NARROWLY DISJUNCT ALLOPATRY BETWEEN BLACK-CAPPED AND CAROLINA CHICKADEES IN NORTHERN INDIANA

PETER G. MERRITT

The Black-capped Chickadee (*Parus atricapillus*) inhabits wooded areas across the northern United States, Canada and high elevations in the southern Appalachian Mountains. This species is replaced geographically by the closely related Carolina Chickadee (*P. carolinensis*) in the mideastern and southern United States (A.O.U. Check-list 1957). Where the ranges adjoin, a variety of situations prevail. In Kansas, the westernmost state where the ranges meet, the southern range of *P. atricapillus* is contiguous with the northern range of *P. carolinensis*. Rising (1968) provided evidence based on multivariate analyses of morphological characters that some interbreeding resulting in hybrid birds may take place there. Following the boundary eastward, the ranges remain contiguous through Missouri and into southern Illinois. There, Brewer (1961, 1963) described a zone of interbreeding where many birds appeared to be hybrids. Eastward from Illinois through Indiana and Ohio, Brewer (1963) reported a narrow gap (about 24 km wide in eastern Illinois) between the breeding ranges. Ward and Ward (1974) reported contiguous ranges in southeastern Pennsylvania and they provided evidence based on song that hybridization may occur there. Johnston (1971) described a hybrid population at the contact zone in the mountains of southwestern Virginia, where the chickadee ranges are separated by elevation. In contrast, Tanner (1952) found an elevational gap of about 180 m (855–1035) between the nesting ranges in the Great Smoky Mountains.

The existence of a narrow gap between the chickadee ranges is peculiar because apparently suitable nesting habitat occurs within the gap regions (Tanner 1952, Brewer 1963). Furthermore, both species appear to be able to exist under essentially the same climatic conditions. In the Great Smoky Mountains where *P. atricapillus* occurs only on some peaks, Tanner (1952) found that *P. carolinensis* nested at higher elevations on the peaks where *P. atricapillus* did not occur. In Illinois, Brewer (1963) found that *P. atricapillus* and *P. carolinensis* occurred along parallel river systems at the same latitude only 32 km apart.

On Mt. LeConte (Great Smoky Mountains), Tanner (1952) observed that *P. atricapillus* dispersed to lower elevations in the winter, invading the range of *P. carolinensis*. As the nesting season approached most *P. atricapillus* withdrew up the slopes resulting in the formation of the gap.

Similar observations are lacking for the latitudinal gap, but the hiatus seems to be most prominent during the breeding season (Brewer 1963). Brewer (1963) suggested that the gap evolved as a reproductive isolating mechanism. Since the hybrid population in Illinois had a relatively low rate of reproductive success (Brewer 1961), selective pressures may have favored an annual movement of chickadees away from the range interface in certain regions; this would act to increase the fitness of these birds. This hypothesis can be falsified by demonstrating that the gap does not form prior to reproduction.

This paper describes a field study examining the range relationship of *P. atricapillus* and *P. carolinensis* in northern Indiana. The study was designed to test the prediction that after a dispersal of either species of chickadee towards the range interface during the winter, these individuals withdraw from that region, forming a gap between the ranges before reproduction takes place.

STUDY AREA AND METHODS

Fieldwork was conducted in Kosciusko, Wabash and adjacent counties in Indiana. Drainage for most of the study area is by way of the Wabash River system which empties south into the Ohio River. The northern part of the study area consists of gently rolling hills characteristic of glacial landforms; the southern part is a flat till plain. Around 1820, beech-maple (*Fagus-Acer*) and oak-hickory (*Quercus-Carya*) forests were the dominant vegetation types in the study area (Lindsey et al. 1965). Today most of the land is farmed, the main crops being corn, wheat and soybeans. Wooded areas occur along river systems or as isolated woodlots. Lindsey (1966) gives additional information on climate and other aspects of natural history of the area.

