ECOLOGICAL AND REPRODUCTIVE RELATIONSHIPS OF BLACK-CAPPED AND CAROLINA CHICKADEES*

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THE pattern of coexistence of populations differentiated in geographical isolation depends on their reproductive and ecological relationships. For distinct populations to exist sympatrically, two conditions must be met: the populations must be reproductively isolated and they must avoid continued competition. When reproductive isolation is lacking, the two forms will not persist sympatrically because swamping-out of differences between them will result in their being reunited as a single species. Continued competition will result in the more successful species spreading throughout the common range and replacing the second, unless a region or situation is met where the second is the more successful (Lack, 1944).

This study is concerned with Black-capped and Carolina chickadees, *Parus atricapillus* and *P. carolinensis*. These two species of birds are extremely similar or identical in every aspect of size, weight, plumage, life history, and voice investigated (Brewer, 1959; also see Dwight, 1900; Odum, 1941, 1941a, 1942; Bent, 1946; Lunk, 1952; Tanner, 1952; Brewer, 1961). The probable origin and dispersal of these two species and their present-day geographical pattern of distribution are examined in light of their ecological and reproductive relationships.

The period of study extended from October 1954 to June 1959, with scattered observations past that date. Most of the field work was done in Illinois, but supplemental observations were made in Indiana, Michigan, Missouri, North Carolina, Tennessee, and Texas. Principal areas of observation in Illinois were located in the following counties: Bond, Champaign, Clinton, Coles, Cumberland, Douglas, Effingham, Fayette, Jackson, Piatt, Randolph, St. Clair, Shelby, Washington, and Williamson.

CONTEMPORARY GEOGRAPHICAL DISTRIBUTION

The Carolina Chickadee occupies the south- and mid-eastern United States (see Brewer, 1959). The Black-capped Chickadee occupies the northern United States north to southern Alaska and middle and southern Canada. It also extends southward in the western mountains and in the Appalachians to West Virginia, with a disjunct population in the southern Appalachians of Tennessee and North Carolina. The geographical relationship of the northern boundary of the Carolina Chickadee's range and the southern boundary of the Black-capped Chickadee's range has been poorly known. The relationship appears to be as follows (locality names are those of counties). From southern Kansas (Meade,

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Greenwood) through southern and middle Missouri (Cole, St. Louis) to southwestern Illinois (Madison, Fayette) the ranges of the two species are contiguous. To the east, the boundary of the breeding range of the Carolina Chickadee runs from mid-eastern Illinois (Coles, Champaign, Vermilion) through middle Indiana (Tippecanoe, Carroll, Jay), middle and northeastern Ohio (Darke, Ashland, Columbiana), central West Virginia (Barbour, Summers), eastern West Virginia (Morgan), northwestern Maryland (Allegany), southeastern Pennsylvania (Cumberland, Bucks), and middle New Jersey (Mercer, Middlesex) to the Atlantic coast. Through much or all of this region, a gap up to several miles wide seemingly is present between the northern range-limits of the Carolina Chickadee and the southern range-limits of the Black-capped Chickadee.

The easternmost point at which the two species are in contact in Illinois is near Vandalia, Fayette County (see Figure 1, F, G). Eastward the gap becomes increasingly evident, so that around Champaign (Champaign County) and elsewhere within 30 to 40 miles of the Indiana border, there seems to be a hiatus of perhaps 15 or more miles where no chickadees occur in the breeding season. The presence of this gap can be shown by indices of abundance based on the time needed to find one or more chickadees.

The method used in obtaining indices was as follows: for each period of field observation, the elapsed time from beginning until the first chickadee was seen or heard was noted. If no chickadees were found, the total time spent in the field was noted. To obtain an index value to any one area, these times were totaled and the sum divided by the total number of cruises on which chickadees were seen. Thus, if on three trips to an area, chickadees were seen after 5, 10, and 15 minutes, while on a fourth trip of 30 minutes no chickadees were seen, the index value of time to first observation would be 20 (60/3). Low index values indicate high chickadee density, and high index values indicate low density. This method, rather than one based on time or distance, was used because of the automatic standardization of effort. Effort was approximately the same on any cruise until the first chickadee was located; afterwards, it might vary according to what features of life history or ecology were being considered. For use in calculating index values, only cruises taken in floodplain and riverbottom woods were used. Variability was undoubtedly introduced into the data through the use of cruises taken at different times of day and, particularly, the use of cruises taken during the non-breeding season.

Index values, obtained as just described, are plotted in Figure 1 for 24 areas in Illinois.

Numbers of cruises (and in parentheses total observational time in minutes for areas where the index value was infinity) were as follows: A, 9 cruises; B, 6; C, 3; D, 1; E, 4; F, 14; G, 6; H, 2; I, 1; J, 3; K, 3; L, 8; M, 8; N, 3 (113); O, 6; P, 7; Q, 5; R, 5 (267); S, 3 (76); T, 14; U, 9; V, 4; W, 3; X, 1.

Areas L, N, Q, R, S, T, U, V, and perhaps W are within the gap where chickadees are rare or absent in the breeding season. It is true that

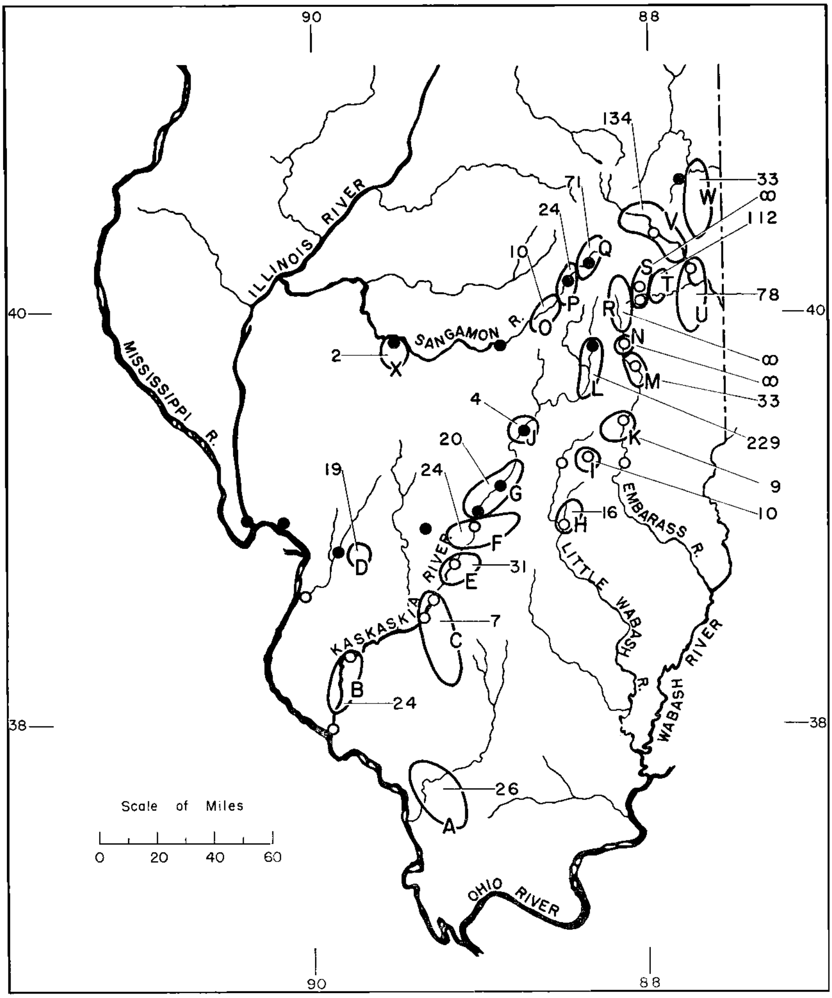

Figure 1. Index values to abundance of chickadees for various areas in Illinois. Large numbers indicate low density and small numbers indicate the reverse. Selected breeding-season records of the two species are indicated by dots (Black-capped Chickadee) and circles (Carolina Chickadee).

much of the area contained in the gap does not contain vegetation optimal for chickadees. Elsewhere, however, chickadees occur in similar somewhat unfavorable situations (city parks, woodlots, etc.); furthermore, large areas of what appear to be perfectly favorable vegetation do occur in the gap. For example, Brownfield and Trelease woods (Champaign County) are mature deciduous forests of about 50 acres each and appear to be suitable for chickadee nesting. Chickadees occur there in small numbers in winter, but are practically nonexistent as nesting birds. Trelease Woods has been censused every year since 1934 and in occasional years previous to that time. During no more than two years have chickadees (Carolina) occurred there during the breeding season.

Although formal cruise data are unavailable, it is likely that the gap begins not far east of area F (Figure 1), runs from there northeastward through area L, and then runs more directly eastward to the Illinois–Indiana border. That the gap continues into Indiana is indicated by the work of Cope. (Full names of persons supplying information through personal communications are given in Acknowledgments.) At the western boundary of the state he found (*in litt.*) a north–south distance of about 40 miles in which chickadees were extremely scarce or absent, between Lafayette (Tippecanoe County) and the Jasper–Pulaski Game Preserve. In the eastern part of the state, the hiatus appeared narrower, extending about 5 miles from Bryant (Jay County) to Geneva (Adams County).

Supplementary evidence for Indiana and for much of the rest of the eastern United States is less quantitative in nature. Burr (*in litt.*) stated that around Lafayette, Indiana, ". . . chickadees are really quite rare . . . in late spring and early summer. For example in our spring day of some 14 hours of field work we are lucky to have three chickadees."

In Ohio, Hicks (1935: 162) stated that the problem of an exact delimitation of breeding ranges was difficult because "both species are usually rather uncommon to rare in areas where their ranges overlap." Aldrich stated (*in litt.*): "I recall that I found what I thought was a hiatus between the ranges of the Carolina and Black-capped Chickadees somewhere south of Cleveland in Summit County."

The range of the two species in Pennsylvania is poorly known. However, Northwood, Curator of the Audubon Shrine and Wildlife Sanctuary, Montgomery County, stated (*in litt.*): "[In six years of daily observation on the 120-acre sanctuary] I have not yet recorded the Carolina Chickadee, though they are supposed to be resident in this area. The Black-capped Chickadee visits us most winters . . . arriving about September 15 and leaving about April 15."

