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## Gap Formation: A Reproductive Isolating Mechanism for *Parus Atricapillus* and *P. Carolinensis* in Northern Indiana

Peter Gorham Merritt

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GAP FORMATION: A REPRODUCTIVE ISOLATING MECHANISM  
FOR *PARUS ATRICAPILLUS* AND *P. CAROLINENSIS*  
IN NORTHERN INDIANA

by

Peter Gorham Merritt

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Submitted to the  
Faculty of The Graduate College  
in partial fulfillment  
of the  
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Western Michigan University  
Kalamazoo, Michigan  
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I extend my sincere gratitude to Richard Brewer for providing direction and guidance throughout all phases of this project. I profited from conversations with Joseph G. Engemann and Rainer R. Erhart and from correspondence with James B. Cope, Russell E. Mumford, Ernest M. Shull, and Gary L. Wilford. I owe particular thanks to those people in Indiana who took interest in my study and aided me during some aspect of the project: Paul E. Steffen (Tippecanoe Audubon Society), David Eiler (Manchester College), Neil Case and Rex Watters (Salamonie Reservoir) and James Bostwick (Mississinewa Reservoir). I thank G. T. Donceel, Jr. of the Indiana Department of Natural Resources for providing me with sleeping quarters at the Salamonie Reservoir. I also thank friends, John Stiner, Doug and Christine Campbell, and John Olson, for assistance with various aspects of the project. In addition, I would like to express my appreciation to the many kind people of Indiana who permitted me to trap or make observations on their property. This project was partially funded by grants from the Frank M. Chapman Memorial Fund of The American Museum of Natural History and the Western Michigan University Research Fund; to each of these I am grateful.

Peter Gorham Merritt

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## CHAPTER I

### INTRODUCTION

#### Range Relationships in the Genus *Parus*

The examination of geographical range relationships of species in the passerine genus *Parus*, titmice and chickadees, has yielded much insight into the evolutionary role of competition in animal populations (Snow, 1954; Dixon, 1961; Lack, 1971). The pressures associated with interspecific competition apparently provide a driving force which eventually allow competing species that are reproductively isolated to become ecologically segregated, thereby permitting coexistence (Lack, 1944; Svärdson, 1949; Udvardy, 1951). Thus interspecific competition has the effect of facilitating species divergence and increasing species diversity.

A comparison of the range relations of European versus North American species of *Parus* reveals one basic difference; six of the nine European species coexist over wide areas, whereas only two of the ten North American species coexist (Lack, 1969). Ecological isolation in the sympatric European species is achieved partially by differences in habitat; however, it is usually by a difference in food and feeding station within the same habitat (Snow, 1954). This comparison suggests, as proposed by Lack (1969), that the North American species of *Parus* are at an earlier stage of evolution than their European counterparts.

The present study is concerned with the geographical relationship of the ranges of two North American species of *Parus*: the Black-capped Chickadee (*Parus atricapillus*) and the Carolina Chickadee (*P. carolinensis*).

These sibling species are extremely similar in all aspects of morphology and ecology (Brewer, 1961, 1963). *P. atricapillus* inhabits wooded areas across the northern United States and Canada and is replaced by *P. carolinensis* in the mideastern and southern United States. Isolated populations of *P. atricapillus* also occur at high elevations in the southern Appalachian Mountains (Tanner, 1952). The ranges, therefore, are essentially allopatric and evidence suggests that, owing to the birds' ecological similarity, competition takes place where the ranges adjoin (Brewer, 1963).

The Range Relationship of  
*P. atricapillus* and *P. carolinensis*

A variety of situations have been reported to prevail where the ranges of *P. atricapillus* and *P. carolinensis* come together. 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 measurements, that some interbreeding resulting in hybrid birds may take place here. Following the boundary eastward, the ranges remain contiguous through Missouri and into southern Illinois. Here, Brewer (1961, 1963) has described a zone of interbreeding where a large proportion of the birds may be hybrids. To the east of the hybrid zone in Illinois and extending through Indiana, Ohio and possibly farther east, a gap containing suitable nesting habitat for either species exists between the ranges (Brewer, 1963). East of this region information on the exact nature of the range interface is sketchy; however, Ward and Ward (1974) reported that the ranges are

contiguous in southeastern Pennsylvania and they provided evidence based on song that hybridization may occur. Johnston (1971) described a hybrid population at the contact zone of *P. atricapillus* and *P. carolinensis* in the mountains of southwestern Virginia, where the ranges are separated altitudinally. In contrast, Tanner (1952) found that in the Great Smoky Mountains an altitudinal gap exists between the nesting ranges of the two species, a situation similar to that found by Brewer (1961, 1963) occurring east of the hybrid zone in Illinois.

Where the ranges of *P. atricapillus* and *P. carolinensis* are contiguous, then, it seems that hybridization occurs, at least to some extent. This is, perhaps, not surprising in view of the morphological and ecological similarities between these two species. However, Brewer (1961) found that the hybrid population in Illinois had a low rate of hatching and fledging of the young. The low rate of nesting success implies that interbreeding wastes reproductive energy. A situation such as this would have a low adaptive value, making it evolutionarily advantageous to restrict or eliminate interbreeding. Brewer (1963) suggested that the reproductive isolating mechanism which evolved in these exceedingly similar species was the formation of a gap between the breeding ranges.

### Purpose

The purpose of this project was to examine the nature of the range interface of *P. atricapillus* and *P. carolinensis* in northern Indiana. Here the range relationship of these species has been of interest to James B. Cope and Russell E. Mumford for more than 20 years; however,

a definitive study confirming the existence and revealing the exact location of a gap between the ranges has not been carried out. I designed my study to test the hypothesis that there would be a dispersal of either species of chickadee towards the range interface during the winter with these individuals withdrawing away from that region forming a gap before reproduction takes place. Data were gathered from the fall of 1975 through the summer of 1976 via trapping, banding and soliciting song responses from chickadees.

## CHAPTER II

### STUDY AREA

Field work for this project was conducted in and near Kosciusko, Wabash and Grant counties (85°45'W. Long., 41°00'N. Lat.) in northern Indiana (Figure 1). Only a brief discussion of the study area with references to habitat will be provided. Additional information pertaining to climate and other aspects of natural history for the area may be found in an authoritative series of papers edited by Lindsey (1966).

#### Drainage and Physiography

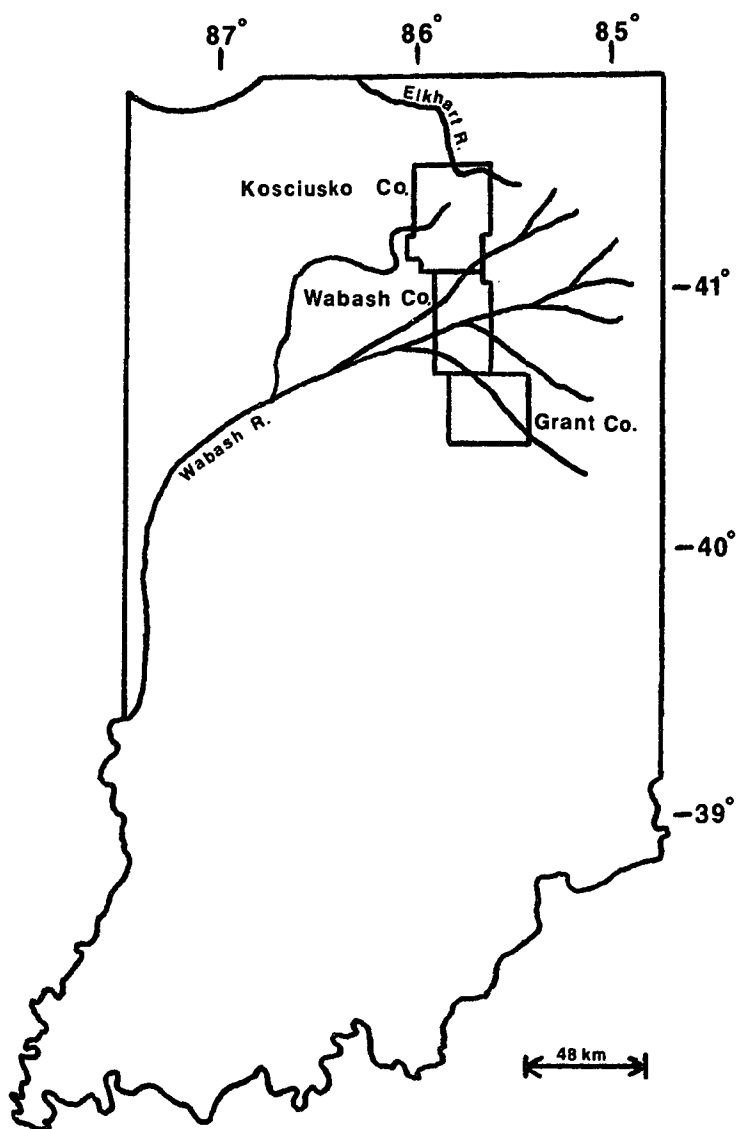
Drainage for most of the study area is by way of the Wabash River System which empties south into the Ohio River. The northern portion of the study area drains north into Lake Michigan via the Elkhart River. The Eel River flows southwest across the study area bisecting it centrally. The land lying north of the Eel River consists of gently rolling hills with variable relief characteristic to morains and other glacial structures. South of the Eel River lies an extensive till plain which has left the land extremely flat in nature.

#### Original Vegetation

Lindsey et al. (1965) provided a generalized map of the presettlement vegetation of Indiana based on the original land survey records and modern soil maps of counties. Their map shows that around 1820 beech-maple forest was predominant south of the Eel River and in a band

Figure 1. Map of Indiana showing the location of counties where trapping was conducted.

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surrounding Kosciusko County. North of the Eel River a strip of oak-hickory forest reached from the southwest and extended up to cover most of Kosciusko County. The prairie peninsula described by Transeau (1935) extended across the northwest portion of Indiana but for the most part was not a dominant vegetation type in the study area. According to the map of Lindsey et al. only isolated patches of wet and dry prairie existed in the study area and were probably most abundant in the northwest corner of Kosciusko County.

#### Present Vegetation

Today most of the land in the study area is farmed with the main crops being corn, wheat and soybeans. The wooded areas occur along river systems or as isolated wood lots dispersed among the farmlands. A detailed description of the riparian vegetation along the Tippecanoe and Wabash Rivers west of the study area by Lindsey et al. (1961) probably provides a fairly accurate description of the same vegetation within the study area. The isolated wood lots are of variable size and quality; a typical one might be from .004 to .008 ha in size and show signs of selective lumbering and grazing in the past. Nearly all wood lots, however, seem to remain relatively undisturbed throughout most of the year and many show a good range of size variation for the constituent trees and shrubs.

