. We split the sample (sexes combined) into three time periods: 1–20 July, 21–31 July, and 1–20 August (Table 2). The median distances were nearly identical.

A possible explanation for the lack of a date-distance relationship lies in our method of trapping, which we believe contained a bias in favor of the more mature juveniles who had developed sufficient social behavior and aggressiveness to respond to playback of songs or calls. In fact we found it difficult to trap any juveniles at all in early July. Using total hours spent in the field as a measure of trapping effort, our success rate in trapping juvenile chickadees was: 1–10 July, 0.09 birds/h; 11–20 July, 0.59; 21–31 July, 1.09; and 1–20 August, 1.43. Thus we believe that the birds trapped in early or mid-July were those that had hatched and become independent earliest and had by that time reached the requisite state of maturity, while later-hatched birds were still dispersing and not responding to our song playbacks. Some confirmation of this was obtained in 1977, an exceptionally early breeding year, when independent juveniles were first noted on 18 June. In the 1–10 July period we had a success rate of 0.98 birds/h, far higher than usual.

Still another question concerned possible differences between the summers of high density and low density juvenile populations. Birds trapped in 1970, 1972, and 1975, the high density years, were compared with those trapped in 1971, 1973, and 1974. The numbers in this case were disparate, 40 in the former group, 63 in the latter, due to the differences in survival rates mentioned previously. For the low density years the median distance from banding point to the next year's territory was 194 m, while for the high density years it was 217 m, but the difference was not significant ($\chi^2 = .554$, $P > 0.05$). In the low density sample 7 birds (11.1%) moved over 500 m, compared with 9 birds (22.5%) in the high density sample. Again, however, the difference was not significant ($t_s = 1.640$, $P = .10$; test for equality of percentages, Sokal and Rohlf 1969).

Movements in winter and spring.—In our study, movements of chickadees in winter or spring should have been detectable as (1) an influx of unbanded birds at the feeders, (2) a permanent disappearance in the spring of birds that had been present at the feeders in winter, or (3) the presence in the breeding population of a substantial number of unbanded birds.

The last alternative was not the case. Although there were some unbanded birds breeding each year near the periphery of the basic study area, there were very few in the central parts. Therefore we assume that any birds entering the central portions of the area between 15 November and 30 April found their way to the feeders and were trapped and color-banded.

Figure 5 shows the monthly patterns of arrival of new birds at the feeders. Only birds of known sex were included (about 85% of the total). Since many birds lived more than 1 yr the number of records of adult arrivals is larger than the number of individual chickadees. The month-to-month patterns of arrival were similar for adult birds and birds banded as juveniles in July and August. Most of these birds along with their unbanded (juvenile) flockmates found the feeders and started using