The range of the Black-capped Chickadee is continuous from Pennsylvania and western Maryland into far southern West Virginia in the Allegany Mountains. Because of the sharp relief, the gap to be looked for here is altitudinal rather than latitudinal. Evidence for its presence

TABLE 1

ABUNDANCE OF CHICKADEES AT VARIOUS ALTITUDES IN EASTERN WEST VIRGINIA AND WESTERN MARYLAND

Altitude (feet)	*Number of censuses*	*Breeding pairs/100 acres*	
		P. atricapillus	*P. carolinensis*
0–499	5	0	9.2
500–999	2	0	0
1,000–1,499	2	0	0
1,500–1,999	4	1.7	0
2,000–2,499	5	4.2	0
2,500–2,999	4	3.1	0
3,000 and above	20	4.1	0

is given in Table 1, which records density of nesting pairs at various altitudes in eastern West Virginia (Jefferson, Randolph, Berkeley, Greenbrier, Tucker, Hardy, Webster, and Pocahontas counties) and western Maryland (Garrett and Allegany counties). Of eight census areas between 500 and 1,999 feet in elevation, only one had at least one pair of breeding chickadees. Hall, who has done considerable field work in the area, stated (*in litt.*) that although he had never tried to correlate the fact with altitude, chickadees of either species are rare in much of mountainous West Virginia.

Tanner (1952) has definitely established the existence of a hiatus between the breeding ranges of the two species in the southern Appalachians (North Carolina and Tennessee). The gap extends through about 600 feet of elevation, from 2,800 to 3,400, although chickadee density is low for some distance above and below these altitudes.

There is little good definite information about the subject from New Jersey. Most sources (e.g., Fables, 1955: 50) rely on Miller's statement (Stone, 1937: 730) that the Raritan River is the dividing line between the two species.

There seems, in summary, to be a considerable volume of evidence supporting the view that in many of the areas where the two species should come into contact, both species are rare or nonexistent in the breeding season.

During late fall and early winter, there is some dispersal of both species. This movement is perhaps predominantly southward, but a general dispersal may also occur and northward movements are the more readily detectable in the Carolina Chickadee (Palmer, 1885; Attwater, 1892: 344; Carter and Hartman, 1947; Tanner, 1952: 417; A. O. U., 1957: 382–385; Irving, 1960: 86). Winter movements of Black-capped Chickadees are more noticeable and seem to involve greater numbers than those of Carolina Chickadees; sometimes particularly east of the

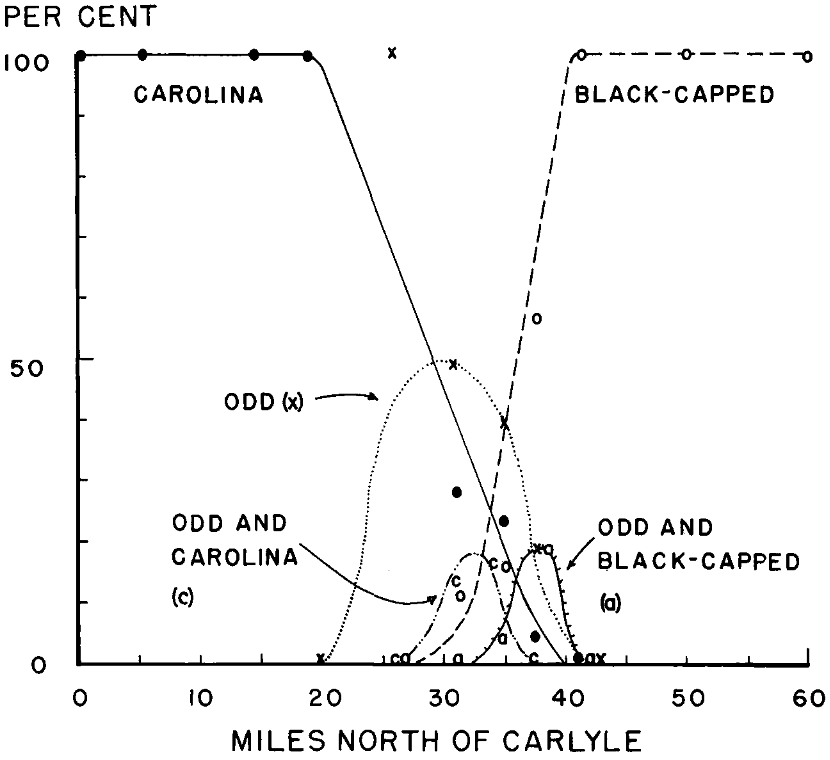

Figure 2. Percentages of birds in five classes with respect to whistled songs at various points along the Kaskaskia River. Observations at 26.5 miles included only three birds. Representative landmarks and their mileages are as follows: Keyesport, 11; Vernon, 18; Vandalia, 30–32; Vera Bridge, 36.5; Wren Bridge, 45.5; Cowden, 57.

85th meridian these reach the proportions of large-scale flights involving thousands of birds (Wallace, 1941: 58; Poor, 1946; Thomas, 1958).

Reproductive Relationships Between the Two Species

Where the two species come together in Illinois and eastern Missouri, hybridization seems to occur. The exact areas in which I have found an apparent hybrid zone are around Vandalia (Fayette County) and between Reno and Sorento (Bond County), Illinois, and in Missouri along the Missouri River from three miles east of Gumbo (St. Louis County) west to near Labadie (Franklin County), and south to below Eureka (Jefferson County). On the Meramec River southeast of St. Clair (Franklin County), I found Carolina Chickadees, but time did not

TABLE 2

MEASUREMENTS OF CHICKADEES TAKEN NEAR VANDALIA, ILLINOIS, FEBRUARY–MAY 1959

Specimen number (RDB)	*Sex*	*Wing length*	*Tail length*	*Length of bill*	*Length of tarsus*	*Tail/wing ratio*
89	♀	60.0	57.5	7.18	16.5	0.958
96	♀	60.5	51.0	6.82	14.0	0.843
92	♀	62.0	53.5	6.81	14.5	0.863
88	♂	62.5	52.5	6.55	15.0	0.840
90	♂	63.5	56.5	7.00	17.0	0.890
91	♂	64.0	55.5	6.97	16.5	0.867
95	♂	65.0	59.5	7.99	16.0	0.915

permit northward delimitation of the zone of apparent hybridization in Missouri.

Evidences of hybridization for the Vandalia population, which was the only one studied at length, are along four main lines:

1. *Atypical vocalizations.* For a distance of about 10 miles along the Kaskaskia River, 40–50 per cent of all birds sing only songs that appear to be outside the range of variation of either Carolina or Black-capped chickadees (Figure 2; for additional detail see Brewer, 1961). An additional percentage sings these peculiar songs in combination with what seem to be occasional normal songs of one species or the other. In all, a distance of about 20 miles exists, centered near Vandalia, in which some proportion of birds sings songs which cannot be reliably attributed to either species. Unusual vocalizations identical to those at Vandalia were noted in the contact zone of eastern Missouri. I believe that the birds which sing unusual songs exclusively may be hybrids of various sorts. The categories of birds which sing both unusual and typical songs could be variously interpreted: two possibilities are that they represent some genetic class, such as back-crosses with the parental species whose song they sing, or that they represent birds of a particular genetic constitution, which have learned songs characteristic of another genetic constitution.

2. *Morphological intermediacy.* Because of the overlap of characteristics between the two species, morphological intermediacy in single specimens is difficult to detect. No adult collected at Vandalia could not be assigned on the basis of measurements to either Black-capped Chickadee (Richard D. Brewer original catalogue numbers 89 and 95) or Carolina Chickadee (RDB 88, 90, 91, 92, and 96) (Table 2). RDB 90 is the only specimen which could perhaps be called intermediate, but it is within the range of normal variation of the Carolina Chickadee. There

TABLE 3

TAIL-TO-WING RATIO IN BLACK-CAPPED CHICKADEES, CAROLINA CHICKADEES, AND CHICKADEES OF THE VANDALIA POPULATION

Sample	*Number*	*Tail-to-wing ratio*				
		0.820–0.859	0.860–0.899	0.900–0.939	0.940–0.979	0.980–1.019
P. atricapillus	19	10.5%	16.0%	58.0%	10.5%	5.0%
Vandalia population	7	29.0	43.0	14.0	14.0	0.0
P. carolinensis	26	69.0	31.0	0.0	0.0	0.0

are, nevertheless, indications that the population as a whole is one that is intermediate in some respects. This intermediacy is illustrated in the two important characters of tail-to-wing ratio and distinctness of edgings on rectrices (Tables 3 and 4).

For analysis of markings of rectrices, Black-capped and Carolina chickadees in the author's collection and in the University of Illinois Natural History Museum were arranged in a series, without regard to species, according to distinctness and lightness of the rectrix margin. Five color classes (1–5) could be distinguished, running from the darkest, least distinct, to the whitest, most distinct. Available specimens from Illinois were then classified as to color.

3. *Mixed mating.* On the basis of both measurements and plumage characters, RDB 95 would be identified as a Black-capped Chickadee, RDB 96 as a Carolina Chickadee (Table 2). These two birds, however, were a pair, observed feeding four fledged young on 19 May and 20 May 1959, on which date they were taken along with two of the young. The male gave songs of a hybrid character, but did not sing frequently enough for the possibility that he also sang Black-capped songs to be eliminated. The young birds resembled Carolina Chickadees. At least two objections can be raised to this observation. First, there is no evidence that the male taken with the female was the bird with which she originally mated and which fathered the young. Second, there is no evidence that this is not actually a hybrid × Carolina or a hybrid × hybrid mating. Even if the male was a replacement for another bird, however, the observation is evidence that, under some conditions, female chickadees of "Carolina" appearance will accept males of "Black-capped" appearance. The second objection, that this is a mating involving hybrids, merely shifts the necessary mixed mating back one or more generations.

Without extensive collection of mated pairs, it is difficult to form any firm judgment as to the presence or absence of preferential mating. Field observations suggest that there may be no particular tendency toward intraspecific mating.

TABLE 4

DISTINCTNESS OF WHITE EDGINGS ON RECTRICES OF BLACK-CAPPED AND CAROLINA CHICKADEES AND CHICKADEES OF THE VANDALIA POPULATIONS*

Sample	*Number*	*Color class*				
		1	*2*	*3*	*4*	*5*
P. atricapillus	9	0%	0%	11%	56%	33%
Vandalia population	7	28.5	43	28.5	0	0
P. carolinensis	41	80.5	19.5	0	0	0

* For discussion, see text.