## CHAPTER III

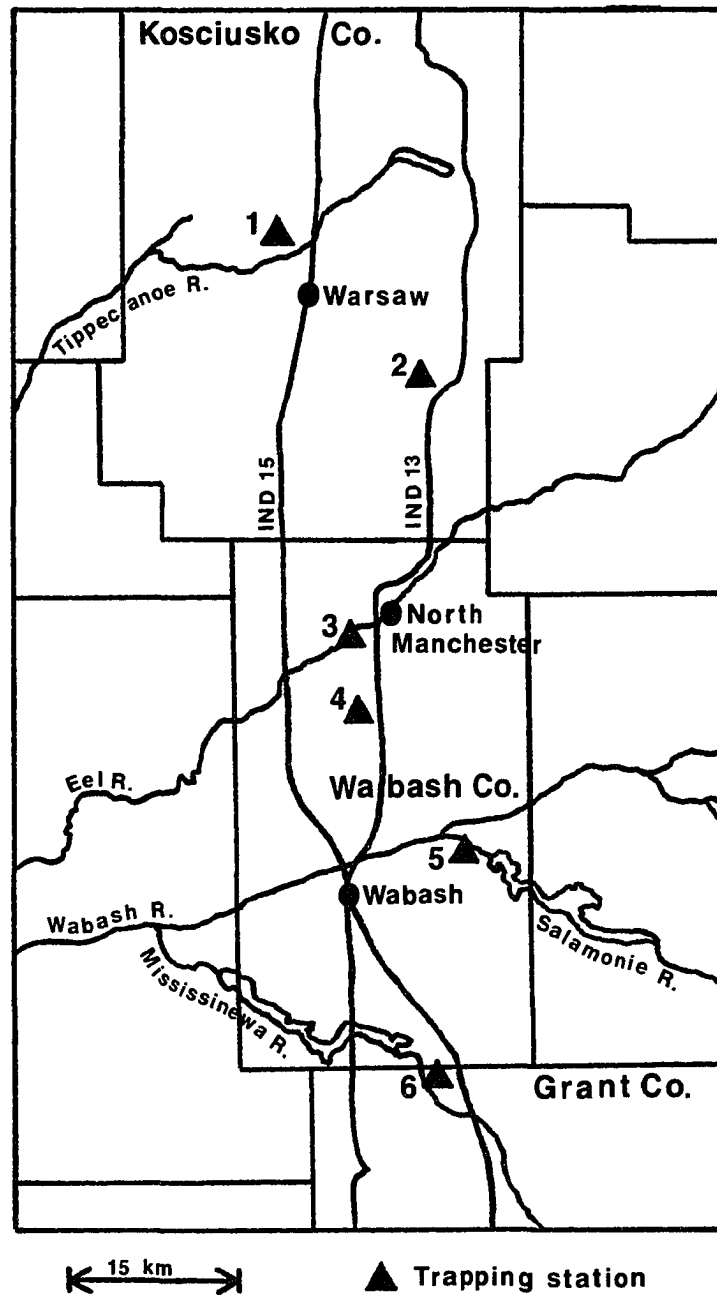
### TRAPPING METHODS

Preliminary field work in 1963 and 1966 by Richard Brewer and by me in 1975 indicated that *P. atricapillus* occurred near the city of Warsaw, Kosciusko County, and *P. carolinensis* occurred along the Wabash River in Wabash County. Little was known of the chickadee populations between these two locations. In order to determine the exact relationship of the ranges, a series of trapping stations was set up on a north-south line transecting the range interface. Criteria for trapping stations was that each had to be relatively undisturbed forest of at least .008 ha with trees showing a good range of size variation. In addition, the areas were chosen to be as similar as possible with respect to tree composition. Figure 2 shows the location of the six trapping areas chosen; the exact location and ownership of each site is listed in Appendix 1.

#### Trapping Stations

Trapping station 1 was a mature beech-maple wood lot of approximately .012 ha. Known as Rosbrugh Woods, the tract has been used as a sugar bush for more than 100 years; the area has been described in Lindsey et al. (1969). The woods had no standing or running water; however, it lies only about a half mile from the Tippecanoe River. Several acres of forest edge and thicket habitat abutted the woods to the east and west.

Figure 2. Map of the study area showing the location of the six trapping stations.



The second trapping station was another isolated wood lot of about .008 ha dominated by beech and sugar maple. The woods had no running water but contained several shallow ponds, each of which were less than an acre in size. Many acres of immature woods, mostly xeric in nature, were in contact with the trapping area directly to the south.

Trapping station 3 was located at the north edge of Ogden Woods, an essentially virgin .008 ha tract of beech-maple forest; a brief description of this area can also be found in Lindsey et al. (1969). The stand is on the upland above the Eel River and grades down a steep slope to a mature and continuous river bottom forest.

Between the Eel and Wabash Rivers much difficulty was encountered in finding a forest type similar to that of the other trapping areas. The woods finally chosen for the fourth trapping station was a diverse one of about .008 ha. The southern part of the woods was mesic, although most of the larger trees had been cut down within the past several years and many tree tops were left on the forest floor making it very dense in spots. The eastern part of the woods was very wet and the northwest portion of the woods consisted of a few acres of red maple swamp. To the east, the swamp graded into a few acres of young oak-hickory woods. The adjacent property to the north and east of the trapping area was also wooded.

The fifth trapping station was located in a deciduous woods of the Salamonie River Forest. It was dominated by beech, maple, oak and hickory and resembles the western mesophytic forests of southern Indiana. The forest ran along the top of an escarpment on the south side of the Salamonie River. Numerous deep gorges cut through the area. The north

side of the river was covered mostly by flood plain vegetation with sycamore, willow and cottonwood trees growing abundantly.

Trapping station 6 was a mature beech-maple woods of at least .008 ha located on land maintained by the Mississinewa Reservoir. It was about 72 km south of station 1. The area was bounded to the east by a small creek which flows into the Mississinewa River; marginal habitat consisted of a strip of lowland thicket and woods that followed along the creek.

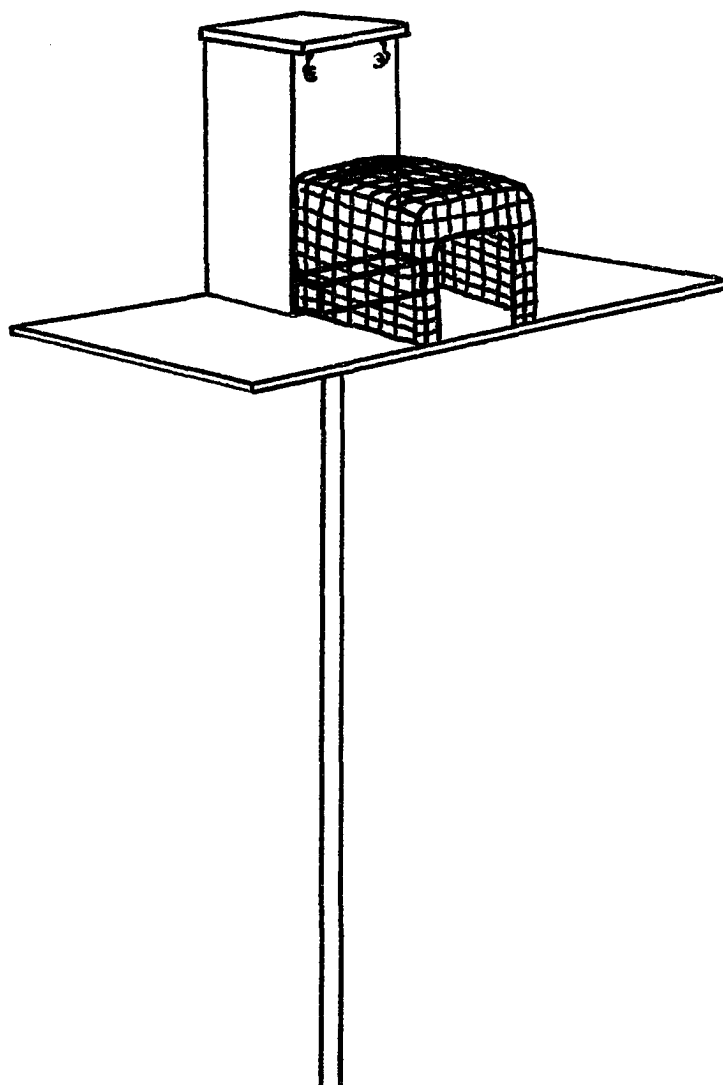
#### Feeder Design and Daily Trapping Procedures

A combination feeding-trapping platform as shown in Figure 3 was erected at stations 1, 2 and 3 on 29 September 1975 and at stations 5 and 6 on 4 October 1975. Owing to difficulty in finding a suitable trapping area, the platform at station 4 was not set up until 6 January 1976. The feeders held about 4.5 kg of sunflower seeds and were mounted on plywood platforms (.6 X .9 m). Each platform was mounted on a steel pole and raised 1.5 m above the ground. A wire mesh frame was attached to the opening of the feeders so that birds would be forced to pass through to obtain seed; it was hoped that this would condition birds to enter a trap type structure readily. The feeders were filled with sunflower seeds when originally set up and a constant supply of seed was maintained until May 1976.

Trapping was conducted on at least four separate days (totaling about 25 hours) at each station from 24 December 1975 through 4 April 1976 (for a list of the exact dates and hours trapped see Appendix 2). The traps were usually operated between 08:00 and 16:00 EST. Upon

Figure 3. A combination feeding-trapping platform, typical of one used at each trapping station.

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arrival at a trapping area six McCamey chickadee traps (McCamey, 1961) were placed on the platform and a cloth hood was placed over the entrance to the permanent feeder. The traps were baited with sunflower seeds, set and left for a half hour to an hour before being checked. Captured birds were removed, placed in a carrying case and transported to a distant location within the woods for banding. Chickadees, Downy Woodpeckers (*Dendrocopos pubescens*), Tufted Titmice (*Parus bicolor*) and White-breasted Nuthatches (*Sitta carolinensis*) were marked with U. S. Fish and Wildlife aluminum bands. Chickadees were also marked with from one to three plastic color bands for individual recognition.

To insure proper identification of all captured chickadees each bird was weighed, body measurements were taken and plumage color was inspected. No attempt was made to age or sex individuals by measurement or plumage since methods are not reliable (Gochfeld, 1977). Body weight was measured to the nearest 0.1 g on a Pesola 30 g scale. Body measurements followed the methods outlined in Baldwin et al. (1931); all measurements were taken to the nearest 0.5 mm. Wing chord was measured by inserting a ruler under the right wing and measuring from the farthest anterior point of the bend of the wing to the tip of the longest primary, without flattening the feathers. Length of tail was measured by parting the feathers at the base of the tail exposing the insertion point of the middle pair of rectrices; measurement was made from this point to the tip of the longest tail feather with the tail closed using a ruler. Culmen length was measured with dividers from the anterior edge of the nostril to the anterior end of the bill. Length of tarsus was measured with dividers from the middle point of the joint between the tibia and

metatarsus behind, to the lower edge of the lowest individual scute on the front part of the junction of the metatarsus with the base of the middle toe. Inspection of plumage color was limited to the outer edge of the lateral tail feathers and the lateral edge of the secondary wing feathers. These areas are characteristically distinct and white in *P. atricapillus* and less distinct and gray in *P. carolinensis*. Notes were taken on the coloration of these feathers as compared to a color chart. The chart consisted of five gradations ranging from white to gray and was constructed by reference to feathers of specimens lent to me by Richard Brewer. The collection included *P. atricapillus*, *P. carolinensis* and suspected hybrids from Illinois.