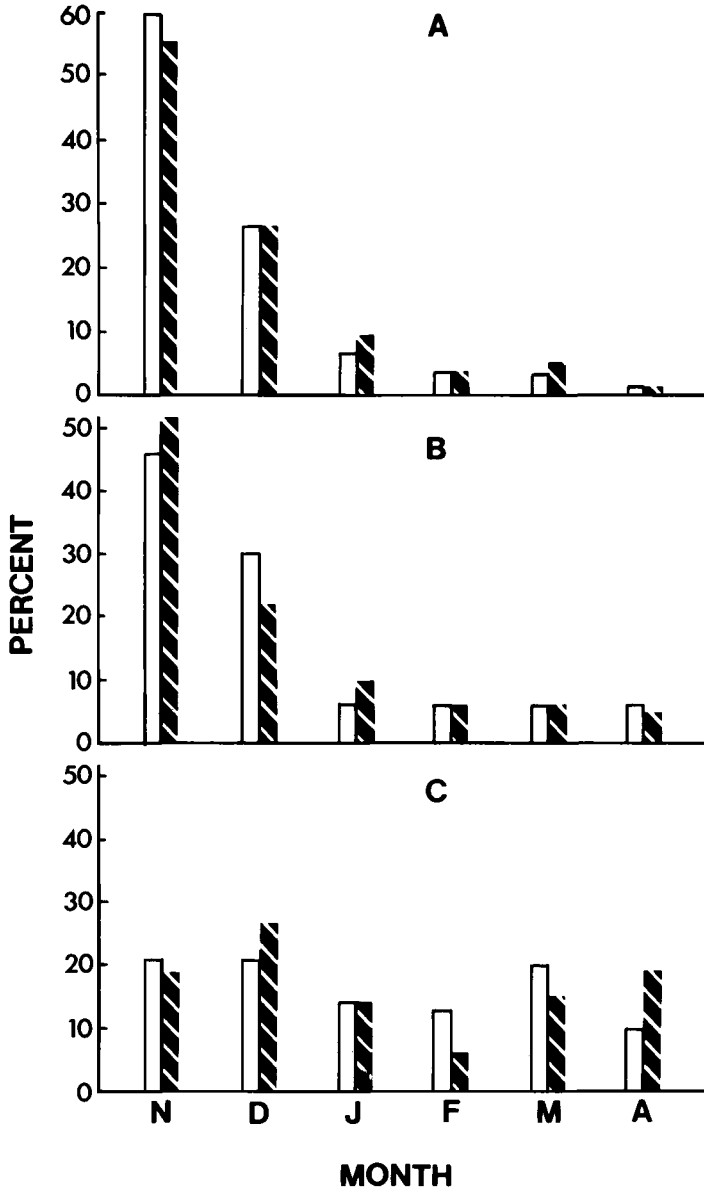


Fig. 5. Month of first arrival of chickadees at UWM winter feeders, expressed as percentage of total for each class and sex. Composite of 6 yr. Sexes as in Fig. 4. A = adults banded in previous years, N = 330 males, 285 females. B = independent juveniles banded in July–August, N = 97 males, 88 females. C = previously unbanded birds (believed to be 90% juveniles), N = 182 males, 223 females.

them shortly after they were set out in mid-November. December arrivals were mostly flocks from near the periphery of the basic study area, and small numbers of such birds continued to arrive throughout the winter. In several cases we could verify that March or April arrivals were flocks that had spent the winter in parts of Cedarburg Bog remote from the feeders. Typically such a flock consisted of 1 or

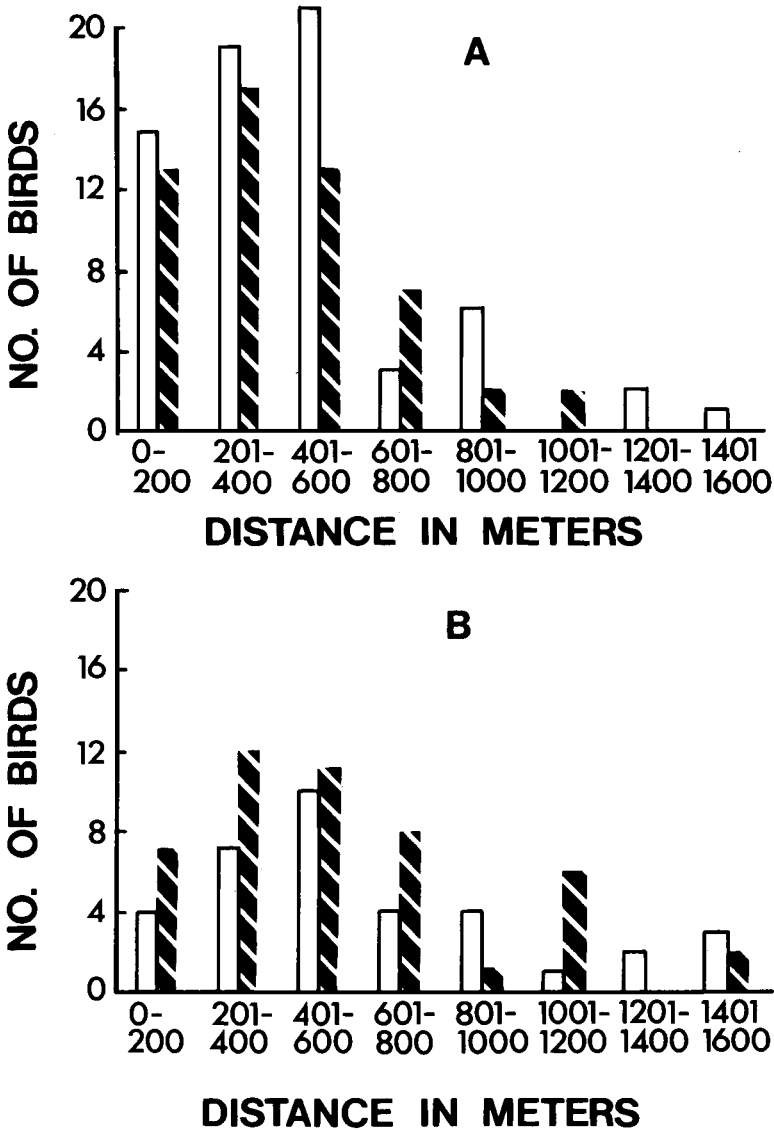


Fig. 6. Distance from winter feeder to territory, comparing previously unbanded chickadees arriving at feeders in early winter with those arriving in spring. Composite of 6 yr. Sexes as in Fig. 4. A = birds arriving 15 November–31 December; males, $N = 66$, median = 380 m; females, $N = 54$, median = 366 m. B = birds arriving 15 March–30 April; males, $N = 35$, median = 531 m; females, $N = 46$, median = 473 m.