Preliminary fieldwork indicated that *P. atricapillus* occurred near the city of Warsaw, Kosciusko Co., and *P. carolinensis* occurred along the Wabash River in Wabash County. Six relatively undisturbed stands of mesic forest were chosen as trapping stations along a 72 km north-south line transecting this region (Merritt 1977). Feeders erected at each trapping station were filled with sunflower seeds when originally set up, and a constant supply of seed was maintained until May 1976. Trapping was conducted with 6 McCamey chickadee traps (McCamey 1961) on at least 4 separate days totaling about 25 h at each station, from 24 December 1975–4 April 1976. Captured chickadees were held briefly for banding, measurement and observation of plumage coloration. The birds were marked with U.S. Fish and Wildlife Service aluminum bands and from 1–3 plastic color leg bands for individual recognition.

Captured chickadees were identified on the basis of tail-to-wing ratio and feather coloration. Wing chord and tail measurements were taken as suggested by Baldwin et al. (1931, see Merritt 1978). Inspection of plumage color was limited to the outer edge of the lateral tail feathers and the lateral edges of the secondary wing feathers. These areas are characteristically distinct and white in *P. atricapillus*, but gray and less distinct in *P. carolinensis*. Notes were taken on the coloration of these feathers as compared with a color chart consisting of 5 gradations ranging from white to gray. The chart was constructed by reference to feathers of specimens of *P. atricapillus*, *P. carolinensis* and suspected hybrids from Illinois.
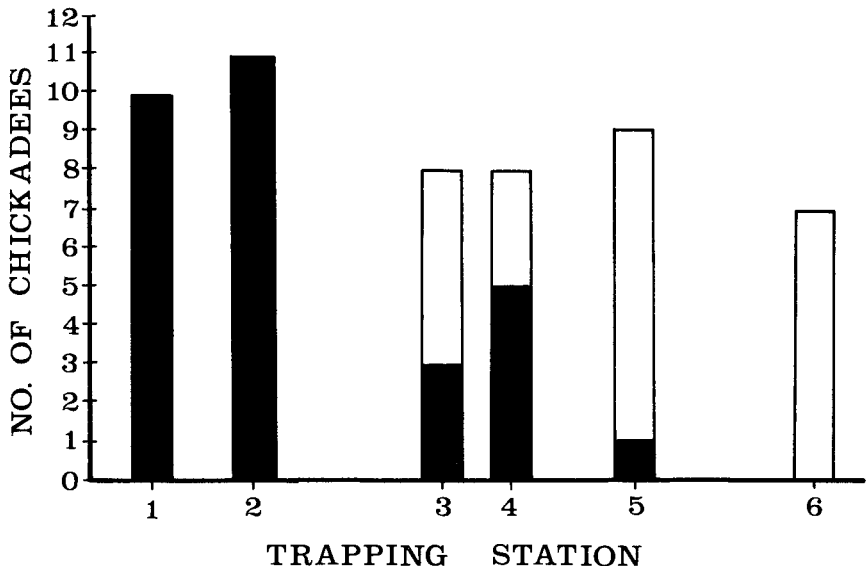
FIG. 1. The number of chickadees banded at each trapping station; *P. atricapillus* is shown in solid bars and *P. carolinensis* in open bars. The relative north-south distance between stations is represented on the abscissa.

Other distributional information was gained by soliciting vocal responses from chickadees in non-trapping areas in the winter (27 January–26 February 1976) and spring (29 April–31 May 1976). *P. atricapillus* typically sings a 2-noted whistle song, *fee-bee*, which is generally distinct from the 4-noted song, *fee-bee-febay*, of *P. carolinensis*. Less distinct, yet diagnostic to each species (especially when an on-the-spot comparison with a pre-recorded tape can be made), is the general call note. *P. atricapillus* gives this as a relatively slow *chickadee-dee-dee*, whereas *P. carolinensis* gives the same call but faster.