## CHAPTER IV

### TRAPPING RESULTS

#### Chickadee Populations

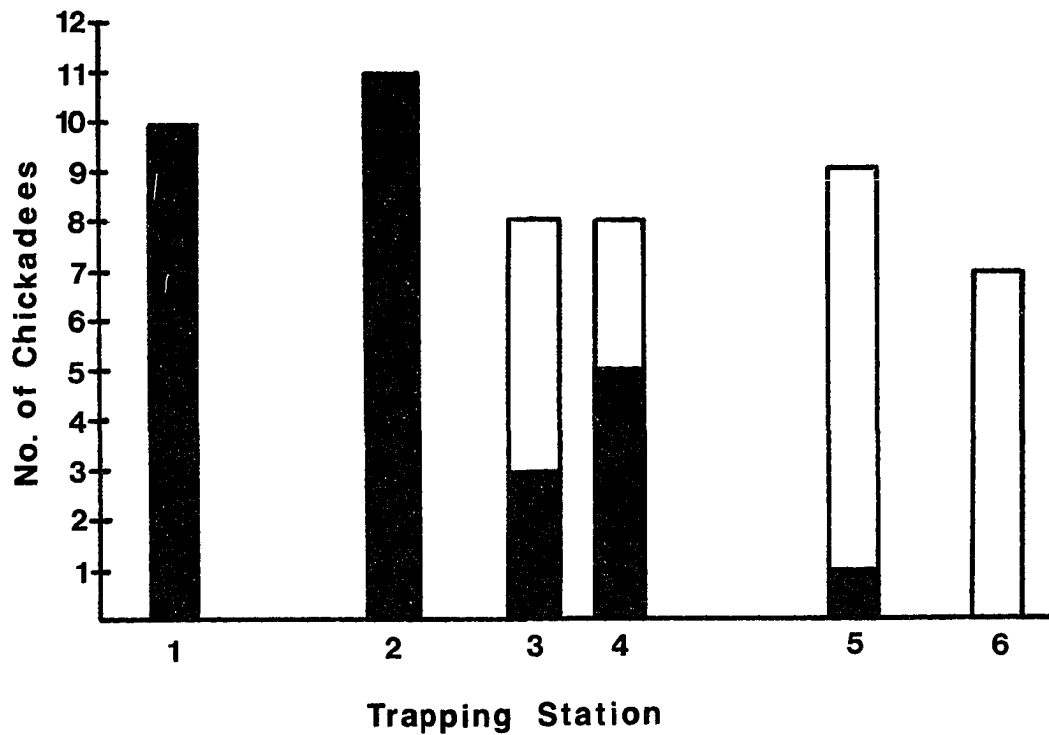
Fifty-three chickadees including 30 *P. atricapillus* and 23 *P. carolinensis* were banded during this study. Only *P. atricapillus* occurred at trapping stations 1 and 2; both species were present at stations 3, 4 and 5; and *P. carolinensis* was the only chickadee found at station 6 (Figure 4).

Several times at trapping stations 3 and 4 both species of chickadee were identified moving together in feeding parties. No unusual behavior was noted but flock interactions were not investigated thoroughly.

There was little suggestion that hybrid populations existed at any of the trapping stations. If an individual chickadee could not be identified by measurement, it was in most cases easily identified by plumage color or vocalizations.

It is doubtful that all of the chickadees wintering at any one area were banded but the relative numbers banded at each station are probably representative. The proportion of *P. atricapillus* to *P. carolinensis* banded at trapping stations 3 and 4 indicates that nearly equal numbers of each species occupied this region during the winter. At trapping station 5 only one *P. atricapillus* was banded compared with eight *P. carolinensis*; this suggests that the ranges graded into one another as opposed to meeting abruptly. Trapping station 2 was located approximately

Figure 4. Number of chickadees banded at each trapping station; *P. atricapillus* in solid bars and *P. carolinensis* in open bars. The distance between stations is represented.



21 km north of trapping station 3 and it seems reasonable to speculate that had station 2 been closer to station 3, a small number of *P. carolinensis* may have been captured there as well. This conjecture is also supported by evidence based on song.

#### Other Species Banded

Because the Downy Woodpecker, Tufted Titmouse and White-breasted Nuthatch utilize a habitat similar to that of the chickadee, the abundance of these species should give some indication of the relative similarity of the habitats trapped. The number of these birds captured at each station shows some variation but no great differences are evident (Table 1). Even though no Downy Woodpeckers were banded at trapping stations 1 and 3, nor White-breasted Nuthatches at trapping station 1, these birds were observed at each of these sites. These data, then, suggest no differences in suitability of habitat over the 72 km transect for chickadees and ecologically similar birds.

Table 1. Number of Downy Woodpeckers, Tufted Titmice and White-breasted Nuthatches banded at each trapping station.

Species	Trapping Station					
	1	2	3	4	5	6
Downy Woodpecker ( <i>Dendrocopos pubescens</i> )	0	3	0	2	1	4
Tufted Titmouse ( <i>Parus bicolor</i> )	5	4	5	4	5	3
White-breasted Nuthatch ( <i>Sitta carolinensis</i> )	0	2	3	2	2	2

## CHAPTER V

### CHARACTERISTICS OF THE BANDED CHICKADEES

Measurements and observations taken from banded chickadees are listed in Appendix 3 for *P. atricapillus* and Appendix 4 for *P. carolinensis*. *P. atricapillus* is characteristically slightly larger than *P. carolinensis* (Lunk, 1952; Tanner, 1952; Brewer, 1963; Olson, 1968; Johnston, 1971). This phenomenon was reflected in all measurements taken on chickadees in northern Indiana; however, all features exhibited some degree of overlap in size.

#### Weight

Body weight of *P. atricapillus* ranged from 9.8 g to 12.4 g with a mean of 11.2 g while individuals of *P. carolinensis* weighed from 9.0 g to 11.7 g with a mean of 10.6 g (Table 2). A plot of the per cent frequency of these weights in Figure 5 shows that for each species several peaks occurred. These deviations from a normal distribution are probably due to sexual differences within each species plus the fact that weights were taken at different times of the day and over a three month period. In any case, extensive overlap in weight was displayed by *P. atricapillus* and *carolinensis* (Figure 5).

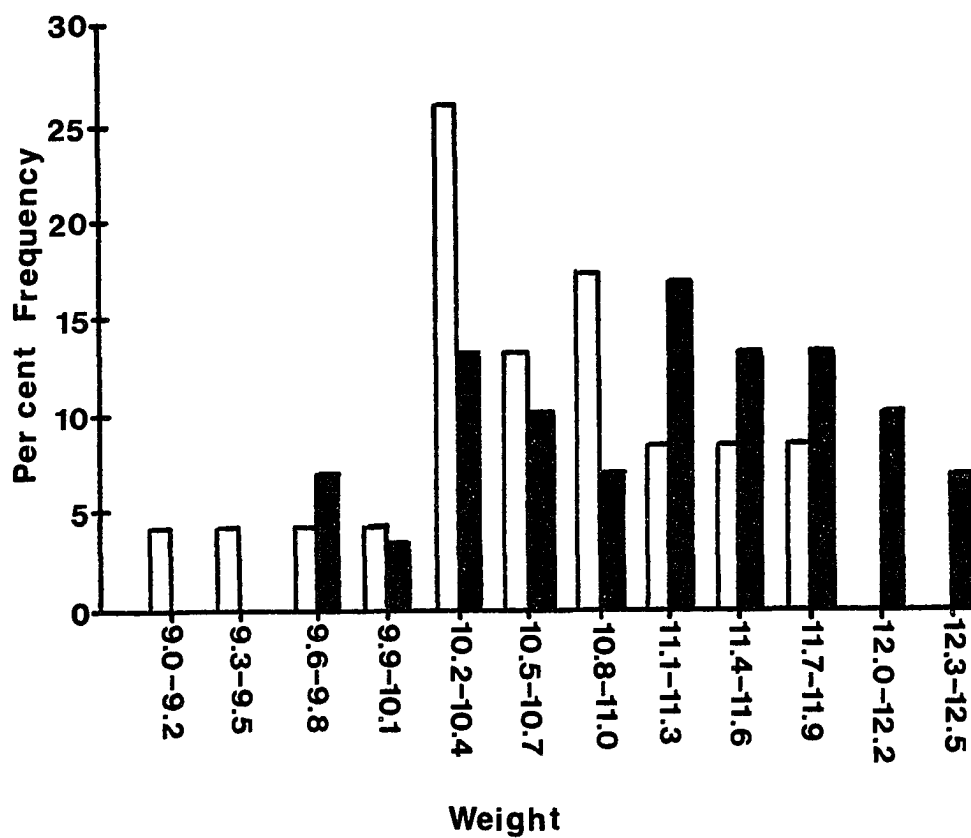
#### Culmen and Tarsus Length

Culmen and tarsus length showed the most overlap in size of all features measured. A plot of the per cent frequency of the culmen lengths

Table 2. Mean, standard deviation and variance of body weight (g), wing chord length (mm), tail length (mm) and tail-to-wing ratio of banded chickadees; N=30 for *P. atricapillus* and N=23 for *P. carolinensis*.

Body Measurement	<i>P. atricapillus</i>			<i>P. carolinensis</i>		
	$\bar{x}$	$s$	$s^2$	$\bar{x}$	$s$	$s^2$
Weight	11.2	0.77	0.59	10.6	0.64	0.41
Wing Chord	63.7	1.55	2.39	62.0	2.27	5.13
Tail	60.9	1.72	2.96	55.2	2.66	7.09
Tail/Wing	.955	.016	-	.890	.023	-

Figure 5. Per cent frequency of body weights (g) of *P. atricapillus* (solid bars) and *P. carolinensis* (open bars) banded.



(Figure 6) shows that each species range from 6.5 mm to 7.5 mm; however, most *P. atricapillus* had culmen lengths between 7.0 mm and 7.5 mm whereas most *P. carolinensis* had a culmen length near 7.0 mm. A plot of the percent frequency of tarsus length (Figure 7) for *P. atricapillus* shows a range from 15.0 mm to 17.5 mm with peaks at 16.0 mm and 17.0 mm, again possibly due to sexual differences. *P. carolinensis*, in turn, had tarsus lengths ranging from 14.5 mm to 17.0 mm with lengths of 15.5 mm and 16.0 mm occurring most frequently but no bimodal distribution was evident.