2 color-banded adults accompanied by 3–6 unbanded flockmates. Birds banded as juveniles the previous summer were seldom present in these flocks because we avoided trapping for juveniles in areas near or beyond the boundaries of the basic study area. In short, the continued arrival in late winter and spring of known adults and some unbanded birds was the result of expansion of the daily foraging range, rather than dispersal in the proper sense. Such birds returned to their remote sources for breeding.

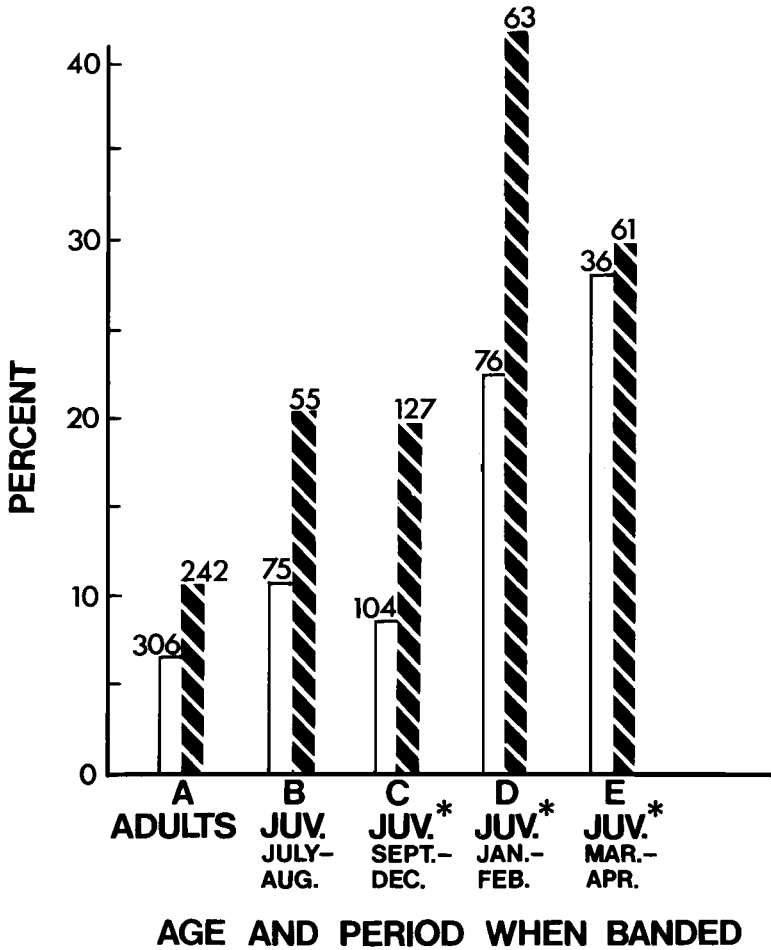


Fig. 7. Losses of chickadees from study area in spring, expressed as percentage of numbers present at feeders in 15 March–30 April period. Composite of 6 yr. Sexes as in Fig. 4. Numbers above bars indicate N in each class. * = birds first trapped after early November that could not be aged. We believe 90% are juveniles (see text).

Nevertheless, the monthly pattern of arrival of previously unbanded birds (Fig. 5C) was sufficiently different from that of adults and summer-banded juveniles to suggest that other factors might be involved. The main difference was that in March there was an increase in the arrivals of unbanded birds of both sexes, in April a further increase in females, but a decline in males. One possible explanation would be that these were birds from remote flocks that were simply expanding their daily foraging ranges, as described above. If so their breeding territories should have been located near the borders of the basic study area, long distances from the feeders. To test this we measured the distance from winter feeders to breeding territory for unbanded birds first arriving at the feeders in March and April as compared with those from flocks from the central part of the basic study area, which arrived at the feeders in November and December (Fig. 6). Of 78 males and 101 females that arrived in November and December, 66 and 54, respectively, were later found on

territory. For the March–April group 55 males and 76 females were recorded, and 36 and 46, respectively, were found on territory. Males arriving at the feeders in spring did have territories significantly farther from the winter feeders than did those arriving in early winter, the medians being 531 m and 380 m respectively ($\chi^2 = 5.25$, $P = 0.05$). In the females, the difference was similar in magnitude, 473 m vs 366 m, but was not significant ($\chi^2 = 2.53$, $P = 0.20$). In both sexes there were larger than expected numbers of the spring arrivals settling to breed within short distances of the feeders, where they almost certainly were not present in the fall or early winter.