A portable cassette tape recorder was used to broadcast pre-recorded chickadee songs. One min of song and call notes for each species was recorded on separate cassettes. Songs of both species and call notes for *P. atricapillus* were recorded from Kellogg and Allen (1971) and call notes for *P. carolinensis* were recorded from Borror (1970). I located wooded areas containing seemingly favorable habitat for chickadees. Up to 30 min were spent walking through each area trying to elicit song responses from chickadees. This was accomplished by continuously broadcasting the pre-recorded tapes (once a minute I would pause to rewind the tape and listen for chickadees). During the winter survey I broadcast the *atricapillus* tape at areas north of the Eel River, the *carolinensis* tape at areas south of the Wabash River and both tapes, interchanging them at 5-min intervals, between the Eel and Wabash rivers. Because of changes in the chickadee populations found at the trapping stations this procedure was modified for the spring survey. The *atricapillus* tape was broadcast at areas north of the Eel River, the *carolinensis* tape at areas south of the Eel River and both tapes at areas along the Eel River. The trapping stations were also included in the spring survey.

Approximately 10 h of observation on 4 separate visits were spent at each of the 6 trapping stations from 6 April–22 May 1976. An additional 3 h of observation were spent at trapping

stations 5 and 6 on 25 May. The observation time was spent searching for and following chickadees.

TRAPPING RESULTS

The winter ranges of the 2 species were found to overlap by at least 20 km (Fig. 1). Thirty individuals of *P. atricapillus* were banded at trapping stations 1–5 and 23 individuals of *P. carolinensis* were banded at stations 3–6. Characteristics of the captured chickadees are described and compared in a separate paper (Merritt 1978); only features necessary for species identification are included in the following discussion.

The tail-to-wing ratio ranged from 0.846–0.938 ($\bar{x}$ = 0.890, SD = ±0.023) in *P. carolinensis* and 0.919–0.992 ($\bar{x}$ = 0.955, SD = ±0.016) in *P. atricapillus*. The overlap in tail-to-wing ratio (9.4% of all chickadees captured) is not uncommon; Lunk (1952), Tanner (1952), Simon (1959), Brewer (1963) and Johnston (1971) have reported slight overlap in the tail-to-wing ratio of these species.

Accurate classification of plumage color was difficult in the field because lighting conditions varied, but some differences in coloration were evident. Four *P. atricapillus* (13.3%) and 4 *P. carolinensis* (17.4%) showed plumage coloration tending towards intermediacy. These percentages of individuals deviating from the characteristic forms are within the range of variation observed by Brewer (1963:16–17) in Illinois.

One *P. atricapillus* banded at station 2 and 1 *P. carolinensis* banded at station 5 were intermediate in tail-to-wing ratio and feather coloration. Their intermediate morphology may have resulted from interbreeding; however, it is not likely that hybridization is widespread within the study area since these individuals represent only 3.8% of all chickadees captured.

WINTER DISTRIBUTION

The winter survey of vocal responses indicated that the ranges of *P. atricapillus* and *P. carolinensis* overlapped by about 25 km (Fig. 2). Differences in time and day of sampling did not seem to affect this survey significantly; chickadees responded with call notes or song at all 58 areas sampled. The distributional map in Fig. 2 may be biased to some extent by the choice of songs broadcast at a particular area. However, this bias is probably minimal since on several occasions an individual of 1 species responded to the taped broadcast of the heterospecific song (Merritt 1978) and the amount of range overlap detected (Fig. 2) corresponds with that found by the trapping (Fig. 1).