#### Wing Chord and Tail Length

The single most important characteristic used to differentiate between *P. atricapillus* and *P. carolinensis* is the tail-to-wing ratio (T/W). According to Tanner (1952) this ratio gives the most consistent difference between the two species, is independent of sex and shows no significant differences between the ratios taken from birds with worn and non-worn feathers. *P. atricapillus* had a mean wing chord length of 63.7 mm, mean tail length of 60.9 mm and a T/W of .955. In contrast, *P. carolinensis* had a slightly lower mean tail length of 55.2 mm and a T/W of .890 (Table 2). In general, *P. atricapillus* has a T/W > .09 whereas *P. carolinensis* has a T/W < .09; however, deviations from this do occur and several researchers (Brewer, 1963; Simon, 1959; Tanner, 1952; Johnston, 1971) have reported a slight overlap in the tail-to-wing ratio for these species.

A plot of the tail-to-wing ratios for chickadees banded in this study shows distinct clusters for *P. atricapillus* and *P. carolinensis* (Figure 8). There is very little overlap here with only two *P.*



Figure 6. Per cent frequency of culmen lengths (mm) of *P. atricapillus* (solid bars) and *P. carolinensis* (open bars) banded.

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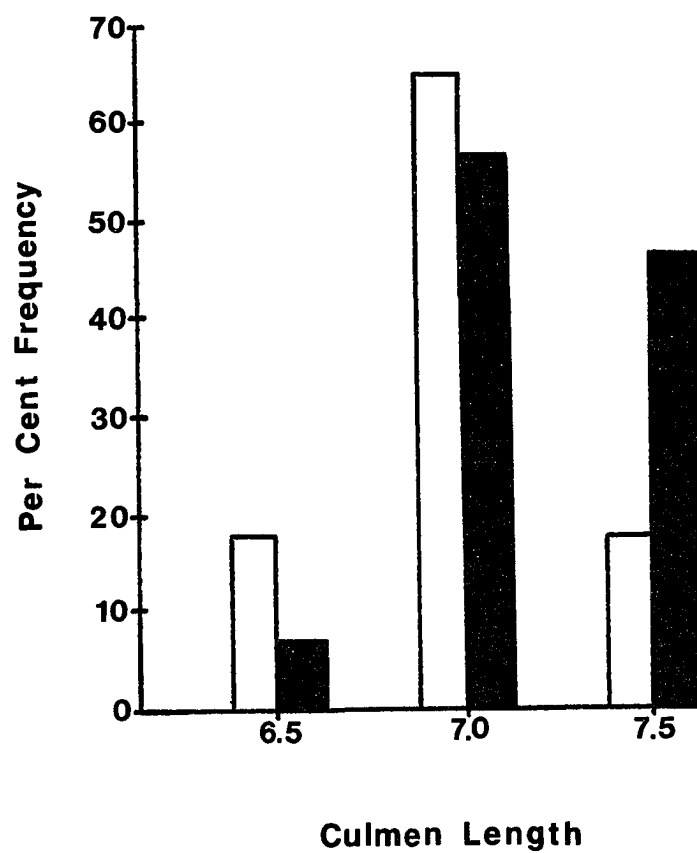
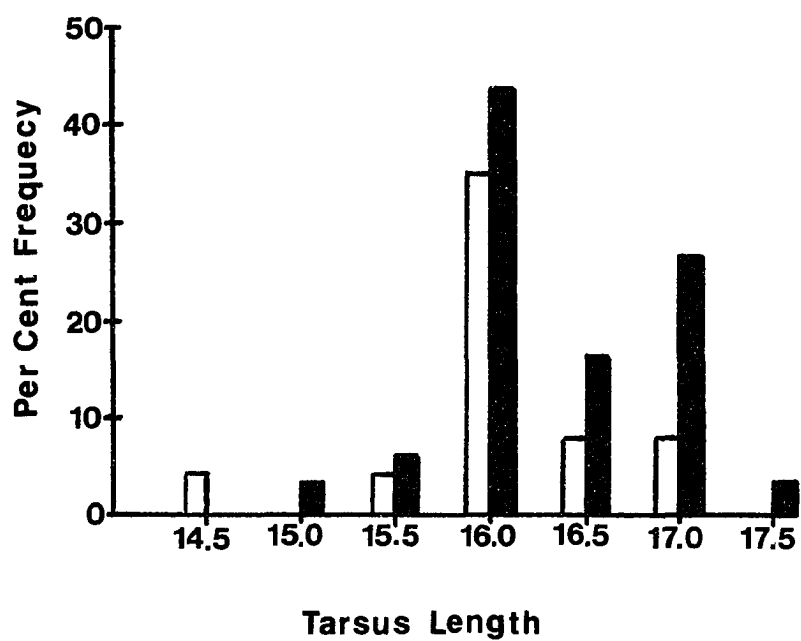


Figure 7. Per cent frequency of tarsus lengths (mm) of *P. atricapillus* (solid bars) and *P. carolinensis* (open bars) banded.

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*atricapillus* (6.7%) falling into the *carolinensis* cluster and only one *P. carolinensis* (4.4%) invading the *atricapillus* cluster. It would seem that the best tail-to-wing ratio used to separate *P. atricapillus* and *P. carolinensis* here might be set at about .925. This value is a little greater than the .9 value commonly used to separate the species. This upward shift is possibly an artifact of the author's measuring techniques or may reflect larger chickadees at this northern portion of the range interface.

#### Feather Coloration

Depending on the degree of grayness (as compared to the color chart described previously) on the edgings of the secondary wing and lateral tail feathers, individuals were classified as "*atricapillus*-like", "*carolinensis*-like" or "intermediate". Accurate classification in the field was difficult owing to variations in lighting conditions; nonetheless, differences in plumage color were detectable. Only four *P. atricapillus* (13.3%) were classified as "intermediate" and none as "*carolinensis*-like"; four *P. carolinensis* (17.4%) were classified as "intermediate" and none as "*atricapillus*-like". The low percentage of individuals deviating from the characteristic forms seems to be within the expected range of variation observed by Brewer (1963).

## CHAPTER VI

### WINTER DISTRIBUTION

#### Methods

From the trapping data gathered no gap was apparent between the ranges of *P. atricapillus* and *P. carolinensis*. In order to examine the range interface on an enlarged scale and to search further for any hiatus not evident from the trapping data, supplementary information in the form of soliciting song responses from chickadees in non-trapping areas was employed. This portion of the study was conducted from 27 January through 26 February 1976 in Fulton, Kosciusko, Whitley, Miami, Wabash, Huntington and Grant counties.

The vocal differences which make this sampling possible are as follows: *P. atricapillus* typically sings a two-noted whistle song, *fee-bee*, which is generally quite distinct from the four-noted whistle song, *fee-bee-fee-bay*, 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 at a more rapid speed.

A General Electric cassette tape recorder (model m83003) was used to broadcast pre-recorded chickadee songs. One minute of song and call notes for each species was recorded on separate cassette cartridges. 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).

Wooded areas containing favorable habitat for chickadees were searched for; upon locating a suitable site, up to 30 minutes were spent walking through the area trying to solicit song responses from chickadees. This was accomplished by continuously broadcasting the pre-recorded tapes (every minute or so I would pause to rewind the tape and listen for chickadees). North of the Eel River I played the *atricapillus* tape, between the Eel and Wabash Rivers I played both tapes, interchanging them, and south of the Wabash River I played the *carolinensis* tape.

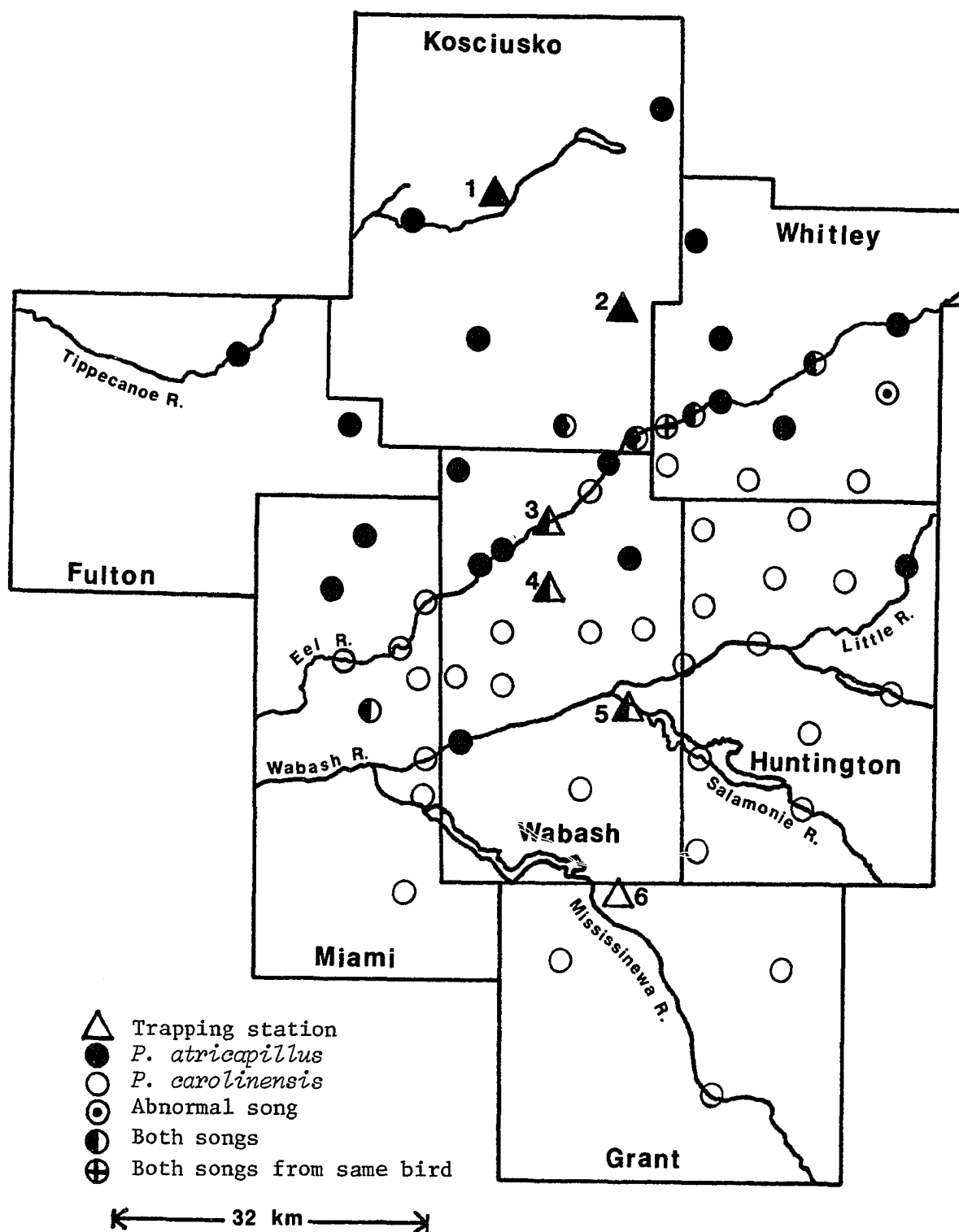
The taped broadcasts often attracted chickadees towards the recorder. Individuals generally issued a vocal response which enabled them to be identified. After this the tape of the congeneric chickadee species was played for a few minutes to see if different responses could be elicited. If chickadees were attracted but not identified, the sampling was repeated on another day until identification was possible.