4. Although some circularity may be involved in the argument, it is possible to regard certain abnormalities in reproduction observed in the Vandalia population as evidences of hybridization. Abnormalities were noted as early as the time of nest excavation (Brewer, 1961: 353). Based on observations at five nest-sites, only one bird excavated; in four cases this was demonstrably the female. In both Black-capped and Carolina chickadees, both sexes excavate, usually working alternately (Brewer, *loc. cit.*).

Although attentiveness in incubation seemed low (68 per cent), this may merely have been a response to high temperature. A striking difference in the Vandalia birds compared with the parental species, with no apparent relation to temperature, appeared in the frequency with which the male fed the female on the nest. At all nests observed except one, the male never visited the nest during incubation and often appeared not to know exactly where it was. In 568 minutes of observation, only four feedings on the nest were seen. This is a rate of 0.6 per hour of attentiveness, to be compared with a rate of 2–3 in Black-capped and Carolina chickadees (Brewer, 1961: 357).

Perhaps the most noticeably abnormal behavior was that shown by a pair in which the female began apparently normal incubation with the laying of the first or second egg. The pair abandoned after 20 days of incubation (or, since 7 eggs were laid, 14 days after laying of the last egg). Of the 7 eggs, 3 contained no embryos, 1 contained a good-sized embryo still several days from hatching, and others contained much smaller embryos.

Reproductive success (number of young fledged/number of eggs laid) was 14.3 per cent at four nests for which complete information was available (Table 5). The percentage hatching was 46.4. Both of these figures are significantly lower (beyond the 0.01 level using chi-square calculated from a 2 × 2 contingency table) than those for either of the

TABLE 5

REPRODUCTIVE SUCCESS AT SIX NESTS AROUND VANDALIA, ILLINOIS

Location of nest (Miles north of Vandalia)	*Hatching*		*Fledging*	
	Number of eggs	*Per cent hatched*	*Number of eggs*	*Per cent fledged*
0.0	6	16.7	6	0.0
1.5	7	100.0	7	0.0
2.0	?	some	?	some
4.0	7	0.0	7	0.0
5.5	8	62.5	8	50.0
6.0	?	some	?	some
Totals for 1, 2, 4, and 5	28	46.4	28	14.3

two parental species. Reproductive failure at these four nests resulted from three causes: infertility or retarded development of eggs (41.7 per cent of the 24 cases of failure), destruction by House Wrens, *Troglodytes aedon* (54.2 per cent), and predation by an unknown animal (4.2 per cent). At two additional nests unknown numbers of eggs were laid, and some young hatched and fledged, but the numbers in both cases were unknown. If it is assumed that these two nests each had 7 eggs and all 14 eggs produced fledged young, then reproductive success for the six nests is 42.8 per cent (18/42). This figure is still significantly lower (at the 0.01 level) than reproductive success as calculated for either of the parental species (Table 6).

It may be noted that the fate of an individual egg is not wholly independent of other eggs inasmuch as some events tend to result in the destruction of a whole clutch or brood. If nests rather than individual eggs are considered, the ratio of successful (some fledged young) to unsuccessful nests for the three populations is 8 : 1 for Carolina Chickadees, 31 : 10 [= 3.1 : 1] for Black-capped Chickadees, and 1 : 3 [+2 uncertain] for the Vandalia population.

Data used for calculation of reproductive success in the two parental species consisted of all records giving eggs laid and young fledged, from correspondence, in my own notes, and in the literature with one restriction, namely that records specifically describing some event which would lower reproductive success were omitted. A priori considerations suggested that such occurrences might tend to be reported in disproportionately large numbers compared with their actual frequency. The figures as calculated should reflect normal infertility, predation, etc.

Two factors which might have produced erroneously low figures for reproductive success at Vandalia were activities of the observer and destruction by House Wrens. The observer spent considerable time in the vicinity of four of the six nests and used a wired-on panel (see Odum, 1941: 315) to allow examination of three of them. The same activities

TABLE 6

REPRODUCTIVE SUCCESS IN BLACK-CAPPED AND CAROLINA CHICKADEES

Species	*Hatching*		*Fledging*	
	Number of eggs	*Per cent hatched*	*Number of eggs*	*Per cent fledged*
P. atricapillus	266	72.6	335	66.3
P. carolinensis	56	92.8	51	86.3

were practiced elsewhere with the parental species with no reduction of nesting success. Destruction by House Wrens is a normal factor in the reproduction of chickadees and is adequately reflected in the figures for Black-capped Chickadees (most of the data for Carolina Chickadees are from areas where House Wrens are absent or rare).

HYBRIDIZATION ELSEWHERE

It will be suggested later that hybridization may be expected in any area where the two species are not at or near the zone where their respective competitive abilities balance one another. This may be the case for the whole area from central Illinois to western Kansas; relevant observations are lacking for areas west of eastern Missouri. In the eastern United States, W. DeWitt Miller is said to have collected a mixed pair (male Black-capped) at Old Bridge, New Jersey (Cruickshank, 1942: 321). Also in New Jersey, Fables (1955) reported that a mixed pair may have been present on a breeding-bird census area near Lakehurst in 1940.

Tanner (1952: 412) concluded that hybridization had probably occurred in certain populations of the southern Appalachians some time in the past on the basis of tail-to-wing ratios of birds taken in the Plott Balsams (mountains southeast of the Great Smokies) of North Carolina. These Black-capped Chickadees had tail-to-wing ratios significantly smaller (at the two per cent level) than Black-capped Chickadees from the Great Smoky Mountains. Tanner found no evidence of active hybridization during the more than three years of his study.

ECOLOGICAL RELATIONSHIPS

COMMUNITY DISTRIBUTION

Both species are, in general, birds of forest and forest-edge. There is no obvious difference in community occurrence; the same community types which support Black-capped Chickadees in the north support Carolina Chickadees in the south. To approach the problem of density within community types, breeding-bird censuses published in *Bird-lore, Audubon Magazine,* and *Audubon Field Notes* from 1937 to 1960 were used.

The following criteria were established for acceptance of a census: (1) only a single vegetational type, described with sufficient thoroughness to allow classification, must be included; (2) at least 11 hours must have been spent on an area of at least 15 acres; (3) coverage must have been otherwise sufficient considering size of census area, its terrain and vegetation, and time of nesting of chickadees; and (4) the census area must not be in or near that zone in the eastern United States which lies between the ranges of the two species.

Unfortunately, censuses satisfying these criteria proved too few to allow any thorough analysis of the effects of community, geographical location, and elevation on density of the two species. Only for mature wet forests (i.e., forests of elms, *Ulmus* spp.; sycamore, *Platanus occidentalis*; silver maples, *Acer saccharinum* and *A. rubrum*; birches, *Betula* spp.; etc., on poorly drained sites) and mature mesic forests (i.e., forests of beech, *Fagus grandifolia*; sugar maple, *Acer saccharum*; basswood, *Tilia americana*; tulip-tree, *Liriodendron tulipifera*; etc., on well-drained sites) of middle latitudes (37.5–42.5° N) and moderate elevations (0–2,000 feet) does any sizable number of censuses exist. The mean density for Carolina Chickadees from this region (using locality as the sampling unit regardless of the number of years censused) was 14.3 pairs per 100 acres in mesic forests (eight localities) and 15.5 in wet forests (three localities). For the Black-capped Chickadee, mean density was 7.9 for mesic forests (five localities) and 8.3 for wet forests (four localities). Even within these data, however, an east–west trend appears to be present at least for density of Carolina Chickadees in mesic forests (the data do not allow any conclusion on the point in the other three cases: all of the mesic forest censuses for the Black-capped Chickadee are in Ohio; all of the wet deciduous forest censuses for the Carolina Chickadee are in Maryland, and of the four wet deciduous forest censuses for the Black-capped Chickadee, two are in Illinois, one in Ohio, and one in Virginia). The trend for Carolina Chickadees in mesic forests appears to be one of decreased density in the east. If the data are restricted longitudinally, only one test is possible; this is a comparison of density between Black-capped and Carolina chickadees in mesic deciduous forests of middle latitudes in the Midwest (or specifically in Ohio). Here on four census areas, Carolina Chickadees had a mean density of 24.6 pairs per hundred acres; Black-capped Chickadees had a mean density of 7.9 (five areas). The difference between these means is significant at the one per cent level ($t = 4.048$).

The reasons for these differences in density are unknown. One speculation, for which no evidence exists, is that Carolina Chickadees, although having the same average requirements for favorable space as Black-capped Chickadees, are able also to occupy less favorable situations more readily. Thus, a given area of forest would tend to be able to support more Carolina Chickadees than Black-capped Chickadees.

TERRITORIAL SPACE

Within the limits of the data available, mean territory size seems to be about the same in the two species of chickadees. The only estimation of territory size for the Carolina Chickadee that I have found is that of Marshall (1944) who gave a figure of 1.3 acres in an upland oak–tulip-tree forest. Two territories that I mapped were 5.4 acres (nine plotted observations in the breeding season, while taking Williams spot-map census; north of Murphysboro, Illinois) and 4.3 acres (more than two hours' observation on pair in egg-laying stage; east of Dubois, Illinois). The mean for these three determinations is 3.67 acres. A number of estimates are available for the Black-capped Chickadee. Most of these were taken from data gathered during spot-map censusing of breeding birds (Longley, 1944; Fawver, 1947; Wallace, 1949; Burton *et al.*, 1953; Martin, 1960: 130; Calef, 1953; personal observations). Others resulted from extended observations of one or more pairs (Butts, 1931: 21; Odum, 1941: 328; Fitch, 1958: 241–245; personal observations). Available estimates were utilized by giving equal weight to each report from an area whether the size of one territory or a mean for several was given. The resulting mean and standard error ($N = 12$) were 3.64 ± 0.96.

Territorial size as reported for the Black-capped Chickadee was extremely variable, ranging from 0.18 (Martin, 1960) to 17.1 acres (Odum, 1941). Although some of this variability surely is real, it seems likely that much of it is spurious and the result of differences in technique. On the basis of the sample available, territory size did not vary in any consistent way with density of the chickadee population.