Typical vocal responses were elicited at most areas permitting species identification, but at 1 location an individual chickadee gave the song of
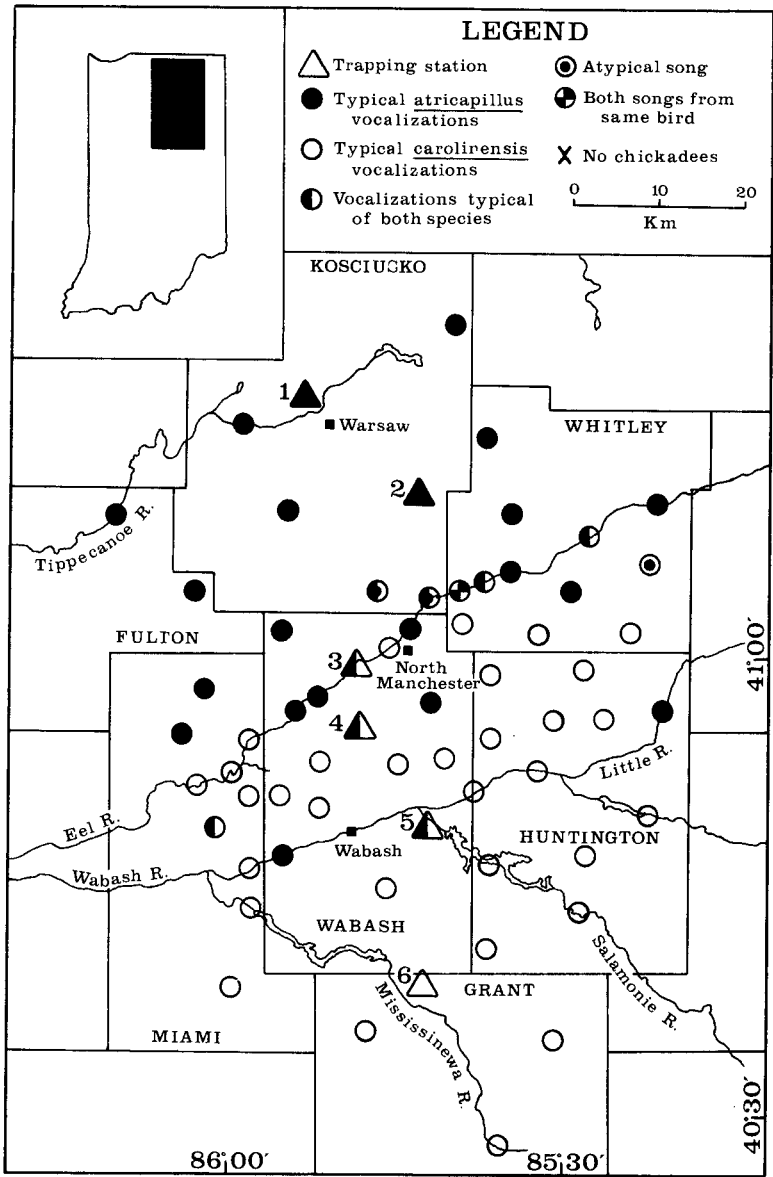
FIG. 2. Winter distribution of chickadees as determined by vocal responses. The trapping station symbols are solid if *P. atricapillus* was present, open if *P. carolinensis* was present and half-filled-in if both species were present.

both species and at 3 other locations abnormal songs were elicited (Merritt 1978). Tanner (1952), Johnston (1971) and Ward and Ward (1974) also observed individual chickadees singing the songs of both species. Similar cases of closely related species singing mixed songs have been described in buntings (*Passerina cyanea* and *P. amoena*), meadowlarks (*Sturnella neglecta* and *S. magna*), towhees (*Pipilo fuscus* and *P. albicollis*), tree-creepers (*Certhia familiaris* and *C. brachydactyla*), Old World warblers (*Acrocephalus scirpaceus* and *A. palustris*, *Phylloscopus trochilus* and *P. collybita*, *Sylvia communis* and *S. atricapilla*) and wrens (*Troglodytes aedon* and *Thryomanes bewickii*) (Lemaire 1977:227–230). As suggested by Emlen et al. (1975) for the case of the buntings (*Passerina cyanea* and *P. amoena*), it is likely that this behavior promotes interspecific recognition and facilitates heterospecific spacing.