### Results

Time of day and weather conditions obviously varied throughout the sampling although they appear to have had little influence in determining whether chickadees would respond or not. The average time required to locate chickadees after entering a wooded area was six minutes for *P. atricapillus* and eight minutes for *P. carolinensis*.

Chickadees were located and identified in the 58 areas shown in Figure 9. No gap between the winter ranges of *P. atricapillus* and *P. carolinensis* is evident. In agreement with the trapping data the ranges

Figure 9. Winter distribution of *P. atricapillus* and *P. carolinensis* in northern Indiana as determined by soliciting song responses.



were found to overlap for a distance of about 30 km. *P. atricapillus* occurred commonly north of the Eel River, sporadically between the Eel and Wabash Rivers and was uncommon south of the Wabash River. *P. carolinensis*, on the other hand, was uncommon north of the Eel River but was abundant along it and south of this region.

On at least three occasions during the sampling I identified both *P. atricapillus* and *P. carolinensis* in the same area. Since both species of chickadee were found together at trapping stations 3, 4 and 5, I suspect that with additional observations both species would be found to occur together in the overlap zone more frequently than shown in Figure 9.

#### Vocal Responses

##### Interspecific recognition of song

On several occasions I found that one species of chickadee was receptive to the song of the congeneric chickadee species. On 7 February I broadcasted the *carolinensis* tape at the edge of a wooded lot between trapping stations 4 and 5. Three chickadees soon approached with one giving the typical four-noted *P. carolinensis* song. The birds hopped around in low branches at the edge of the woods seemingly trying to find the individual whose song was coming from the tape recorder. I shut off the recorder and walked down the edge of the woods about 50 m. I then played the *atricapillus* tape and the three chickadees again moved towards the recorder. As the birds approached within a few meters one of the chickadees continued to sing the *P. carolinensis* song. No difference in



behavior between the birds' responses to the *carolinensis* or *atricapillus* tapes was noticed. Similarly, I was broadcasting the *carolinensis* tape on 14 February in a river bottom forest along the Little River in Huntington County. After about five minutes I heard a distinct two-noted *P. atricapillus* song from the forest. The bird never approached closely but continued to repeat its song.

Interspecific recognition of song playbacks was also noted by Ward and Ward (1974) in southeastern Pennsylvania. Their results seem to indicate that interspecific recognition in chickadees is restricted to the contact zone; away from this zone recognition is limited to conspecifics.

#### Duality of song

One bird gave the songs of both *P. atricapillus* and *P. carolinensis*. This occurred on 31 January in a river bottom forest along the Eel River near Collamer, Whitley County. I began by playing the *carolinensis* tape and immediately two chickadees approached; one answered with a typical *P. carolinensis* song. One of the chickadees flew away but the other remained and continued to sing in the tree above me. I then broadcasted the *atricapillus* tape and the remaining bird responded by changing to the *P. atricapillus* song. After singing about ten two-noted whistle songs, the bird switched back and sang the *P. carolinensis* song. I observed the bird sing the *P. atricapillus* song one more time before leaving.

Duality of song as reported here has been described by Tanner (1952) in the Great Smoky Mountains, Johnston (1971) in southwestern Virginia

and Ward and Ward (1974) in southeastern Pennsylvania. Tanner and Johnston each described only one individual that sang both songs; however, in southeastern Pennsylvania the Wards reported that from eight different locations they solicited both songs from individual chickadees. It is unknown whether the singing of both songs by one individual is a learned behavior acquired through association with the other species in the overlap zone or due to a trait inherited through interbreeding.

#### Abnormal songs

Abnormal song responses were solicited from chickadees three times during my sampling. On 27 January along the Eel River in Kosciusko County, a chickadee responded vigorously to a broadcast of the *atricapillus* tape with a whistle song in a 1-2, 1-2 pattern; all the notes were of the same high pitch. The bird responded similarly to a broadcast of the *carolinensis* tape. On 31 January I visited this area again but a typical *P. atricapillus* song was the only response elicited. On 3 February in a mesic woods several kilometers west of the previous sighting I solicited a number of typical song responses from *P. atricapillus*. One chickadee, however, responded with an abnormal four-noted song similar to the one just described. On 12 February in a woodlot in Whitley County, I solicited another chickadee singing an abnormal song. This bird answered the *atricapillus* tape with a high pitched trill followed by three high and equally pitched whistle notes in a 1-2-3 pattern.

In each of the above cases the birds gave their abnormal songs in a high pitch and with more intensity than usually issued by chickadees. The songs more closely resembled those of *P. carolinensis* whose song is

of a more variable nature than that of *P. atricapillus* (personal observation; Ward, 1966; Smith, 1972), but I believe that these songs were outside the normal range of variation for *P. carolinensis*.

Similar vocal anomalies have been reported in areas where the ranges of *P. atricapillus* and *P. carolinensis* come together in Illinois (Brewer, 1961), Kansas (Rising, 1968) and southeastern Pennsylvania (Ward and Ward, 1974). Little is known about the genetic nature of these songs but hybridization is a likely explanation since some interbreeding is suspected in each of these areas.

## CHAPTER VII

### SPRING OBSERVATIONS

Approximately ten hours of observation was spent at each of the six trapping stations from 6 April through 22 May 1976. Observations were made on four separate visits to each area. An additional three hours of observations were spent at trapping stations 5 and 6 on 25 May. Most of the observation time was spent searching for and following chickadees; individuals were identified by their colored leg bands. The date of banding along with the dates of subsequent observation of each chickadee are chronologically summarized for each trapping area in Figures 10-15.

#### Trapping Station 1

Of the ten *P. atricapillus* banded at trapping station 1 (Figure 10) none was observed and no other chickadees were seen or heard in the area after 20 March.

#### Trapping Station 2

Eleven *P. atricapillus* were banded at trapping station 2 (Figure 11) but only one individual was found to remain in the area past March. This chickadee, seen on both 8 and 15 April, was accompanied by its apparent mate, an unbanded male that I observed singing on 8 April. I suspect that the birds were nesting in the swampy woods adjacent to the south end of the trapping area where they were last seen foraging together on 15 April.

Figure 10. Spring observations for trapping station 1. Chickadee numbers correspond with those listed in Appendices 3 and 4. Squares indicate the bird was trapped; circles indicate that it was observed. *P. atricapillus* is represented by solid figures and *P. carolinensis* by open figures.

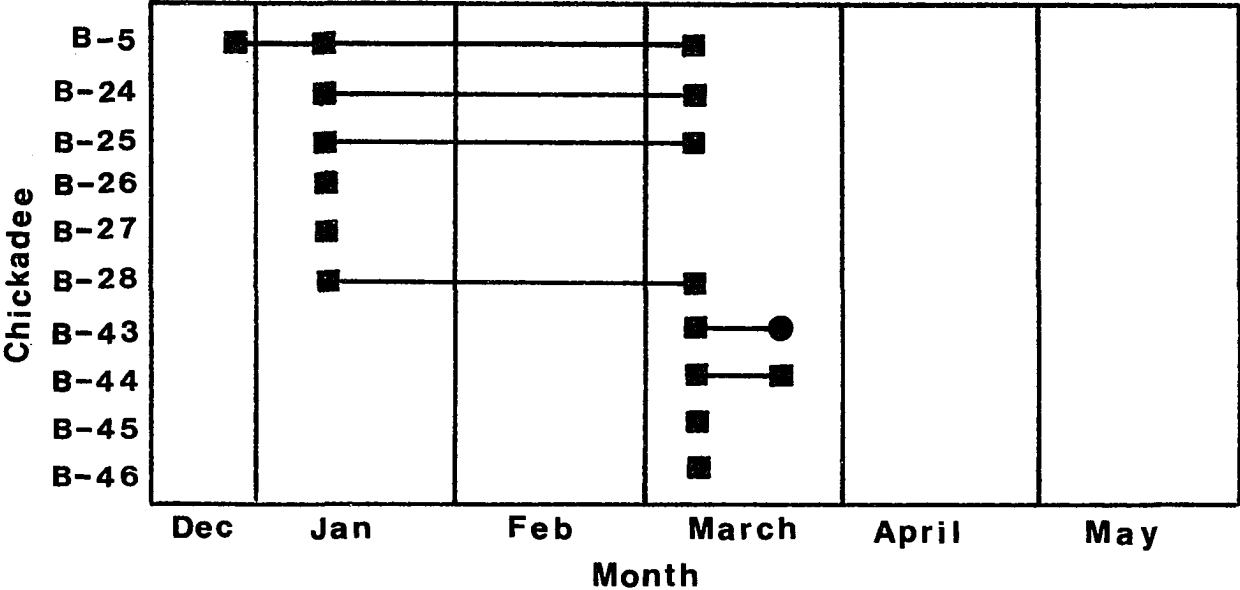


Figure 11. Spring observations for trapping station 2.

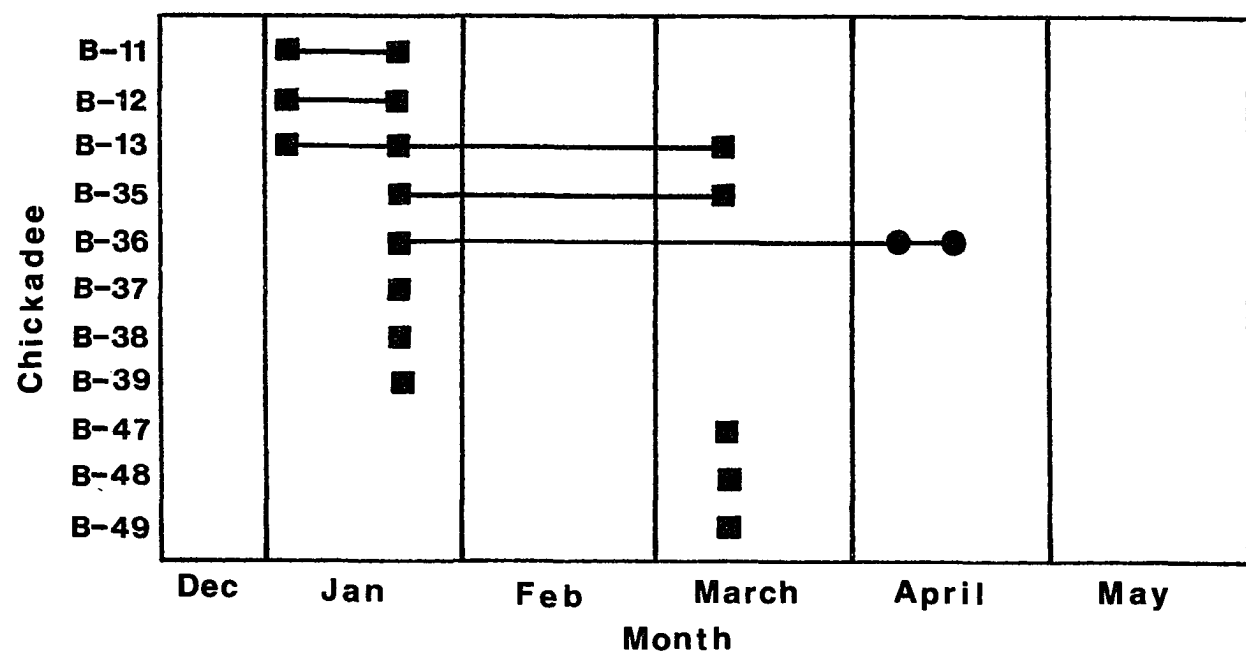


Figure 12. Spring observations for trapping station 3.