Probably most competition for territorial space is intraspecific. Interspecific territorial defense by chickadees (except against other chickadees; see "Competition between Black-capped and Carolina Chickadees") is extremely rare. Several species, however, may defend all or part of their territory against chickadees. Species which have been observed in apparent territorial defense against chickadees are the following: Red-headed Woodpecker, *Melanerpes erythrocephalus*; Eastern Wood Pewee, *Contopus virens*; Tufted Titmouse, *Parus bicolor*; Red-eyed Vireo, *Vireo olivaceus*; Prothonotary Warbler, *Protonotaria citrea*; Yellow Warbler, *Dendroica petechia*; Black-throated Green Warbler, *Dendroica virens*; Yellowthroat, *Geothlypis trichas*; and Summer Tanager, *Piranga rubra*. Probably few of these species defend the whole of their territories against chickadees throughout the breeding season. Stewart (1953: 105), for

TABLE 7

TREE DENSITY (MEAN NUMBER OF TREES PER ACRE) AROUND NEST STUBS AND AROUND APPARENTLY SUITABLE BUT UNUSED STUBS 125 FEET FROM NEST

Species	*Tree density*			
	Around nest stub		*Around unused stub*	
	All trees	*Trees more than 2.9 inches d.b.h.*	*All trees*	*Trees more than 2.9 inches d.b.h.*
P. atricapillus	164.3	82.2	595.7	328.6
P. carolinensis	446.7	215.7	862.7	338.9

example, stated that male Yellowthroats defend their territories interspecifically only during the period from establishment to arrival of females. My own observations suggest, further, that territorial activities of these species may not be particularly successful in preventing trespass by chickadees.

Although the Tufted Titmouse occasionally exhibits territorial behavior towards both species of chickadees, this is less usual than might be expected on the basis of their taxonomic proximity. Territorial space occupied by chickadees and titmice shows considerable overlap, further suggesting that territorial behavior between them is not very important.

NESTING AND ROOSTING SITES

Vegetation. Vegetational characters of nest sites were studied by tallying and measuring all trees within a 15-foot radius (707 square feet) of three nests of the Black-capped Chickadee and four of the Carolina Chickadee. Herbaceous vegetation was ignored because it is low or has not sprouted at the time nest sites are selected. Other samples of 15-foot radius were taken, using as centers apparently suitable but unused trees which were located closest to a point 125 feet in a randomly determined direction from each nest stub. Two arrays of figures were thus made available, giving tree density around nest stubs, and around dead trees apparently suitable but unused for nesting that were within the cruising radius (and in some cases demonstrably within the territory) of each pair of chickadees. The results indicate that nests of both species tend to be in relatively open portions of the forests where they are located (Table 7). Comparisons between the two species are not appropriate because of the different nature of the two forests considered (mature mesic for Carolina Chickadee, second-growth floodplain for Black-capped). Odum (1941: 330) pointed out the tendency of Black-capped Chickadees to nest in edge situations but to forage in the forest. His

TABLE 8

DIAMETER, HEIGHT, AND HEIGHT OF NEST HOLE FOR NESTING STUBS OF BLACK-CAPPED AND CAROLINA CHICKADEES (IN CM)

Species	*Diameter*		*Height*		*Hole height*	
	Number	*Mean ± S.E.*	*Number*	*Mean ± S.E.*	*Number*	*Mean ± S.E.*
P. atricapillus	9	11.4 ± 2.9	11	196.3 ± 40.5	26	175.0 ± 26.1
P. carolinensis	9	12.9 ± 1.2	19	187.4 ± 5.6	35	179.5 ± 19.0

conclusion that this dual habitat preference is the result of the need for a nest tree of soft wood is not fully substantiated here, since equally suitable stubs in denser forest were not used. The possibility exists that the ecological niche requirement resulting in nesting in relatively open situations is for such trees and the presence of characteristics associated with edge situations (where soft trees would be more frequent) are merely "sign-posts" used by the birds as an aid in finding such trees.

Nest stubs. The nest stub used by chickadees is, on the average, 180–200 cm in height and 11–13 cm in diameter where the hole is placed (Table 8). The entrance hole is usually within 25 cm of the top of the stub. In none of these characters is there a significant difference between the two species.

At least 29 species of trees have been recorded as nest sites for one or the other chickadee. Most of these are trees with fairly soft wood, with utilization of *Pinus*, *Populus*, *Salix*, *Betula*, *Pyrus*, and *Prunus* being particularly frequent. (Plant names follow Fernald, 1950.) Trees which in life possess hard wood are also used, if in death the inner portion is softened by decay. In this category are blue beech, *Carpinus caroliniana*, which is the most frequently used tree in mature mesic forests of central Illinois; beech; sugar maple; and oaks, *Quercus* spp.

It is difficult to know which features of nest stubs actually determine their use and which are merely concomitants of these features. It is plausible that the two most important features are height and suitability for excavation. The species of tree is probably unimportant in itself. Trees satisfying the two conditions above would often be between 10 and 15 cm in diameter. The tendency toward nesting near the top of the stub may depend on the fact that spots of decay reaching the outer surface are more frequent there and excavation is thus easier.

Roosting. Little information is available on roosting. In both species, the female of a nesting pair spends the night in the cavity from the time of nest-building until the nestlings are several days old. During the fall for the female and during the summer and fall for the male, roosting may be on sheltered branches or vines (Jones, 1910: 178; Odum, 1942: 517). During the coldest part of the winter, or perhaps during the whole period from late fall to spring, birds of both sexes may roost singly in cavities. From the scattered observations available there is no evident difference in frequency of hole-roosting between the two species (Sutton, 1928: 233; Hutchinson *et al.*, 1943: 3–4; Thomas, 1946: 147; Fitch, 1958: 242–243).

Competition for nesting and roosting sites. Because chickadees excavate their own cavities and begin nesting early, conflicts for nest sites usually involve attempts by other small hole-nesting birds to occupy cavities already claimed by chickadees. Fitch (1958) related that a pair of Black-capped Chickadees was driven away from a hole where Eastern Bluebirds, *Sialia sialis,* were nesting, but the chickadees were evidently merely inspecting the cavity rather than trying to take possession of it. Black-capped Chickadees have been observed defending the nest stub or its immediate vicinity against such hole-nesting species as Hairy Woodpeckers, *Dendrocopos villosus*; Downy Woodpeckers, *Dendrocopos pubescens*; White-breasted Nuthatches, *Sitta carolinensis*; House Wrens; and House Sparrows, *Passer domesticus.* A similar list for the Carolina Chickadee includes House Wrens as well as the open-nesting Catbird, *Dumetella carolinensis,* and Canada Warbler, *Wilsonia canadensis.* Birds of the Vandalia population were observed defending the nest stub against House Wrens and Prothonotary Warblers. Probably both species will attack most small birds that venture too near the nest. Except in encounters with House Wrens, chickadees are usually successful in protecting the nest. Walkinshaw (1941: 17), however, reported that a cavity of the Black-capped Chickadee containing seven eggs was taken over by a Prothonotary Warbler. Later a House Wren evicted the warblers and emptied the cavity.

Competitive relations between chickadees and House Wrens appear to be concerned primarily with nest sites. Overlap of House Wren and chickadee territories suggests that the territories themselves are not defended by either species against the other. While attempting to evict chickadees, a House Wren moves about silently and, when the pair of chickadees is absent, enters the cavity and throws out the nest and eggs or young, if present. If this is accomplished, the wren prevents reoccupation by song, display, and chases. A critical point appears to be removal of the major portion of the contents of the cavity. Before this is achieved, the wren is easily chased from the vicinity of the nest; afterwards, the wren apparently gains dominance. The main methods of defense against House Wrens as well as other nest-site competitors seem to be chasing by either member of the pair of chickadees, hissing of the incubating or brooding female, and hissing by nestlings. These methods are sometimes successful against House Wrens, but because of the wrens' extreme persistence often are not. House Wrens are probably the most constant and successful competitors for nest sites of both species of chickadees over much of their ranges (for notes see Ridgway, 1905; Kendeigh, 1941: 31–33).

Defense of holes used for winter roosting has been observed against Tufted Titmice in the Black-capped Chickadee (Fitch, 1958: 244) and against Downy Woodpeckers in the Carolina Chickadee (Thomas, 1946: 47). It seems likely that chickadees of either species defend their roosting holes against most other small birds that utilize cavities.

FEEDING

Only casual observations are necessary to establish that, qualitatively, the foraging of the two species is very similar. They move from perch to perch frequently and often use their acrobatic ability to reach otherwise inaccessible spots. Most food is gleaned from the bark of twigs, branches, and boles of trees or from their foliage, fruits, and flowers. If the food item is small enough, it is eaten as soon as taken, but if it is too large, the chickadee may pin the prey down with one foot to facilitate feeding. When a relatively large prey animal is taken on the ground, the bird nearly always flies up to perch on a limb, perhaps because manipulation of the food is difficult for a chickadee standing on the ground. Weed-feeding does not differ from feeding on trees, except that chickadees occasionally pound on weed stems in a woodpecker-like manner. Presumably these birds are either dislodging pieces of cuticle with insect eggs or attempting to break through into the center of the stem to search for larvae or pupae.

Some of the aspects of feeding that lent themselves to quantitative treatment were studied by means of standardized observations, observations of foraging rate, and compilations of food-habit analyses. Standardized observations were taken in a manner similar to that of Hartley (1953). The plant species, height from the ground, and position were recorded for feeding individuals. For *position*, the categories were ground, herb, shrub, vine, and in trees, small branch, large branch (more than one-half inch in diameter), bole, fruits and flowers, and foliage. Height was estimated and was believed to be accurate within 5 feet, at least at lower levels; however, intervals of 10 feet were used for analysis. In order to eliminate community and geographical variation as much as possible, analysis of standardized observations was restricted to floodplain and riverbottom forests in Illinois.

Standardized observations. Two relatively distinct periods were found to exist in the feeding niche as reflected by standardized observations: winter (October–March) and summer (April–September).