The atypical songs given by 2 chickadees consisted of 4 high-pitched whistle notes of equal tone. The other atypical song consisted of a trill followed by 3 high-pitched whistle notes. In each case, these songs seemed to be given with unusually high intensity. Vocal anomalies apparently similar to these were also reported in Illinois (Brewer 1961, 1963), Kansas (Rising 1968), southwestern Virginia (Johnston 1971) and southeastern Pennsylvania (Ward and Ward 1974). Brewer (1963) and Johnston (1971) noted an unusually high percentage of atypical vocalizations near the hybrid zones in Illinois and Virginia, respectively. It seems probable that the vocal anomalies are the result of interbreeding. In this study only 3 individuals in the 58 areas surveyed responded with abnormal songs. This suggests, as does the trapping data, that isolated cases of interbreeding may occur in northern Indiana but a significant zone of hybridization is not present.

SPRING DISTRIBUTION

The spring survey of vocal responses revealed that the ranges of *P. atricapillus* and *P. carolinensis* were separated by a gap of about 30 km (Fig. 3). In general, chickadees of both species were sparse throughout the region surveyed; rarely did more than 1 chickadee in any particular area respond to the taped broadcast. Most chickadees occurred in river bottom forests or lowland woods along streams. This was especially true for *P. atricapillus*; only twice were individuals located in isolated wood-lots.

Only 1 *P. atricapillus* was found south of the Tippecanoe River and only 1 *P. carolinensis* was found north of the Eel River. Perhaps the most striking feature of the gap was the absence of chickadees along the Eel River northeast of trapping station 3. This area offers habitat similar to that existing along the Elkhart, Tippecanoe and Wabash rivers, yet in

spite of repeated tries at various times on different days no chickadees could be found here.

Of the 30 banded individuals of *P. atricapillus*, only 9 were seen past the middle of March and only 2 were observed after 1 April (Fig. 4). One of these (at station 2) was seen on both 8 and 15 April accompanied by an unbanded individual. Of the 23 banded individuals of *P. carolinensis*, 16 were observed in April and 4 individuals (at stations 4, 5 and 6) were seen near the end of May. During the observations at stations 5 and 6, typical *carolinensis* songs were commonly heard and a few instances of what appeared to be territorial combat were observed.

The only other sightings of chickadees at any of the trapping stations during April and May were as follows: On 3 April, I followed 3 unbanded chickadees from 16:00–16:10 as they foraged from the center of station 2 to the north edge of the woods. At least one of the birds gave the 2-noted whistle song characteristic of *P. atricapillus* several times, but the song was given softly. When they reached the edge of the woods they hesitated for a minute, then flew north over a corn field out of sight. On 13 April and 16 May, I observed an unbanded chickadee foraging in woods along the Eel River about 0.4 km north of station 3; no vocalizations were heard. On 25 May, I saw a group of 4 chickadees as they foraged slowly through some dense vegetation at station 6. One bird wore a band and appeared to be a parent leading young.

DISCUSSION

Comparison of the spring distribution (Fig. 3) with the winter distribution (Fig. 2) makes it evident that most *P. atricapillus* withdrew from the range interface. Observations at the trapping stations indicate that this took place primarily during the last 2 weeks of March (Fig. 4). The withdrawal included *P. atricapillus* occupying woodlots in Elkhart County as far as 80 km north of the range interface. Interestingly, most of the chickadees found in this region were in riparian habitat. In Kalamazoo County, Michigan, 175 km north of the range interface, *P. atricapillus* is common in woodlots as well as riparian habitat at all times of the year (pers. obs.). It seems likely that in northern Indiana chickadees were found mainly in riparian habitat because the only continuous stretches of woodland habitat occur along the river systems and these areas act as avenues of dispersion for the southernmost breeding *P. atricapillus*.