If there was immigration into the study area in March and April it stands to reason that there would be a corresponding emigration. Figure 7 shows the losses of birds from the basic study area in the 15 March–30 April period. These were birds that were never recorded again after having been present at the feeders during that period of a particular year. Assuming that the adult male loss rate of 7% is entirely due to mortality and that the mortality of young birds had by this time of year become identical to that of adults, we can subtract the adult loss rate from the total percentage loss and attribute the rest to emigration movements. Thus, for juvenile males that were known to be in the central part of the study area in summer, fall, or early winter (Fig. 7, B and C) only about 3–5% of the birds dispersed in the spring. In those previously unbanded males (believed to be nearly all juveniles) arriving in mid-winter about 16% moved away permanently at the beginning of the breeding season, as did 21% of those arriving in early spring.

The adult female loss rate was 11%. Assuming this to be mortality and subtracting as above, we conclude that about 9% of the juvenile females present before mid-winter dispersed in the spring. For those arriving in mid-winter about 29% moved away, and for spring arrivals about 18%.

DISCUSSION AND CONCLUSIONS

We infer from these data the following picture of Black-capped Chickadee dispersal. After fledging the young remain with their parents for about 3 weeks, moving around within or near the parental territory. Territorial defense by adults is diminishing at this time. As soon as the family group dissolves the young begin relatively rapid and long-distance movements away from their birthplaces. They do not merely drift gradually from their parents' territory to adjacent territories, but exhibit a positive behavior pattern involving movements of longer distance than would be necessary simply for feeding or escaping the aggressiveness of other birds. This is not to imply that the movements are continuous or straight-line flights, or that some birds may not end up near their places of origin. This dispersal phase persists for only a few weeks and carries the birds a median distance of 1.1 km; a small proportion of the movements may exceed several km.

By mid- or late July this dispersal movement is diminishing and the birds are developing site attachments in their new locations. We believe that little dispersal occurs in late summer or fall, despite the fact that a large number (296 of 481) of the birds banded in July and August were not recovered in winter or thereafter. We believe this loss was due mainly to mortality. Our argument is that if the summer to winter loss were due to dispersal, with birds moving about the area searching for suitable places to settle, the emigration would be offset by immigration of unbanded juveniles, as our study area is surrounded by extensive areas of chickadee habitat.

Thus in the years when the juvenile density in summer was high, and the observed recovery rate in winter was low, there should have been large numbers of immigrating unbanded juveniles trapped in our fall netting operation. In years when the summer density was low and recovery rate in winter high, there should have been lower numbers trapped in fall. Instead, the opposite was observed. There was a direct relationship between recovery rate and the number of unbanded birds trapped in fall. Our second argument against continued dispersal in the fall is based on Fig. 4. Since we could have detected movements up to 2,400 m we hypothesized that if much dispersal occurred after the July–August banding period we should have distances broadly distributed over the full range of the graph. Instead, they were strongly concentrated at the short end of the range.

Probably the cessation of the dispersal movement is related in some way to the maturation of social behavior and aggressiveness, which leads the juveniles in late July and August to join adults in localized areas and form small flocks that will persist until spring. Our observations, including retrap records of summer-banded juveniles and sight records of color-banded adults, indicate that the range of movement of each flock is quite restricted at this time (late summer). Later in the fall and early winter the flocks expand their ranges considerably. While this brings birds to areas where they have not been seen before, e.g. residential areas or bird feeders, it is not true dispersal, as the birds will return to breed within the range occupied by the flock in late summer.

A fraction of the first-year birds, especially females, undertake some permanent movements in the winter or spring away from the places where they were found in late summer. The questions are: how large is the fraction, and what causes them to move? Analysis of the permanent disappearances of birds from the feeders in March and April suggests that about 5% of the males and 9% of the females in the first-year population undertake spring movements. Presumably the winter and spring influxes and losses at our feeders represent the movements of this fraction of the large reservoir of yearling chickadees in the Cedarburg Bog area. Whether these are entirely spacing movements or are due to some birds failing to develop site tenacity cannot be answered.