During the winter months, both species fed in trees about 70 per cent of the time (Table 9). The vertical distributions of the two species were

TABLE 9

FOREAGING POSITIONS OF BLACK-CAPPED AND CAROLINA CHICKADEES

Foraging position	*P. atricapillus*				*P. carolinensis*			
	October–March		*April–September*		*October–March*		*April–September*	
	Number	*Per cent*	*Number*	*Per cent*	*Number*	*Per cent*	*Number*	*Per cent*
Ground	13	9.6	0	0.0	13	7.5	0	0.0
Herb	18	13.2	3	5.2	10	5.8	4	4.0
Shrub	4	2.9	0	0.0	12	7.0	7	7.0
Vine	9	6.6	2	3.4	8	4.8	6	6.0
Tree	92	67.6	53	91.4	129	75.0	83	83.0
Small branches	49	43.6	17	39.9	45	42.2	16	24.3
Large branches	14	12.4	5	11.7	15	14.1	8	12.0
Bole	13	11.6	8	18.7	16	15.0	8	12.0
Fruits and flowers	0	0.0	3	7.0	4	3.8	11	16.6
Foliage	0	0.0	6	14.1	0	0.0	12	18.1
Totals of major categories	136		58		172		100	

nearly identical, each feeding below 10 feet about 45 per cent of the time and below 30 feet about 75 per cent of the time (Table 10). This finding is in agreement with the observations of Van Deventer (1936) for the Black-capped Chickadee in New York. Within trees, each species fed about 60 per cent of the time on small branches (Table 9). Most of the differences between the two species are probably explainable on the basis of differences in vegetation and differences in foraging action under different climatic conditions. This is true of the apparent greater tendency of the Black-capped Chickadee to feed on the ground and on weeds.

TABLE 10

FEEDING HEIGHTS OF BLACK-CAPPED AND CAROLINA CHICKADEES (IN FEET)

Feeding height	*P. atricapillus*				*P. carolinensis*			
	October–March		*April–September*		*October–March*		*April–September*	
	Number	*Per cent*	*Number*	*Per cent*	*Number*	*Per cent*	*Number*	*Per cent*
0–9	64	46.0	12	24.5	67	44.6	26	24.1
10–19	22	15.8	6	12.3	25	16.6	21	19.4
20–29	15	10.8	11	22.4	22	14.6	16	14.8
30–39	10	7.2	10	20.4	12	8.0	22	20.4
40–49	14	10.1	5	10.2	15	10.0	15	13.9
50–59	7	5.0	3	6.1	2	1.3	7	6.5
above 59	7	5.0	2	4.1	7	4.6	1	0.9
Totals	139		49		150		108	

TABLE 11

UTILIZATION OF PLANT SPECIES BY BLACK-CAPPED[1] AND CAROLINA CHICKADEES[2]

Plant species	*P. atricapillus*		*P. carolinensis*	
	October–March	*April–September*	*October–March*	*April–September*
Elms, *Ulmus americana* and *rubra*	24.2%	36.2%	27.6%	23.0%
Oaks, *Quercus* spp.	7.2	10.3	10.7	7.0
Black willow, *Salix nigra*	4.8	6.9	10.0	11.0
Sycamore, *Platanus occidentalis*	1.6	1.7	6.3	2.0
Soft maple, *Acer saccharinum*	12.1	8.6	5.0	11.0
Cottonwood, *Populus deltoides*	1.6	0.0	3.8	0.0
Sweet gum, *Liquidambar styraciflua*	0.0	0.0	3.8	0.0
Grape, *Vitis* spp.	7.2	0.0	3.1	4.0
Ragweed, *Ambrosia trifida*	11.3	0.0	3.1	0.0
Hackberry, *Celtis occidentalis*	3.2	0.0	1.9	0.0
White ash, *Fraxinus americana*	0.8	0.0	1.3	0.0
Honey locust, *Gleditsia triacanthos*	3.2	0.0	0.6	0.0
Hawthorn, *Crataegus* spp.	2.4	0.0	0.0	0.0
Other trees	12.9	27.6	10.0	29.0
Shrubs and other vines	4.0	3.5	9.4	9.0
Other herbs	3.2	5.2	3.1	4.0

[1] Number of observations: 124 October–March, 58 April–September.
[2] Number of observations: 159 October–March, 100 April–September.

Chickadees tend to utilize these situations most from December to March, when food presumably is scarcest. Probably woody growth in areas where observations were made on Carolina Chickadees (from a few to 200 miles south of most of those made on Black-capped Chickadees) provided enough food throughout the winter so that little recourse to herbaceous vegetation or litter was necessary. A comparison of foraging positions of Carolina Chickadees in southern Illinois and central Illinois supports this hypothesis. Utilizing only records from central Illinois (Coles County and northward), about 23 per cent of all records were of birds on the ground or on weeds—a percentage nearly identical to that for the Black-capped Chickadee. The percentage of non-woody feeding sites in southern Illinois was much lower (7 per cent).

Rather marked differences existed in the utilization of plant species by the two chickadees (Table 11). It seems clear, however, that utilization depends primarily on availability and that the differences observed are merely the result of different frequencies of occurrence for the various

TABLE 12

USE OF TREE SPECIES BY BLACK-CAPPED CHICKADEES ALONG SANGAMON RIVER AND THEIR RELATIVE ABUNDANCES IN THE SAME AREAS*

Tree species	*Utilization by P. atricapillus*		*Relative abundance*	
	Number of observations	*Per cent of total observations*	*Number of trees*	*Per cent of total trees*
Elms	30	32.6	213	32.4
Soft maple	15	16.3	79	12.0
Oaks	9	9.8	52	7.9
Black willow	6	6.5	26	4.0
Hackberry	4	4.3	56	8.5
Honey locust	4	4.3	27	4.1
Hawthorn	3	3.3	23	3.5
Cottonwood	2	2.2	2	0.3
Sycamore	2	2.2	22	3.3
White ash	1	1.1	59	9.0
Other species	16	17.4	97	14.8
Totals	92		656	

* Data on trees from Martin, 1955.

plants in different geographical areas. This conclusion is based on two facts: (1) the utilization of tree species by Black-capped Chickadees followed very closely the relative abundance of the species as determined by Martin (1955) for the areas in which observations were made (Table 12), and (2) the differences between Black-capped Chickadees and Carolina Chickadees and between Black-capped Chickadees and chickadees of the Vandalia population were those which, through observation, would be expected were availability the primary factor in utilization. For example, chickadees at Vandalia showed a much higher utilization of cottonwoods than did either Black-capped or Carolina chickadees, this difference corresponding to an obvious greater respresentation of that tree in the forests of Vandalia.

It is possible to obtain an index to the degree of distinctness of the two chickadees with regard to foraging position by summing the differences between the percentages of feeding done by each species in the various positions. For small branches the difference between percentages (for the winter) is 1.4 (43.6–42.2); for the ground, it is 2.1; and so on (Table 9). Summing these figures results in a value that reflects the degree to which the species do not overlap in their feeding position. When the same procedure is followed for other pairs of species for which standardized observations are available, the resulting array of figures compares, although not necessarily linearly, the distinctness in foraging position of Black-capped and Carolina chickadees and the various other

TABLE 13

TOTAL PERCENTAGE DIFFERENCE IN FORAGING POSITION BETWEEN BLACK-CAPPED AND CAROLINA CHICKADEES IN WINTER AND BETWEEN OTHER PAIRS OF BIRD SPECIES

Species	*Number of position categories*	*Total percentage difference*	*Source*
P. atricapillus : *P. carolinensis*	8	25.7	this study
Black-crested Titmouse, *P. atricristatus* : Tufted Titmouse	5	121.9	Dixon, 1955
Great Tit, *P. major* : Blue Tit, *P. caeruleus*	6	99.9	Gibb, 1954
Chestnut-backed Chickadee, *P. rufescens* : Plain Titmouse, *P. inornatus*	6	69.0	Dixon, 1954
Great Tit : Coal Tit, *P. ater*	6	57.0	Gibb, 1954
Great Tit : Marsh Tit, *P. palustris*	6	56.0	Gibb, 1954
Blue Tit : Coal Tit	6	51.3	Gibb, 1954
Blackburnian Warbler, *Dendroica fusca* : Cape May Warbler, *D. tigrina*	4	48.4	MacArthur, 1958
Black-throated Green Warbler : Bay-breasted Warbler, *D. castanea*	4	46.4	MacArthur, 1958
Coal Tit : Marsh Tit	6	33.4	Gibb, 1954

species pairs. This comparison, of which a sample is presented in Table 13, indicates that Black-capped and Carolina chickadees are more similar in their foraging positions than any of the other pairs of species considered. The very low total difference figure for these two species is approached only by the Coal Tit : Marsh Tit combination. These two species of birds, however, tend to occur in different communities, the Marsh Tit occupying broadleaved communities, the Coal Tit occupying coniferous forests. Thus Black-capped and Carolina chickadees are more similar in foraging position than any other pair of species considered, even including those, which because of occupancy of different communities, have no contemporary need for distinctness in foraging position.

Chickadees spent an even greater portion of their time foraging in trees in summer than in winter (Table 9). The distribution of foraging height was more even in summer, although there was a slight tendency towards foraging below 10 feet (Table 10). Ground- and weed-feeding almost disappeared in the summer months, and a large portion of foraging time was given over to searching leaves, flowers, and fruits (Table 9). Differences between the species, both in these features and in utilization of plant species (Table 11), are probably the result of differences in vegetation and differences in foraging action under different climatic conditions.

Foraging rate. Foraging rate of the two chickadees was studied by recording the number of times per minute a bird moved to a new perch or changed position on the same perch while foraging. Both species foraged at a higher rate in winter than in summer (about 30 movements per minute in winter compared with 20 in summer). This is probably a reflection of the stress placed on the birds by low temperature. There was no discernible difference in foraging rate between the two species, at least in the range of temperatures at which observations were made.

Horizontal area exploited. Both species appear to cover about the same horizontal area in search of food. Territory size (see "Territorial Space") and probably winter home range (see Brewer, 1961: 350) are about the same in the two species. It is interesting that size of home range tends to increase from early to late winter (Batts, 1957). This perhaps indicates that the area traversed by a bird in winter is related closely to the food supply.

Diet. Besides exploiting the same sources and foraging at the same rate, the two species seem to take about the same kinds of food. The diet of each consists of about 50 per cent animal food in the winter and 80–90 per cent animal food in the spring, summer, and fall (Martin *et al.*, 1951). Published reports and a small number of stomach analyses by me indicate that the taxonomic groups best represented in the birds' diets show a close correspondence (Forbes, 1882; Sanderson, 1898; Weed, 1898; Beal *et al.*, 1916; Kalter, 1932; Terres, 1940; Martin *et al.*, 1951). The most important insect families in the diet of each appear to be Tettigoniidae, Pentatomidae, Membracidae, Cicadellidae, Coccidae, Aphididae, Chrysomelidae, Curculionidae, Phalaenidae, Olethreutidae, Geometridae, and Lasiocampidae. Spiders are regularly taken by both species, and the fruits of ragweed, *Ambrosia* spp., and poison ivy, *Rhus radicans*, are two important plant foods.