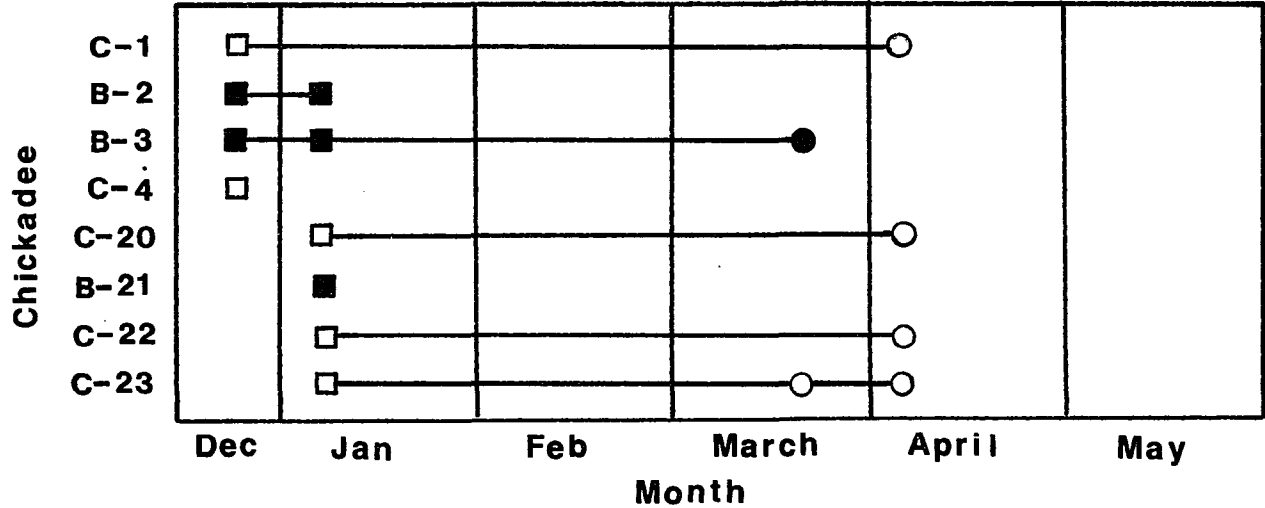


Figure 13. Spring observations for trapping station 4.

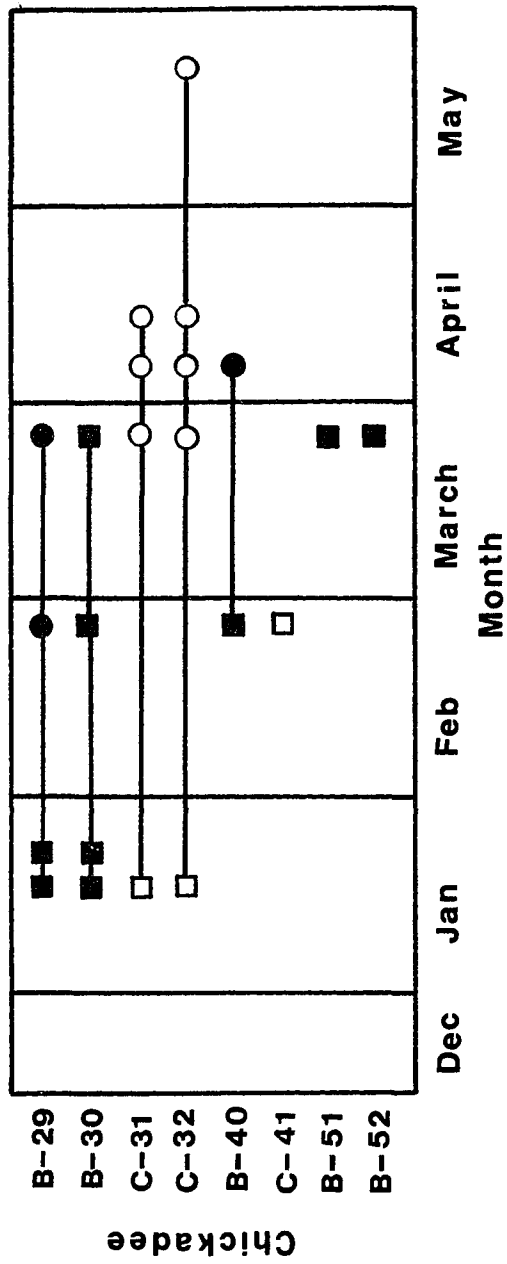




Figure 14. Spring observations for trapping station 5.

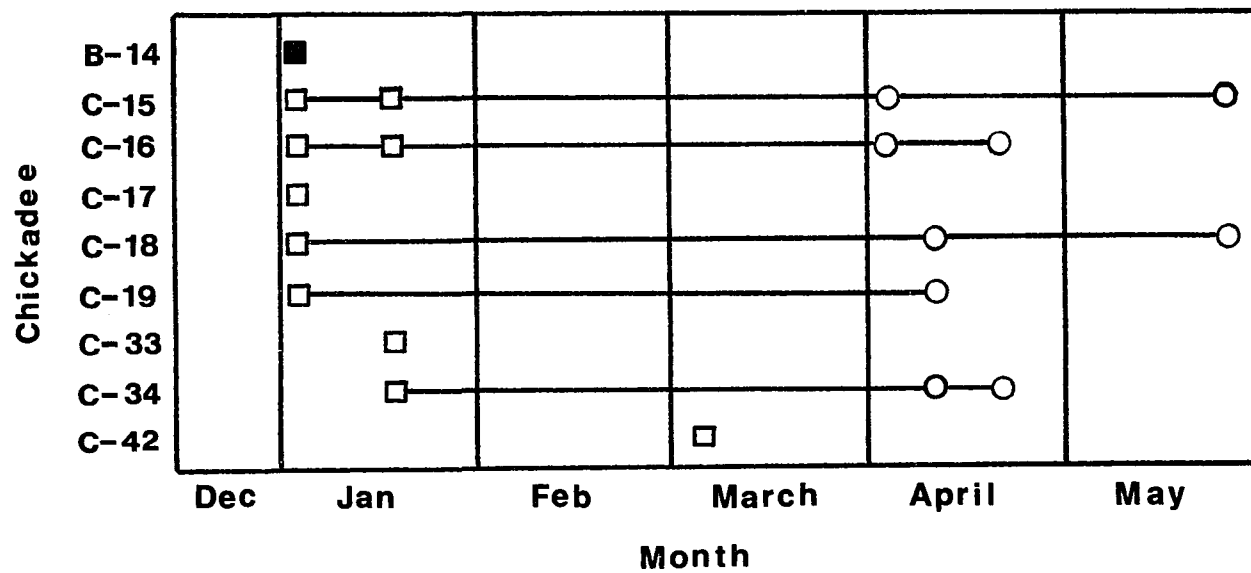
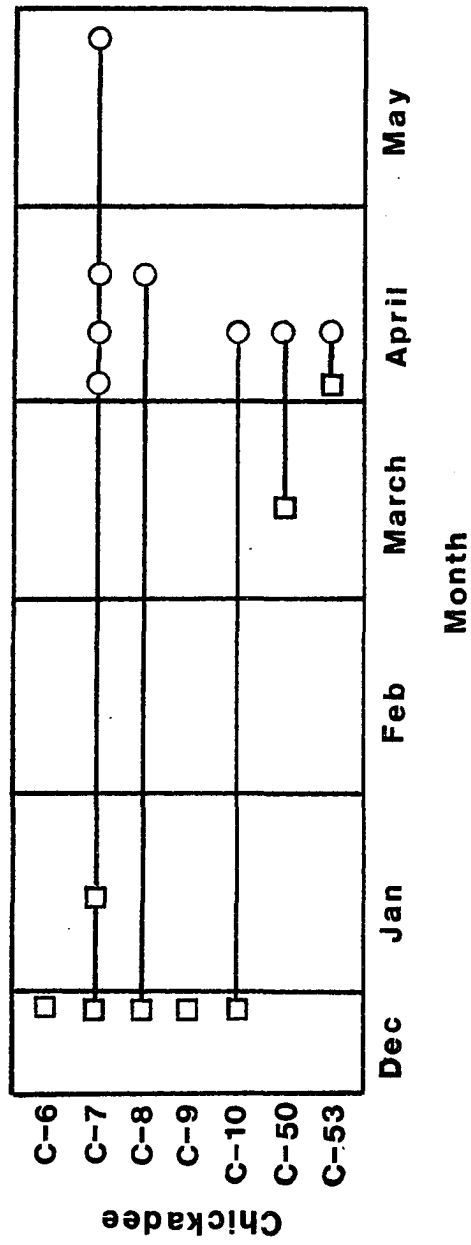


Figure 15. Spring observations for trapping station 6.



### Trapping Station 3

Of the three *P. atricapillus* banded at trapping area 3 (Figure 12) only one individual was seen on 23 March and none was observed after this date. Four of the five *P. carolinensis* banded at this area were observed at or near the feeder on 6 April. On subsequent observation dates, however, none of these individuals could be found. The only other sightings of chickadees in the area were on 13 April and 16 May; each time I observed an unbanded chickadee foraging along the Eel River about .4 km north of the trapping area.

### Trapping Station 4

Four of the five *P. atricapillus* and two of the three *P. carolinensis* banded at trapping station 4 (Figure 13) were trapped or observed on 27 and 28 March. After this date there was only one sighting of *P. atricapillus* which occurred on 6 April. The pair of *P. carolinensis* previously seen were again observed foraging together on 6 and 13 April and one of these individuals was seen again on 22 May. The pair possibly remained in the area to nest.

### Trapping Station 5

The only *P. atricapillus* banded at trapping station 5 (Figure 14) was never observed again after its release on 3 January. Five of the eight *P. carolinensis* banded at this area were seen on 6, 10 and 22 April. During these observations, typical four-noted songs were commonly heard and few instances of what appeared to be territorial combat

were observed. Chickadees could not be found in the area on 28 April and 8 May but two banded individuals were observed again on 28 May.