Seasonal migration in *P. atricapillus* has been discussed by Butts (1931), Wallace (1941), Bent (1946) and Lawrence (1958). Examination of unpublished banding records obtained in December 1978 from the U.S.
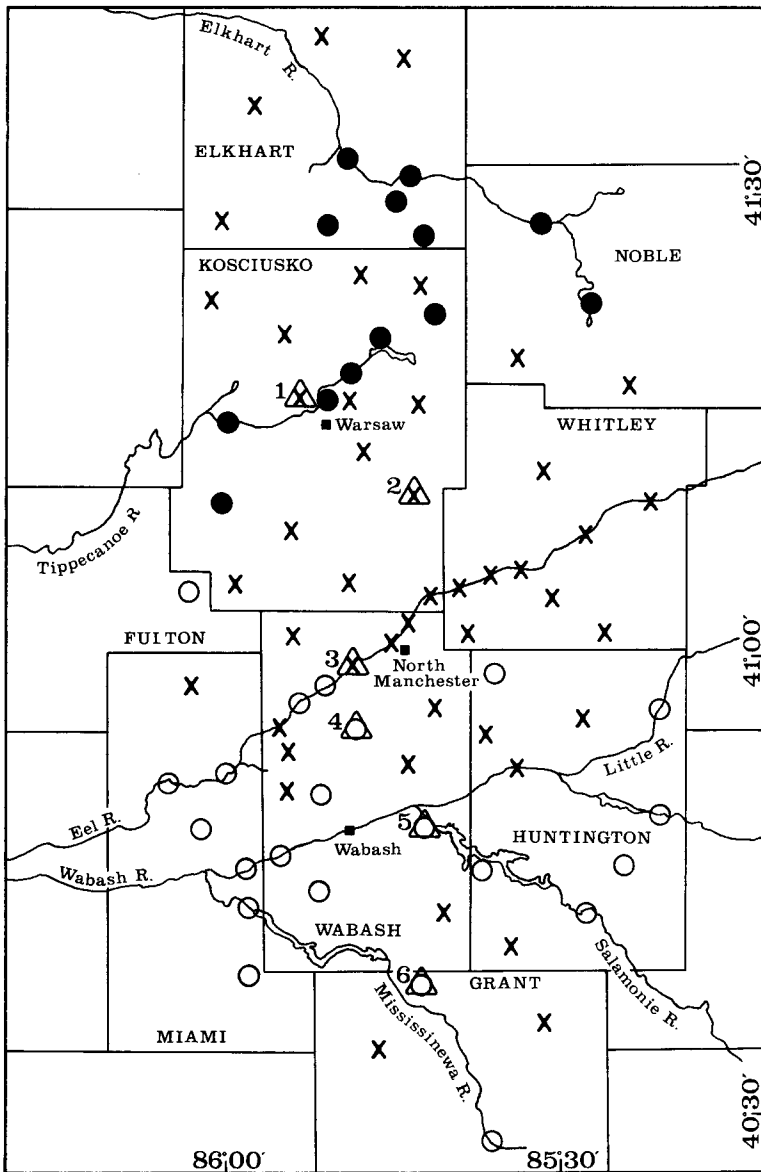
FIG. 3. Spring distribution of *P. atricapillus* and *P. carolinensis*. (Refer to legend in Fig. 2.)
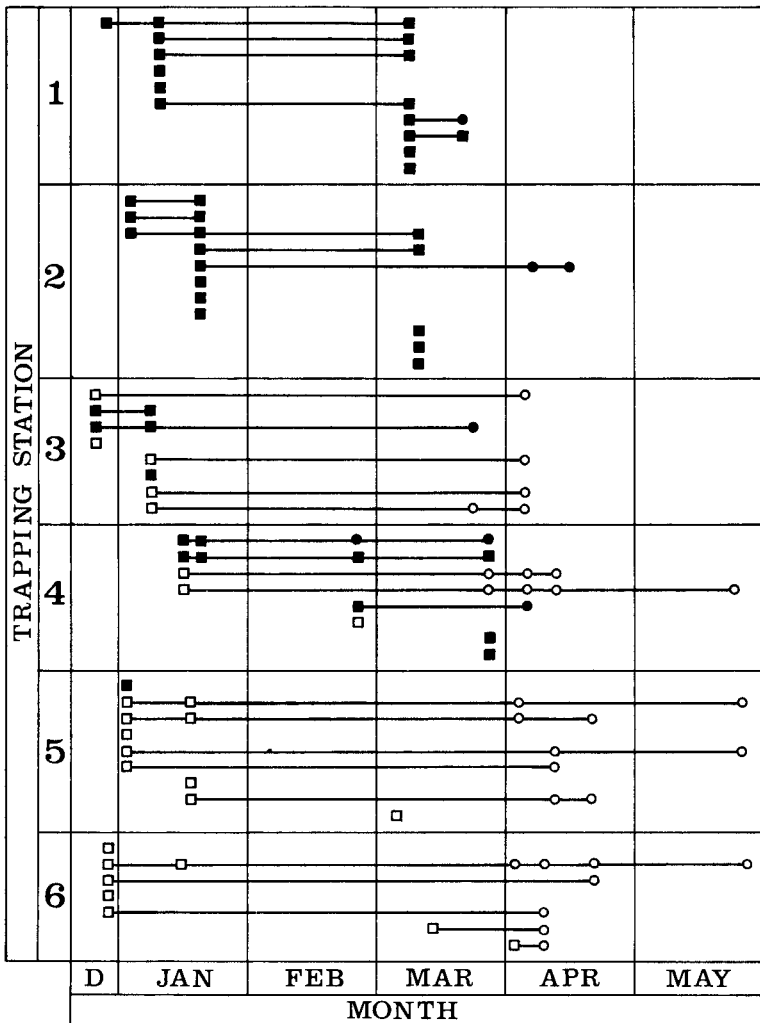
FIG. 4.   Summary of captures and observations at the trapping stations. Squares indicate the bird was captured and circles indicate it was observed. *P. atricapillus* is represented by solid symbols and *P. carolinensis* by open symbols.