The diets of many organisms appear to be determined, within the organism's ability to take food, and its knowledge of food, by the relative availability of the various food items (see, for example, Scott and Klimstra, 1955). Available evidence suggests that this generalization also applies to chickadees. It is clear, merely through observation, that most items appear in stomachs with a frequency roughly proportional to their relative frequencies in nature; for example, eggs of many forms are most frequent in winter; lepidopteran larvae reach a peak in April, May, and June. The opportunistic tendencies of the two species also point to this conclusion. Roth (1928) reported that a pair of Carolina Chickadees nesting near a feeder fed their young only beef suet. Hamerstrom (1942: 40) stated that the largest flock of Black-capped Chickadees she had ever observed away from human habitation was in the vicinity of a dead skunk. The summer of 1959 was, in central Illinois, one in which periodic cicadas (Cicadidae) were extremely abundant. During this period, chickadees spent much of their foraging time in pursuit of these insects. The birds would look about, spot a cicada, and then fly up and perch near it. Often the insect flew before the chickadee could grasp it, but the lack of adroitness on the part of the birds apparently was compensated for by the size and abundance of the insects.

Food-storing. In early winter, both species may store food in crevices in bark (Weed, 1898; Van Sant, 1901; Forbush, 1929: 371; Odum, 1942: 514; Laskey, 1957: 137). I have observed this practice only once in Illinois, by a bird of the Vandalia population. The single instance occurred on 26 February 1958, and involved storing a seed of trumpet creeper, *Campsis radicans*, under the bark of a grape vine, *Vitis* sp., about 6 inches above the ground. To what degree food-storing is important for survival, either at the latitude of Illinois or farther north is uncertain.

Competition for food. Chickadees are not particularly specialized in their foraging; consequently they share food sources with many species and probably come into occasional competition with some of them. One indication, obviously only partially satisfactory, of species with which chickadees might compete is the occurrence of supplanting attacks or chases between feeding birds. I have observed such occurrences involving the Tufted Titmouse; Downy Woodpecker; White-breasted Nuthatch; Ruby-throated Hummingbird, *Archilochus colubris*; House Wren; Black-and-white Warbler, *Mniotilta varia*; and American Redstart, *Setophaga ruticilla*. The least likely of these possible competitors might seem to be the hummingbird. During some parts of the year, however, both hummingbirds and chickadees feed on insects attracted to or caught in the sap coming from woodpecker borings on tree trunks and limbs. Chickadees may even hover to make use of this food source. In 12 instances of interspecific strife that I have observed, it was always the chickadee which was supplanted or chased.

The food stores of chickadees are said to be raided by other species such as Tufted Titmice (Laskey, 1957: 137) and Blue Jays, *Cyanocitta cristata* (Weed, 1898).

COMPETITION BETWEEN BLACK-CAPPED AND CAROLINA CHICKADEES

Organisms survive and reproduce only within certain ranges of various environmental elements (or *requisites* in the terminology of Nicholson [1954]). Determination of the limits and degrees of favorability of these elements is basically an experimental matter, although estimates, biased to varying degrees, are available through observation. To the degree that the combined demands of two or more species in a given area exceed the supply of any depletable requisite, these species are in competition. For competing species to exist contemporaneously in the same area, each must inhibit its own further increase more than it inhibits the further increase of the other species (Crombie, 1945; see also MacFadyen, 1957; MacArthur, 1958: 600; Park, 1948; Birch *et al.*, 1951). In the preceding sections estimates of the pattern of utilization of certain depletable environmental elements were given. The patterns of utilization are so similar in the two species that competition would appear to be inevitable in any time and place of short supply.

The question now arises as to the effect of competition upon the coexistence of the two species. Is there evidence that each species might inhibit its own further increase more than the further increase of the other? Because there is no real area of geographical overlap of the two species, good observational evidence on the point is difficult to produce. The following observations are offered as evidence that territorial and aggressive activities are the same interspecifically as intraspecifically and that these activities, to the degree that they affect population size, will affect it at least as strongly interspecifically as intraspecifically.

In the contact zone at Vandalia, Illinois, chickadees appeared to defend their territories against any other chickadee, Black-capped, Carolina, or presumed hybrid. For example, on 27 March 1958, two birds, one singing a Carolina song and the other a Black-capped song, engaged in a vocal duel that seemed identical to those of intraspecific nature. The presumed Carolina Chickadee was the male of a pair which was excavating in the area and which nested there. The presumed Black-capped Chickadee was not seen or heard in the vicinity afterwards. Other examples involving other combinations were recorded.

The following observations on caged birds are inconclusive, but also suggest that for certain purposes the species do not distinguish between one another. Five Black-capped Chickadees which had hatched 13 days previously and one adult parent were introduced into a flight cage adjacent to a cage containing four Carolina Chickadees which had left the nest four days previously. The adult Black-capped Chickadee forced itself through a small hole in the wire partition and was discovered feeding the young Carolina Chickadees. The adult was returned to the cage containing its own young and the hole blocked, but for some days thereafter it occasionally tried to enter the adjacent cage and also to feed the young Carolina Chickadees through the mesh. As the young Carolina Chickadees grew more independent and exhibited begging behavior less frequently, the adult became more and more aggressive and would fly towards the young giving dominance notes. When the two Carolina Chickadees which were still alive 11 days after fledging were introduced into the cage containing the Black-capped Chickadee, the adult showed a curious ambivalence of behavior. When the young Carolina Chickadees begged, the adult would feed them, although it often by-passed them to feed its own young several times first. Once, after feeding one of the young Carolina Chickadees, the adult suddenly flew up from its perch and landed on the young with both feet. One young ceased giving begging behavior and was chased repeatedly. Sometimes the young bird would be unable to avoid the adult and they would grapple in mid-air. After 75 minutes the attacks on the young chickadees became so intense that I removed them. As the young Black-capped Chickadees grew older and more mature in behavior and appearance, the adult began to react to them in the same way.

Although reactions of solicitude to begging young and of hostility to young of adult appearance do occur interspecifically in some groups of birds, the fact that the actions were so similar whether Black-capped or Carolina chickadees were involved, and the rarity of interspecific hostile reactions in chickadees suggest that in this case the adult made no distinction between its own species and the Carolina Chickadee.

The next question regarding coexistence of the two species is this: is there evidence that, given favorable conditions for both species, the presence of one species prevents the occurrence of the other? The best evidence on this point is the work of Tanner (1952) in the Great Smoky Mountains. Here in the breeding season, Carolina Chickadees occur upward only to about 2,800 feet elevation on mountains where Black-capped Chickadees occur on the summit, but occur up to 4,000 feet on mountains where Black-capped Chickadees are absent.

The final question as to the coexistence of the two species deals with relative competitive abilities. Specifically, what features make Carolina Chickadees more successful in the south and Black-capped Chickadees more successful in the north? Most aspects of life history, behavior, and morphology can be eliminated from consideration because of the obvious extreme similarity of the two species. The following were thought worthy of particular attention.

Mortality. Mortality in the nest appears not to differ between the two species. The apparently poorer hatching and fledging rate of the Black-capped Chickadee (Table 6) can be traced almost entirely to the heavy losses to House Wrens in one sample, that of Kluyver (1961). Most of the data for Carolina Chickadees are from areas where House Wrens are rare; where House Wrens are present in numbers, Carolina Chickadees appear to be equally subject to their attacks.

Mean annual mortality rates for post-nestling birds were calculated from bird-banding records of the U. S. Fish and Wildlife Service.

TABLE 14

MEAN ANNUAL MORTALITY (*M*), MEAN ANNUAL SURVIVAL (*S*), AND MEAN LIFETIME AFTER FIRST 1 JANUARY (*Y*) OF BLACK-CAPPED AND CAROLINA CHICKADEES IN ZONE OF POSSIBLE CONTACT

Species	*Number of returns and recoveries*	*M (per cent)*	*S (per cent)*	*Y (years)*
P. atricapillus	1,276	60.6	39.4	1.07
P. carolinensis	316	59.5	40.5	1.12

Calculations were made by the method of Farner (1949: 69 ff.) except that birds banded at all ages and both living and dead birds were used. The initial date was the first 1 January after banding. Mortality figures obtained in this way are subject to several sources of error. The data obtained from the Fish and Wildlife Service are not perfect: they may contain clerical errors; they do not have repeat records; they may not include all of an individual bander's records, and they include stations which were in operation only a short time. These difficulties can be largely eliminated by using individual station records. As a check on the results obtained using all records, up-to-date records for the Carolina Chickadee from two stations (those of Robbins and Laskey) were used to calculate mortality. The mean annual mortality rate calculated (about 61 per cent) is close enough to the figure calculated using all records to suggest that at least in the case of the Carolina Chickadee, the difficulties listed may not be serious. A second source of error when trapping data, as well as dead birds, are used is that there is sometimes a trap bias in favor of young birds. This, of course, tends to give an erroneously high mortality rate. Unfortunately, the reports of dead birds were so few and so evidently secured haphazardly that using only dead birds, or even comparing results using dead birds with those in which both living and dead birds were used, produces results of doubtful validity. The mortality rates presented here, then, may be erroneously high. Evidence that this is the case results from studies by Wallace (1941: 62–64), Odum (1942a), and Dixon (*in litt.*). Both Odum for the Black-capped Chickadee and Dixon for the Carolina Chickadee calculated an annual mortality rate of about 44 per cent. Wallace's results suggest the extremely low rate of about 15 per cent. All of these studies covered only a few years, however, and dealt with a small sample, most birds of which were breeding adults. Whether or not the mean annual mortality figures presented here are completely unbiased estimates, they should offer an index to mortality that is comparable between the two species.

Banding data were used from the zone across the eastern United States where contact between the two species might occur. Included were records from Delaware, District of Columbia, and Missouri (Carolina Chickadee only); Illinois, Maryland, New Jersey, Ohio, Pennsylvania, and Kansas (both species); and West Virginia (Black-capped Chickadee only).

Both species seemingly average about 60 per cent mean annual mortality (Table 14). Thus, in areas where the two populations might come into contact, there was no difference in mortality rates.