#### Trapping Station 6

Results of observations at trapping station 6 (Figure 15) were similar to those found at trapping area 5. Four banded individuals (one of which was seen in association with an unbanded companion) were observed on 18 April. During these observations songs were heard commonly. Observations on 28 April and 8 May failed to yield any chickadees but on 25 May I observed a group of four chickadees chattering as they slowly foraged through some dense vegetation. Only one of these individuals was banded and it appeared to be a parent bird leading its young.

## CHAPTER VIII

### SPRING DISTRIBUTION

#### Methods

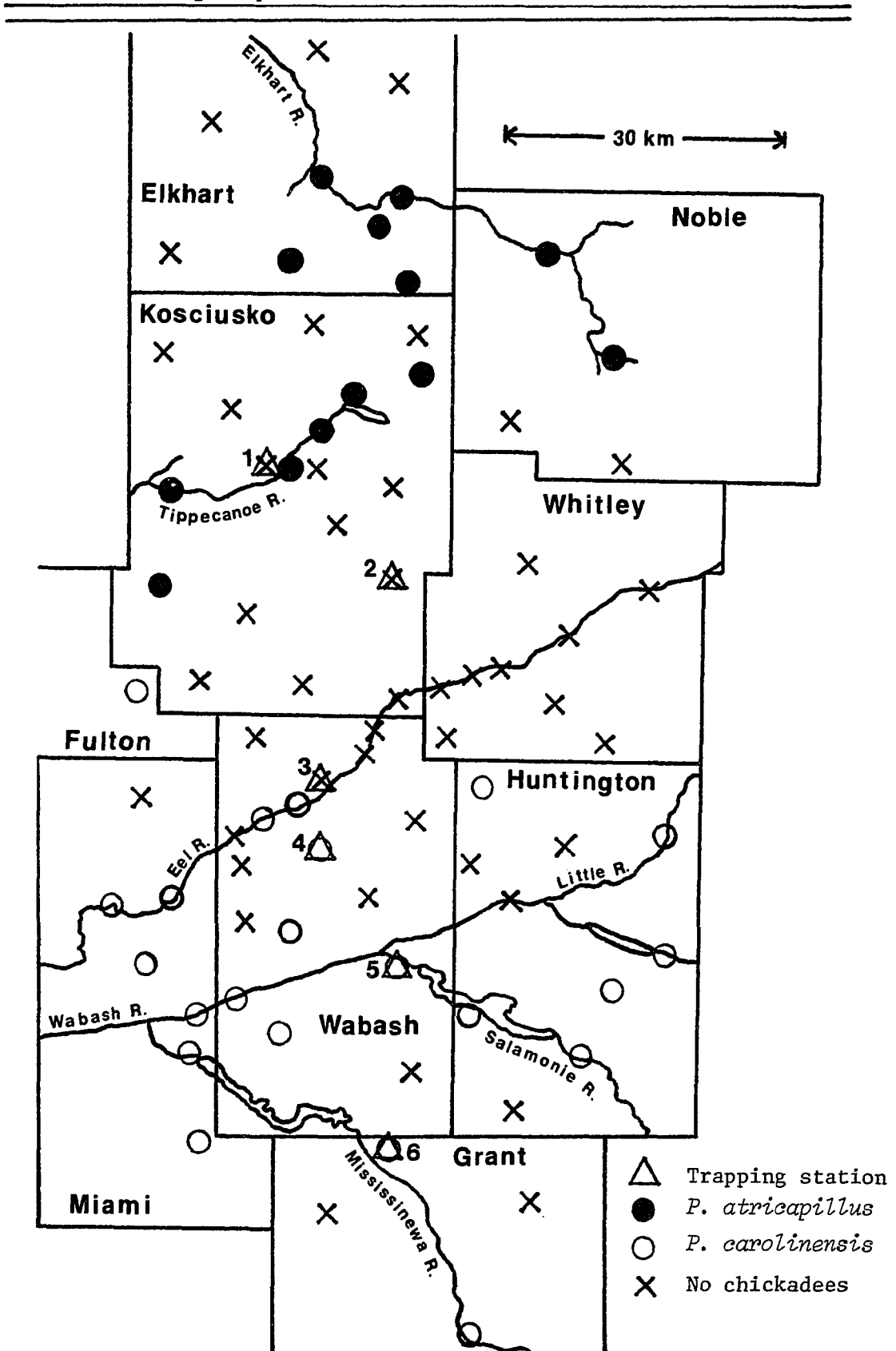
The spring distribution of *P. atricapillus* and *P. carolinensis* was analyzed from 29 April through 31 May 1976 by soliciting song responses. The spring methodology differed from the winter sampling in the following ways: (1) in the spring, a full 30 minutes were spent in each area regardless of whether or not chickadees were found; (2) the *atricapillus* tape was played at all areas north of the Eel River, the *carolinensis* tape was played at all areas south of the Eel River and both tapes were played at areas along the Eel River; and (3) when one species of chickadee responded to the taped broadcast, the tape of the other chickadee species was not played.

#### Results

The spring ranges of *P. atricapillus* and *P. carolinensis* in northern Indiana were found to be separated by a gap of about 30 km (Figure 16). In general, chickadees of both species seemed to be sparse throughout the whole region; rarely did I hear a response from more than one chickadee in any particular area. At the sites where chickadees were found, the average time required to gain a response was ten minutes for *P. atricapillus* and eleven minutes for *P. carolinensis*.

Most chickadees found occurred in river bottom forests or lowland woods along streams. This was especially true for *P. atricapillus*; only

Figure 16. Spring distribution of *P. atricapillus* and *P. carolinensis* in northern Indiana as determined by soliciting song responses.



twice were individuals found in isolated wood lots. Interestingly, chickadees could be found along the Tippecanoe River only about .8 km away from trapping station 1 which had been deserted by chickadees by late March.

Only one *P. atricapillus* was found south of the Tippecanoe River and only one *P. carolinensis* was found north of the Eel River. These sightings, plus the fact that a few individuals remained in trapping stations 2 and 4, seems to indicate that the hiatus is not perfect and probably meager populations of both species of chickadees occupy this region during the spring.

Perhaps the most striking feature of the gap was the absence of chickadees along the Eel River north of trapping area 3. This region offers a lush habitat similar to that existing along the Elkhart, Tippecanoe and Wabash Rivers yet no chickadees could be found here.

## CHAPTER IX

### SUMMER OBSERVATIONS

On 12 July and 8 September I spent one half hour soliciting song responses from chickadees in each of the six trapping stations. On 12 July I got no responses from chickadees at trapping stations 1, 3 and 6. At trapping station 2 one unbanded *P. atricapillus* responded to the taped broadcast. At trapping stations 4 and 5 typical *carolinensis* songs were solicited from one individual at each area. On 8 September two unbanded *P. atricapillus* responded to the taped broadcast and were observed at each of trapping stations 1 and 2. Responses from *P. carolinensis* were heard at trapping stations 3, 4 and 5; however, no chickadees were found at trapping station 6.

Weise and Meyer (1976) have found that the main dispersal of juvenile chickadees (*P. atricapillus*) takes place in late June and early July. Since summer observations at the range interface seemed to show a pattern like that of the spring, it can be concluded that dispersal of juvenile chickadees is probably not heavily responsible for filling in the gap.



## CHAPTER X

### DISCUSSION

#### Formation of the Gap

By comparing the spring distributions in Figure 16 to the winter distributions in Figure 9 it is evident that both *P. atricapillus* and, to a much lesser extent, *P. carolinensis* withdrew from the range interface. Observations in the trapping areas clearly show that most *P. atricapillus* withdrew during the last two weeks of March. The time of withdrawal is less obvious for *P. carolinensis* because individuals remained in trapping areas 4, 5 and 6 probably to breed. From observations at trapping area 3, however, it is apparent that the withdrawal took place soon after 6 April.

The expected date of first egg laying by chickadees at the range interface in northern Indiana can be calculated by adjusting data provided by Brewer (1961) for chickadees nesting in Illinois. Since both species tend to begin laying about three and one half to four and one half days later for each degree of latitude northward, the first egg laying at 41° N latitude should occur from 20 April to 26 May for *P. atricapillus* and 30 April to 21 May for *P. carolinensis*. Nest building, excavation and the establishment of territorial boundaries precede the event by about twenty days. It therefore can be concluded that chickadees remaining in the area might engage in these activities as early as 1 April for *P. atricapillus* and 10 April for *P. carolinensis*. Since

chickadees of both species withdrew from the range interface before or near these dates, it appears that formation of the gap is coordinated to occur just prior to these reproductive activities.

These results are congruent with those of Tanner (1952) in the Great Smoky Mountains. On Mt. LeConte where an isolated population of *P. atricapillus* occupies the higher elevations and *P. carolinensis* occupies the lower elevations, Tanner noted that in the winter *P. atricapillus* dispersed down to lower elevations and invaded the range of *P. carolinensis*. As the nesting season approached, though, most *P. atricapillus* withdrew back up the slopes resulting in the formation of a gap of about 600 feet in elevation (2800 to 3400) between the ranges. Even though the gap contained suitable nesting habitat, neither species of chickadee was found to breed in this region. The similarity between Tanner's results and mine suggests that the mechanism by which the gap is formed is the same at both locations.

Another study corroborating my results was conducted by Gary L. Wilform (personal communication) at Forest Glen Preserve, Vermilion County, in east-central Illinois. Here, both species of chickadees were banded during the winter of 1975-1976. Sometime in March, however, *P. atricapillus* disappeared from the area leaving only *P. carolinensis*. Some of the remaining *P. carolinensis* were later observed nesting in the area. Thus, at a locale approximately 200 km to the southwest of the present study area, the gap also seems to form in a similar fashion.

Historical evidence supporting my results was provided by observations from 1935 to 1939 by Ernest M. Shull. During these years Shull frequently went on early morning walks from Manchester College along the

Eel River, upstream about 3.2 km to Liberty Mills and then back. This area lies only a few kilometers northeast of trapping station 3. Sightings of birds along this route were recorded in an unpublished book (Shull, 1938). His records show that for species such as the Downy Woodpecker, Tufted Titmouse and White-breasted Nuthatch sightings were common during every month of the year. For *P. atricapillus*, however, he has sightings in January through April and September through December, but none in May or July and only one in each of June and August. Shull lists only three sightings for *P. carolinensis* which occurred on 2 March 1938, 8 January and 18 February 1939. These observations seem to indicate that the gap existed some 40 years ago and since the time of Shull's observations, the location of the gap may have advanced northward slightly. This is evidenced particularly by the low number of sightings of *P. carolinensis* in the area as compared with the present study.

#### Possible Explanations for the Gap

Since there are no apparent barriers to either species, it is perplexing that such a narrow gap could persist between the ranges of *P. atricapillus* and *P. carolinensis*. It seems reasonable to assume that some factor might limit the southern range of *P. atricapillus* and the northern range of *P. carolinensis*, thereby causing the gap to occur. Of the usual factors which tend to limit the distributions of organisms (see Krebs, 1972), those applicable to bird populations would include dispersal, behavior (i.e., habitat selection), physiological tolerance to the environment (i.e., temperature, moisture, etc.) and interrelations with other organisms (i.e., predation, parasitism, disease and competition).