Fish and Wildlife Service indicates that long distance movements of *P. atricapillus* are most common in a northeast-southwest direction throughout the eastern and midwestern U.S. and southeastern Canada. Since numerous banding studies show that many individuals of *P. atricapillus* are permanent residents in this region (e.g., Odum 1942, Glase 1973,

Weise and Meyer 1979), it appears that during the winter the gap between the ranges may become occupied by individuals of *P. atricapillus* from the northeast. The gap becomes apparent only after the withdrawal of *P. atricapillus* in the spring. Observations in Ohio by Thomas (1958) also agree with this conclusion.

The disjunct nature of the breeding ranges of *P. atricapillus* and *P. carolinensis* appears to be relatively stable; the gap has remained at approximately the same latitude in northern Indiana for at least 40 years. From 1935–1939 Ernest M. Shull frequently went on early morning walks from Manchester College along the Eel River, upstream about 3.2 km to the town of Liberty Mills and then back. This area lies only a few kilometers northeast of trapping station 3. Shull (unpubl.) recorded sightings of all birds along this route. Downy Woodpeckers (*Picoides pubescens*), Tufted Titmice (*P. bicolor*) and White-breasted Nuthatches (*Sitta carolinensis*) were common during every month of the year. Chickadees (most reported to be *P. atricapillus*), however, were found in January through April and September through December, but none in May or July and only 1 in each of June and August during these years.

It is still not clear what factors cause the gap to occur. The fact that the elevational gap found by Tanner (1952) in the Great Smoky Mountains and the latitudinal gap found in northern Indiana both occurred only during the breeding season and became obvious after a withdrawal of *P. atricapillus* suggests that similar factors maintain the gap at both locales. Considering ultimate factors, Brewer (1963) suggested that the gap evolved as a reproductive isolating mechanism functioning to reduce unsuccessful interbreeding. No active chickadee nests were found in this study so to test Brewer's reproductive isolation hypothesis it is necessary to estimate the time of reproduction. The expected date of first egg-laying by chickadees at the range interface in northern Indiana can be approximated by adjusting data for chickadees nesting in Illinois. Both species tend to begin laying about 3.5–4.5 days later for each degree of latitude northward (Brewer 1961), so the first egg-laying at 41°N latitude should occur from 20 April–26 May for *P. atricapillus* and 30 April–21 May for *P. carolinensis*. Nest-building, excavation and the establishment of territorial boundaries precede the first egg-laying by about 20 days. Therefore, chickadees remaining in the study area might engage in reproductive activities as early as 1 April for *P. atricapillus* and 10 April for *P. carolinensis*. The main withdrawal of chickadees away from the range interface took place prior to these dates so the prediction that the gap forms before nesting activities begin is supported. This, plus the fact that only a few possible hybrid individuals were found in this study, indicate that the gap functions as a reproductive isolating mechanism, but it is not clear that the gap