On the basis of 60 per cent annual mortality, the mean lifetime after the first 1 January (calculated by the method of Farner, 1949: formula

7) is about 1.1 years in both species (Table 14). Potential natural longevity, likewise, seems to be closely similar in both species. In the "border" states considered, the chickadees surviving longest (after banding at an unknown age) were a Carolina Chickadee in Ohio which was trapped and released 7 years, 200 days after banding and a Black-capped Chickadee in Pennsylvania trapped and released 7 years, 290 days after banding. Both birds had been banded in the winter, making it certain that each lived more than eight years. Black-capped Chickadees more than nine years old have been reported from the northeastern states (Wallace, 1941: 61; Wharton, 1946). Absence of records of Carolina Chickadees of comparable age probably results from the small numbers of this species banded in comparison with the Black-capped Chickadee (5,495 compared with 76,759 as of 1957).

Predation and parasitism. There is little basis for judgment on the severity of predation on chickadee populations. Using banding data from "border" states as listed previously, predation accounted for 20 per cent of the deaths for which cause was given (after trapping accidents were eliminated) in Carolina Chickadees and for 51 per cent in Black-capped Chickadees. The samples are so small (15 and 30) and so evidently secured haphazardly that little confidence can be placed in these figures.

Chickadees appear not to form more than an insignificant fraction of the diet of any predator, although many of the usual predators of small birds take them. Evidence of predation on chickadees exists for at least seven species of birds and six species of mammals, with no noticeable differences between the chickadee species.

Likewise, evidence regarding parasitism is too slight to justify any firm comparison between the two species. Peters (1936: 20), Herman (1937: 163; 1944: 103), and Malcomson (1960: 195) have given the few reported instances of parasitism in the two species. Miller (1913) attributed the illness and death of a Black-capped Chickadee to infestation with lice.

Both species have been reported as being victimized by Brown-headed Cowbirds, *Molothrus ater* (Friedmann, 1938: 47), but such occurrences are rare. Not only do chickadees vigorously defend the nest stub against cowbirds, but also the entrance hole of a chickadee cavity is too small to accommodate a cowbird readily. When parasitism by cowbirds does occur, nesting success is reduced by ejection of chickadee eggs and starvation of young (Packard, 1936).

Temperature relations. There is no direct evidence that the two species differ either in the extremes of temperature which they can tolerate or in the range of temperatures over which they can maintain a favorable energy balance. Nevertheless, certain points suggest that such differences

TABLE 15

Numbers of Complete Clutches of Various Sizes, by Latitude, in Black-capped and Carolina Chickadees*

Latitude (° N)	*Number of eggs*							
	2	*3*	*4*	*5*	*6*	*7*	*8*	*9*
Below 30.1								
P. atricapillus	–	–	–	–	–	–	–	–
P. carolinensis	0	0	2	0	1	0	0	0
30.1–32.0								
P. atricapillus	–	–	–	–	–	–	–	–
P. carolinensis	0	0	0	4	1	0	0	0
32.1–34.0								
P. atricapillus	–	–	–	–	–	–	–	–
P. carolinensis	0	0	0	5	5	0	0	0
34.1–36.0								
P. atricapillus	–	–	–	–	–	–	–	–
P. carolinensis	0	0	0	1	1	0	0	0
36.1–38.0								
P. atricapillus	–	–	–	–	–	–	–	–
P. carolinensis	0	0	0	2	3	3	1	0
38.1–40.0								
P. atricapillus	0	0	0	0	3	2	0	0
P. carolinensis	0	0	1	3	5	2	1	5
40.1–42.0								
P. atricapillus	1	2	0	2	5	13	6	0
P. carolinensis	–	–	–	–	–	–	–	–
42.1–44.0								
P. atricapillus	0	0	0	2	10	21	5	0
P. carolinensis	–	–	–	–	–	–	–	–
44.1–46.0								
P. atricapillus	0	0	0	1	2	3	1	1
P. carolinensis	–	–	–	–	–	–	–	–
Above 46.0								
P. atricapillus	0	0	0	0	0	0	2	0
P. carolinensis	–	–	–	–	–	–	–	–

* One clutch of 13 eggs for *P. atricapillus* at 42.1–44.0° N lat. is omitted.

may be present. First, such differences evidently are present in the genus *Parus*, for F. L. Farley (quoted in Bent, 1946: 373) stated that in severe cold spells in Alberta, Canada, Black-capped Chickadees are often found dead, whereas Boreal Chickadees, *P. hudsonicus*, do not succumb. Second, the greater size of Black-capped Chickadees compared with Carolina Chickadees suggests adaptation to lower temperatures, even though the size difference in itself might produce only a slight difference in temperature response (see Scholander, 1955: 22).

Clutch size. Information on clutch size was obtained from literature, correspondence, and my own observations. Complete clutches from throughout the range of the Carolina Chickadee, and from the range of the Black-capped Chickadee within the longitudes where the Carolina Chickadee occurs, were used. Both species showed a trend of increasing clutch size with increasing latitude northward (Table 15). The relationship was essentially linear for the Carolina Chickadee but deviated from linearity in the Black-capped Chickadee. From 39.5 to 40.5° N lat.—perhaps the median area of separation of the two species—mean clutch size for the Carolina Chickadee was 7.3 eggs ($N = 9$, Standard Error = 0.65) and for the Black-capped Chickadee was 5.6 ($N = 11$, S.E. = 0.43). The difference between these means is significant at the five per cent level ($t = 2.246$).

Population size. Evidence has been given that, at least in mesic deciduous forests of Ohio, Carolina Chickadees occur at an average density three times that of Black-capped Chickadees. There is some suggestion that this situation may be more generally true in both mesic and wet forests of middle latitudes. If Carolina Chickadees do, in fact, reach higher densities than Black-capped Chickadees, the ability to do so could be of considerable competitive advantage. If we suppose that a number of areas, previously unoccupied by chickadees, are exposed to immigration by two or three times as many Carolina Chickadees as Black-capped Chickadees (as would presumably be true were Carolina Chickadees twice or three times as abundant in the surrounding region), and that these areas were each too small to allow the establishment of territories by all of the birds seeking them, then the outcome would tend to be as follows: the modal situation would be a population where 75 per cent of all territories would be occupied by Carolina Chickadees and 25 per cent by Black-capped Chickadees (assuming Carolina Chickadees to be three times as abundant as Black-capped). The frequency distribution would be skewed, with 90 per cent of all areas having one-half or more of the territories occupied by Carolina Chickadees. This would be the expected outcome under the assumptions of interspecific territoriality, identical territory size, and equal success in establishment and maintenance of territories. On the basis of present information all of these assumptions seem justified. The modal situation—¾ Carolina Chickadees : ¼ Black-capped Chickadees—would tend to perpetuate itself except that Carolina Chickadees reproduce at a faster rate than do Black-capped Chickadees. Under this condition, we would expect Black-capped Chickadees to tend toward extinction.

Also to the advantage of the Carolina Chickadee is the fact that on most of the areas, it would be the more common species. For this reason, any catastrophic event that tended to destroy much of the total chickadee population would completely exterminate the Black-capped Chickadees in an area, while allowing some Carolina Chickadees to survive, more frequently than the reverse.

I suggest that competition is one factor tending to produce the lack of sympatry in the distribution of the two species. The boundary between the two is set through the interplay of competitive advantages, certain factors of which may be the greater rate of reproduction and ability to reach higher densities in certain forest types of the Carolina Chickadee, and perhaps better adaptation to cold of the Black-capped Chickadee.

DISCUSSION

Black-capped and Carolina chickadees are extremely similar in appearance, behavior, and ecology. They occupy allopatric breeding ranges, with a gap between the ranges in the eastern United States, but none in the midwestern United States. Where the two species come in contact, hybridization occurs with the production of a population which apparently has low success compared with the parents. These appear to be some of the more important facts regarding the present-day relationships of the two species. How did these relationships come about?

I suggest that the two chickadees arose from portions of a stock which were isolated from one another during some pre-Wisconsin glaciation. The portion of the stock giving rise to the Black-capped Chickadee may have been isolated in forests of the mountains of western North America, the portion giving rise to the Carolina Chickadee may have been south of the glacier in eastern North America. With the advent of the next interglacial period, the two populations dispersed and came together.

With subsequent glaciation, the two populations moved southward (although certain groups of the population from which the Black-capped Chickadee was derived probably remained at higher latitudes in Alaska, the western mountains of the United States, etc.). During the glacial periods, the Carolina Chickadee may have occurred in the area north of the Gulf of Mexico, the Black-capped Chickadee north from the northern range-boundary of the Carolina Chickadee to near the southern edge of the glacier (plus those birds in other refugia). When the glaciers receded, approximately the reverse of the movements during their advance occurred. Black-capped Chickadees in the southeastern United States dispersed northward; Carolina Chickadees did likewise, replacing as they did so the Black-capped Chickadees still present in the southern part of that species' glacial period range.

Hypothetical reconstructions of this sort are rarely susceptible of proof. Certain features, nevertheless, can be demonstrated as probable. The two species are believed to have differentiated from a common stock in North America because of their extreme similarity: they are much more similar to one another than to any Palaearctic tit. The closest Palaearctic relative appears to be the Willow Tit, *P. montanus* Conrad, formerly considered conspecific with *P. atricapillus* but actually quite dissimilar in many details of plumage, life history, and voice (see Duvall, 1945: 51; Parkes, 1954: 160; Snow, 1956: 29; Mayr, 1956). Whether the stock that eventually gave rise to the two species of chickadees crossed the Bering land bridge into North America very early or later—perhaps early in the Pleistocene—is uncertain. The similarities that do exist between *P. montanus* and *P. atricapillus* and *carolinensis* perhaps favor the second possibility.

The earliest date at which speciation could have begun, then, is believed to be sometime after dispersal of the common stock into North America. The latest possible date would seem to be the Wisconsin glacial period, but speciation then should be ruled out for this reason: no geographically isolated areas seem to have existed during Wisconsin glaciation from which could have come two species of forest birds having the contemporary distributional patterns of the two chickadees. The two most likely possible refugia for a population giving rise to the Black-capped Chickadee in the Wisconsin would have been (1) the driftless area of southern Wisconsin, northwestern Illinois, and adjacent states, or (2) the southwestern United States. In each case, the population giving rise to Carolina Chickadees would be located in the southeastern United States, and in each case, the relict population of Black-capped Chickadees in the Appalachians of North Carolina and Tennessee poses an insurmountable obstacle. It is difficult to believe that Black-capped Chickadees from Wisconsin or Texas could reach the Great Smoky Mountains ahead of Carolina Chickadees from Florida. The Illinoian period is perhaps the most likely time of differentiation. It appears to be the latest time in which conditions were suitable for isolating populations which could have given rise to the two chickadees, and their extreme similarity perhaps argues for a relatively recent divergence.