This interpretation of the spring dispersal is somewhat at variance with those of others who have studied this species. Butts (1931), Bowdish (1938), and Odum (1942) suggested or implied that substantial movements of chickadees occur in spring at the time of territorial establishment. Smith (1967) reported that many (32–49%) of the birds that wintered in her study area disappeared within a 2-week period in spring, concomitant with the appearance of large numbers of unbanded birds (none of which remained in the area to breed, however). Glase (1973) also reported a “general” movement at this time, during which 47.5% of the wintering birds disappeared. In our study we did not find such high loss rates even among the yearlings. Our data indicate that while there are certainly movements in the spring, only a small proportion of the yearling population is involved.

In other respects, our data are consistent with those of others. Median dispersal distances (hatching site to breeding site) reported for a variety of small song birds are: Great Tit (*Parus major*) 500 m (Kluijver 1951), Blue Tit (*Parus caeruleus*) 700 m (Berndt and Sternberg 1968), European Nuthatch (*Sitta europaea*) 900 m (Berndt and Sternberg 1968), Pied Flycatcher (*Ficedula hypoleuca*) 1,000 m (Berndt and Sternberg 1968), Song Sparrow (*Melospiza melodia*) 285 m in Ohio and 185 m in a

California salt marsh population (Johnston 1956). English and Belgian populations of the Great Tit have dispersal distances similar to those reported by Kluijver (Perrens 1965, Dhondt and Hublé 1968). Other investigators (Butts 1931, Odum 1941, Kluijver 1961, Glase 1973) have banded nestling Black-capped Chickadees. Aside from one of Butts' birds which may have bred about 2 km away, in all these studies it was simply reported that none of the birds was found later as a breeding bird in the study areas, implying relatively long dispersal distances consistent with the 1.1 km median distance reported here.

Goodbody (1952) found an explosive dispersal in the Great Tit beginning within a couple of weeks after fledging and peaking within a short time. This is similar to what we observed in the chickadee, although he concluded that "thereafter birds continue to move outwards from their birthplaces." Johnston (1956) also found a similar limited period of movement in salt marsh Song Sparrows, reporting that these movements ceased and the birds developed site attachments by late summer. Dhondt (1971) suggested that site attachment might develop before autumn in Belgian Great Tits. We believe our data concerning juveniles trapped in summer provide further evidence for the development of site attachment at that time, although homing experiments would be required to prove this conclusively. We concur with Brewer and Harrison (1975) that site (or habitat) selection probably takes place in late summer in many species, since the ultimate factors affecting breeding success (food supply, vegetative cover, etc.) would be more readily discernible then than they would be in the spring at the time of territory establishment.

One question that arises from these findings is whether the summer dispersal movement of juvenile chickadees is an innate dispersal mechanism or an environmentally forced spacing movement. We believe the evidence favors the former. First, at the time of family breakup the adults are no longer rigorously defending their territories and do not attack juveniles unless the latter approach very closely. Second, while aggression between parents and young is at least partly responsible for the dissolution of the family (Holleback 1974), the young would need to move only a short distance—a few tens of meters, perhaps—to escape. Third, if competition for food, foraging sites, or other resources were a driving factor in the dispersal it is likely that short distance movements and a diffuse dispersion pattern would result, rather than the observed long distance movements culminating in flock formation. Such competition might have some influence on the total distances traveled and on where the dispersal terminated, without being the driving or initiating force. Finally, since young are dispersing in all directions, those emigrating from a particular area are replaced by immigrants from another, with little net change in numbers. Little is gained in terms of reduction of competition. Since we cannot discern any external causes we hypothesize that in the chickadee this dispersal behavior is an evolved, innately-programmed adaptation.

The evolution of such an adaptation need not be based on group selection, as suggested by Howard (1960). The chickadee is a highly social species in which survival is enhanced by supposedly altruistic behavior, such as antipredator warning calls. Trivers (1971), in listing the situations favoring the selection of altruistic behavior, suggests the case in which the dispersal rate is low during all or a significant portion of the lifetime, so that the individual interacts repeatedly with the same neighbors. This idea can be turned around to state that it would be advantageous for an individual of a species with altruistic behavior to have its dispersal confined

to a brief period as early in its life as possible, so that it spends most of its life among familiar neighbors or flock members. Likewise, the advantages of late summer habitat and site selection alluded to above should also favor the evolution of a brief, early dispersal mechanism.

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