evolved for this purpose. If an individual chickadee's fitness can be increased by migrating to another area to breed, then natural selection may have favored the spring withdrawal of *P. atricapillus* from the range interface; however, this hypothesis remains speculative.

Two other hypotheses attempting to explain narrowly disjunct allopatry in general, and thought possibly to apply to the case of the chickadees, rely chiefly on proximate factors. Cornell (1974) suggested that parasites might be transmitted between chickadee species in the overlap zone. If these had an adverse effect on the reproductive success of chickadees breeding at the range interface a gap could develop. Expanding on MacArthur's (1972) model of exploitative competition, Slade and Robertson (1977) suggested that a change in resource availability as a result of the cost of interspecific competition in the overlap zone may have caused a competitively-induced gap. These hypotheses do not assume that the withdrawal of *P. atricapillus* is related to the maintenance of the gap. They both require that interspecific contact occurs between chickadees that are permanent residents at the range interface. If the interactions severely reduce the fitness of chickadees attempting to breed in this region a gap might develop. For an hypothesis of this type 2 predictions can be made: (1) the width of the gap should be dependent upon the degree of overlap exhibited by sedentary individuals of both species; and (2) the width of the gap should fluctuate in time according to the rate of recolonization. A gap developing under these circumstances might persist for a relatively long period of time if the rate of recolonization is low. Therefore, these hypotheses might only be testable by a long term study monitoring the distribution and abundance of permanent residents at the range interface.

It is also possible that the gap is caused and maintained by the winter influx of *P. atricapillus*. These individuals might provide additional competition for limiting food resources, which may result in decreasing the winter survival rate of resident chickadees of both species at the range interface. This might be especially important in forming the gap if hybrid chickadees are inferior competitors. This hypothesis could be examined by testing the prediction that year-to-year fluctuations in sedentary chickadee populations near the range interface are directly related to the intensity of the winter influx of *P. atricapillus*.

SUMMARY

During the winter and early spring of 1975–1976 the ranges of *Parus atricapillus* and *P. carolinensis* overlapped by about 25 km in northern Indiana. Evidence based on morphology and song suggest that isolated cases of interbreeding may occur. During the last 2 weeks of March most *P. atricapillus* withdrew from the range interface. A survey of vocal responses

conducted from 29 April–31 May revealed that the breeding ranges were separated by a gap of about 30 km. The withdrawal of *P. atricapillus* included individuals occupying woodlots as far as 80 km north of the range interface.

It is still not clear what factors cause the gap to occur. The resemblance of the elevational gap found by Tanner (1952) in the Great Smoky Mountains and the latitudinal gap found in northern Indiana suggests that the gap is maintained by similar factors at both locations. Since the gap becomes obvious with the withdrawal of *P. atricapillus* just prior to the breeding season, it is possible that these movements were selected for as a reproductive isolating mechanism.

Other hypotheses attempting to explain the presence of the gap rely chiefly on proximate factors. The most likely of these hypotheses are: (1) the gap forms as a direct result of interspecific interactions between sedentary chickadees at the range interface; and (2) the gap is caused and maintained by the winter movement of *P. atricapillus* to the range interface. Competitive interactions reducing the fitness of sedentary chickadees in and near the gap may be important for either hypothesis.

ACKNOWLEDGMENTS

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DEPT. BIOLOGY, UNIV. MIAMI, CORAL GABLES, FLORIDA 33124.