Replacement of Black-capped Chickadees by Carolina Chickadees over a considerable area of the central and southern United States in the approximately 11,000 years since the Wisconsin glaciers receded (Flint, 1957) seems almost a certainty. The relict population of Black-capped Chickadees in the southern Appalachians is, in itself, one indication that this species must have occurred over a much greater area in the middle United States—at least as far south as Tennessee and North Carolina.

The occurrence of the Black-capped Chickadee at the headwaters of such a stream as the Kaskaskia River in Illinois, with the Carolina Chickadee occupying the southern, downstream, part suggests that the Black-capped Chickadee must have once occupied the whole state, but has since been replaced, first in the forests of southern Illinois and then in the forests bordering streams reaching into the central part of the state (Figure 1). Occurrence of the reverse, that is, replacement of Carolina Chickadees by Black-capped Chickadees, seems unlikely. For this to have occurred, Black-capped Chickadees would have had to disperse southward across the several miles of prairie or farmland between the headwaters of the Kaskaskia and Sangamon rivers. There is, furthermore, some direct evidence of the eviction of the Black-capped Chickadee in Illinois. In 1910, Hess (1910: 31) found Black-capped Chickadees breeding south on the Embarass River at least four to six miles below Philo (Champaign County). His identification of the birds as this species is substantiated by three sets of eggs which he took (now in the University of Illinois Natural History Museum). The mean size of 18 of the 19 eggs (one damaged) is 15.5 × 12.1 mm. Bent (1946: 325, 347) gives the size of 50 eggs of *P. a. atricapillus* as 15.2 × 12.2 mm and of 50 eggs of *P. c. carolinensis* as 14.8 × 11.5 mm. Mere inspection of the data suggests that the eggs Hess collected are those of Black-capped Chickadees. The mean length of 129 eggs of Carolina Chickadees (three subspecies) as given by Bent (1946) is 14.9. Assuming that this is a good estimate of the population mean, a statistically significant difference exists between the sample of Hess (mean length ± standard error = 15.5 ± 0.148) and the population represented by the Carolina Chickadee eggs ($t = 4.05$, $P < 0.001$). The presumption is strong that the eggs taken by Hess in 1910 were those of the Black-capped Chickadee. At present only Carolina Chickadees breed around Philo—or anywhere on the Embarass River. The nearest breeding Black-capped Chickadees are now at least 30 miles to the north.

The contemporary pattern of distribution in Kansas, Missouri, Indiana, Ohio, and western Pennsylvania likewise seems explainable by supposing that Carolina Chickadees moving north along river systems have replaced Black-capped Chickadees. To the eastward, replacement may have been along the Appalachian Plateau and the Atlantic coastal plain. Evidence that replacement has taken place within the last hundred years is lacking for any locality east of Ohio. In Ohio, the facts of replacement are obscured by the failure of many early ornithologists to separate the two species. It seems clear, nevertheless, that Black-capped Chickadees regularly wintered around Columbus (Franklyn County) previous to 1880. The species now reaches Columbus only as a rare straggler or in years of very heavy flights, such as 1954–1955 (Thomas, 1958). Baker (*in litt.*) has given me a well-documented description of the northward spread of Carolina Chickadees in eastern Ohio. Around 1932, Carolina Chickadees occurred only in the southern part of Columbiana County. During the 20 years until 1952, they gradually became more numerous northward. At a breeding-bird census area in northern Columbiana County, Baker found only Black-capped Chickadees breeding through 1951. On 11 November 1951, Black-capped Chickadees were still present on the area. Carolina Chickadees appeared in June 1952 and apparently have been the only breeding chickadee since that time.

There has been so little ornithological work in the areas of Indiana, Missouri, and Kansas where replacement might have occurred that no conclusion on the subject seems possible. The fact that none of the early catalogues of Kansas birds (e.g., Goss, 1891; Snow, 1903) lists *P. carolinensis,* although it now breeds throughout the southern tier of counties, may be evidence for an advance of the species.

The situation at the end of Illinoian (or earlier) glaciation may have been one in which, after the two populations had re-established contact, competition between them resulted in one replacing the other until some line of equilibrium was reached where their respective competitive advantages balanced one another. A zone of overlap along this line would be expected, although possibly a narrow one because of the extreme ecological similarity of the two populations. These two populations, however, are believed to have undergone changes during isolation that, while affecting most aspects of their appearance, behavior, and ecology very little, resulted in differences such that in interbreeding one or more of the factors of hybrid inviability, hybrid sterility, or hybrid breakdown (*sensu* Dobzhansky, 1951: 181) was present. I suggest that because of the strong similarity between the two populations in every respect, the genetically simplest mechanism for preventing this disadvantageous hybridization proved to be the production of a gap between the breeding ranges.

It is difficult to explain the presence of the gap on any other basis. All indications are that, were one species completely absent, the other species would occupy the gap and probably portions of the range of the first species as well. One clear suggestion of this is the work of Tanner (1952: 413) already cited showing that on peaks in the southern Appalachians where Black-capped Chickadees are absent, Carolina Chickadees breed throughout the altitudes of the gap and well into the altitudes occupied on other peaks by Black-capped Chickadees. Further, in Illinois, forests of the Kaskaskia River are occupied by Black-capped Chickadees north of 39° N lat., but two parallel stream systems (the Little Wabash and the Embarass), lying as little as 20 miles to the east, support Carolina Chickadees through the same range of latitudes (Figure 1). No vegetational or climatic factors can be adduced to explain these patterns; they are understandable only in terms of the model given here.

How the gap was produced evolutionarily and on what features of the ecology or behavior of the birds it depends are questions that are, at present, unanswerable. To give one avenue of speculation, the gap could have come about as follows: at the equilibrium line a zone would exist where the population was composed of hybrid birds, Black-capped Chickadees, and Carolina Chickadees. Going away from this zone one would find only one parental species or the other. Individuals of parental species which tended to disperse into the hybrid zone would, unless they returned before time for mating, be less successful than those that were sedentary (because of matings with the other species or with hybrids). Selection, then, would be for sedentariness or for a high degree of *Ortstreue*. With the near-elimination of immigration for breeding purposes, the population in the hybrid zone, with its low rate of reproduction, would tend to die out. Perhaps production of the gap could take place only in a region where neither species was extremely successful (i.e., at or near the line of equilibrium), because elsewhere the selective advantage might lie with continued dispersal to relieve population pressure rather than with restricted dispersal to prevent occasional mismatings.

The gap, acting as a reproductive isolating mechanism, was established, if the preceding portions of this hypothesis are correct, sometime during the 135,000 years between Illinoian and Wisconsin glaciation. Since the advance of the Wisconsin glaciers and the accompanying temperature change were gradual, it is conceivable that the two species were merely displaced southward, maintaining the same positions relative to one another and not interbreeding. Temperature change following recession of the glaciers may have occurred more rapidly than northward dispersal of the birds. I suspect that interbreeding occurred at the boundary between the two species until they reached the point where once again they could re-establish the gap that had been hit upon as a reproductive isolating mechanism. (If divergence was pre-Illinoian, these movements presumably occurred with each subsequent glacial advance and retreat.) In most of the eastern United States, I propose, this has been accomplished in the 10,000 to 15,000 years since withdrawal of the Wisconsin glaciers. In the Midwest, it has not. Here, northward dispersal of the Carolina Chickadee and replacement of the Black-capped Chickadee are probably still occurring.

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SUMMARY

The present-day pattern of coexistence of two sibling species of birds, the Black-capped and Carolina chickadees, *Parus atricapillus* and *P. carolinensis*, was investigated from 1954 to 1959.

The Carolina Chickadee occupies the south- and mid-eastern United States. The Black-capped Chickadee occupies the northern United States north to southern Alaska and Canada. From Kansas to central Illinois, the breeding ranges of the two species appear to be contiguous. Eastward, from central Illinois to the Atlantic coast, available evidence suggests that a gap up to several miles wide may be present between the southern boundary of the range of the Black-capped Chickadee and the northern boundary of the range of the Carolina Chickadee. Where the two species are in contact in western Illinois and eastern Missouri (and perhaps in the whole area from western Illinois and eastern Missouri to western Kansas), interbreeding apparently occurs with the production of a zone in which a large proportion of the chickadee population may be hybrid.

Ecologically, the two species are very similar or identical in every aspect investigated. Their demands for territorial space are similar. Each chooses the same kind of nest stub, located in vegetation somewhat less dense than that elsewhere in the immediate area. In feeding, the rate, the horizontal area covered, the sources exploited, and the food items taken all seem essentially identical. The species occur in the same kinds of vegetation, but Carolina Chickadees apparently can reach higher densities in mesic and perhaps wet forests, at least at middle latitudes in the Midwest. These extreme similarities suggest that competition between the two species would be inevitable unless no requisites were in short supply. The presence of competition is believed to be one reason for the allopatric distribution of the two species. The boundary between the two ranges may be set through the interplay of differing competitive advantages, including a higher rate of reproduction (larger clutch size), and an ability to reach higher densities in certain forest types on the part of the Carolina Chickadee and possible better adaptation to low temperature in the Black-capped Chickadee.

It is suggested that the two species diverged in isolation enforced by

a pre-Wisconsin (perhaps Illinoian) glaciation. Upon withdrawal of the glacier, the two populations dispersed and came together. Eventually, a point was reached where their respective competitive advantages balanced one another. This would appear to be a situation which would result in a (perhaps narrow) zone of overlap. I believe, however, that these two populations were interbreeding with low success. Because of the great similarity between the two species in every aspect of morphology and life history, the genetically simplest mechanism for the prevention of disadvantageous hybridization may have been the production of a gap between the breeding ranges. This gap, acting as a reproductive isolating mechanism, was established during some interglacial period (the Sangamon, if divergence began during Illinoian glaciation). With subsequent glaciations, the two species may have been forced southward. Following glacial retreat, interbreeding may have occurred at the boundary between the two populations throughout the period of their dispersal northward, until they reached a point where once again the gap between their ranges could be re-established. In most of the United States, the time since withdrawal of Wisconsin glaciers has been sufficient for this to be accomplished. In the Midwest northward dispersal of the Carolina Chickadee and replacement of the Black-capped Chickadee may still be occurring.

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