Because both species of chickadees are capable of, and indeed do, invade the gap on a temporary basis, dispersal obviously is not range limiting here.

The withdrawal of chickadees prior to reproduction suggests that there could be a lack of suitable nesting habitat within the gap. Both *P. atricapillus* and *P. carolinensis* commonly breed in forest and forest edge habitats and have extremely similar nesting and territorial requirements (Brewer, 1963). Subjectively, as least, there appears to be very little difference in the abundance of wooded areas occurring from the north end of the study area to the south. It seems highly unlikely that the quality of habitat within the gap is such that it is not favorable to breeding chickadees; White-breasted Nuthatches, Tufted Titmice, Downy Woodpeckers and other ecologically similar species were present during the breeding season. It was also concluded by Brewer (1963) in Illinois and Tanner (1952) in the Great Smoky Mountains that the gap zone in these regions contained suitable nesting habitat for either species of chickadee.

The north-south separation of *P. atricapillus* and *carolinensis* across the eastern United States and the altitudinal separation in the Great Smoky Mountains suggests that a climatic factor such as temperature might be limiting to the ranges. This premise, however, can be refuted by several lines of evidence. First, environmental stress would probably be most severe and limiting to *P. carolinensis* during the cold winter months; however, in northern Indiana this species occupies the gap region during the winter and survives. Second, the southern range of *P. atricapillus* is possibly limited by high temperatures during the

summer, but *P. atricapillus* breeds successfully at more southern latitudes in Illinois, Missouri and Kansas. Third, in Illinois Brewer (1963) found that *P. atricapillus* and *P. carolinensis* occur along parallel river systems at the same latitude only 32 km apart; this indicates that both species can successfully reproduce under essentially the same climatic conditions. Finally, in the Great Smoky Mountains where *P. atricapillus* occurs only on some peaks, Tanner (1952) found that *P. carolinensis* nests at higher elevations on the peaks where *P. atricapillus* does not occur. These accounts suggest, then, that the two species overlap in their physiological tolerance to the environment which makes it highly improbable that the ranges are limited by climatic factors alone.

There is little basis for believing that predation, parasitism or disease could limit the ranges of both chickadee species in such a way as to cause the gap to form. Such occurrences would probably exist only temporarily or would affect larger portions of the populations rather than two disjunct locations along the range interface.

The fact that the ranges of *P. atricapillus* and *carolinensis* are essentially contiguous and allopatric is suggestive that interspecific competition takes place where the ranges come together. This is supported by the aforementioned finding of Tanner (1952); occupancy of *P. atricapillus* on some peaks in the Great Smoky Mountains appears to prevent the habitation of *P. carolinensis* at higher elevations. Additional evidence supporting interspecific competition is provided by ecological assessments by Brewer (1963) indicating that all aspects related to nesting and feeding are extremely similar for both species.

It was proposed by Tanner (1952) that competition between these species probably occurs during the early nesting season when territories are established and nest sites are procured. Since new nests can be and often are excavated each year by both species, I believe that the acquisition of nesting territory is the principal source of competition. Existing evidence seems to enhance the credibility of this supposition. For both species of chickadee the whistle song appears to function in proclamation and defense of territory (Odum, 1941; Brewer, 1961; Dixon and Stefanski, 1970; Smith, 1972). It was found by Ward and Ward (1974) in Pennsylvania and by me in Indiana that interspecific recognition and response to the song of the congeneric chickadee species is common at the range interface. Furthermore, at the contact zone in Illinois, Brewer (1963) found that chickadees of either species appeared to defend their territories against any other chickadees, regardless of species.

If the preceding arguments are valid, then it is evident that where the ranges of *P. atricapillus* and *P. carolinensis* come in contact interspecific competition will occur. In accordance with principles demonstrated by Gause (1934), the mere presence of one species during the breeding season would inhibit the presence of the other. It is understandable, then, how interspecific competition might act to limit the ranges; however, this does not explain how the ranges could be limited and separated by a gap. The problem of what causes the gap to form might best be answered by examining the circumstances under which the ranges of these two species originally met.

### Evolutionary Relationship of the Ranges

It was postulated by Brewer (1963) that *P. atricapillus* and *P. carolinensis* arose from common stock separated during pre-Wisconsin glaciation. It is believed that secondary contact was made during an interglacial period when *P. atricapillus* came to occupy the northern portion of the chickadee range and *P. carolinensis* the southern.

The evolutionary consequences of a secondary contact such as this are dependent upon the ecological similarities and the degree of reproductive isolation existing between the two populations; these are based on genetic differentiation achieved during the period of geographic isolation. These ecological and reproductive aspects, however, are usually considered independently.

Lack (1944) was the first to recognize fully the importance of ecological isolation and to elaborate on how selective pressures associated with interspecific competition favor ecological diversity. Further discussions of the competitive aspects of secondary contact are in Svårdson (1949), Udvardy (1951), Orians and Willson (1964) and Rowley (1967); Moynihan (1968) discusses the problem giving brief consideration to the situation where reproductive isolation is only partial.

On the other hand, many authors have given treatment to the evolutionary consequences related to incomplete reproductive isolation and hybridization at the zone of secondary contact (e.g., Mayr, 1942, 1963; Blair, 1951; Dobzhansky, 1951; Sibley, 1961; Bigelow, 1965; Short, 1969).

The competitive relationship between *P. atricapillus* and *P. carolinensis* has already been reviewed. Considering the reproductive

relationship, it appears that intrinsic isolating mechanisms have not developed sufficiently to prevent interbreeding where the ranges adjoin; hybridization has been described by Brewer (1961, 1963) and Johnston (1971) and at least suspected by Rising (1968) and Ward and Ward (1974). Brewer's findings indicate, however, that interspecific crosses occur with a low rate of success; this is apparently due to postmating isolating mechanisms (i.e., hybrid inviability and sterility). Since interbreeding in this case produces reproductively inferior individuals and wastes gametes, selection would favor the elimination of hybridization. Brewer (1963) suggested that the genetically simplest mechanism to this end was the formation of a gap between the ranges. In view of the fact that premating isolating mechanisms in these species probably have not developed to a point where they can be strengthened (see Dobzhansky, 1940 and Sibley, 1957) and the improvement of postmating isolating mechanisms is difficult and indirect (Mayr, 1963), Brewer's hypothesis seems reasonable.

Nevertheless the question arises: Why should a gap develop between the ranges of *P. atricapillus* and *P. carolinensis* and not between the ranges of the numerous other allopatric bird species pairs whose ranges are known to meet in zones of hybridization? (Many such examples are cited in Mayr, 1963 and Short, 1969.) It seems likely that a particular set of circumstances unique to *P. atricapillus* and *P. carolinensis* may have prevailed at the time of secondary contact which prompted the gap to form. This will be examined by considering the potential evolutionary outcomes of secondary contact.



### The Evolution of Range Relationships

A model for the evolution of geographical range relationships in bird species is offered in Figure 17. In it I have attempted to interrelate both the competitive and reproductive factors associated with secondary contact. The model starts by assuming that a parental species is geographically separated into two daughter populations. Depending on the rate of adaptive change and the length of time separated, the daughter populations may acquire genetic differences leading to the formation of two new species. The extent to which these differences accumulate prior to secondary contact affects the eventual outcome of the range relationship.

If the daughter populations are reproductively isolated at the time of secondary contact and interspecific competition does not occur to a limiting degree, both forms could be expected to coexist, ecologically isolated by habitat or food, food size, feeding station, etc. (outcome 1, Figure 17). A more complete description of the requirements necessary for coexistence is provided by MacArthur (1958). Sympatry in this case would most likely occur between forms isolated for relatively long periods of time and might represent species which have undergone changes at the taxonomic level of genus or higher.

If intense competition occurs between the two species, the resulting outcome should follow the competitive exclusion principle (Hardin, 1960). If one species is better adapted to the environment, it may eliminate the other by replacing it throughout its range. The competitively inferior species will be extirpated if replacement is complete.



Replacement may proceed, however, to an environmental zone where neither species is better adapted, thereby establishing a competitive equilibrium. At this point selective pressures would favor ecological isolation to reduce competition. This may be achieved by means of character displacement as described by Brown and Wilson (1959). Depending on the kinds of differences that have developed in allopatry, selective pressures might favor displacement of either habitat (outcome 2) or feeding requirements (outcome 3) to reduce competition and permit coexistence (the problem of which of these is most easily selected for is further discussed by Shoener, 1965).

Where reproductive isolation is not complete at the time of secondary contact the situation is more complicated. Adaptive differences may have accumulated so that interspecific competition does not occur to a limiting degree between the two forms. If interbreeding is frequent with a high success rate, the gene pools of the two forms may merge; however, owing to the nature of their competitive avoidance it seems unlikely that interbreeding would occur with a high degree of success or frequency. Selective pressures favoring the reduction of wasted reproductive energy would operate to strengthen any pre-existing modes of reproductive isolation; e.g., habitat isolation (outcome 14), ethological isolation (outcome 12) or temporal isolation (outcome 13). Mechanical isolation does not seem to be popular in birds.

If at secondary contact reproductive isolation is incomplete and niche overlap is such that interspecific competition occurs, the eventual outcome (and the observed relationship in nature) will depend on a number of variables including the following: the nature and intensity of

competition, the density, diversity and availability of limiting resources (i.e., food or habitat), the type and degree of reproductive isolating mechanisms developed, the rate of barrier removal or breakdown and the dispersal characteristics of the organisms involved. In this situation it is clear that interspecific competition is on a continuum with intraspecific competition and the degree to which either of these exists depends on the frequency and success of interbreeding. Suffice it to say here that situations in nature are more complex than the model. Nevertheless, the model may still predict evolutionary outcomes.

Where reproductive isolation is incomplete and interspecific competition occurs, it is expected that one form would competitively eliminate the other (outcome 5) or a competitive equilibrium would be established. If in the latter case the two forms interbreed with low frequency, it is probably due to insufficient premating isolating mechanisms. Here, selective pressures would favor both reduced competition and the reduction of wasted reproductive energy. Where competition is primarily for habitat and genetic differences gained during geographic isolation render one species better adapted to a particular habitat than the other, these selective pressures would work together to promote habitat displacement and allow coexistence (outcome 11). Where competition is mainly for food selective pressures favoring reduced competition would promote displacement of feeding requirements. Simultaneously, perhaps, selective pressures favoring reduced interbreeding would act to strengthen existing ethological or temporal reproductive isolating mechanisms to permit coexistence (outcome 10). The two Eurasian Rock Nuthatches described by Vaurie (1951), *Sitta neummaer* and *S. tephronota* seem to be an example of

this line of evolution. In the zone of overlap these species occupy the same habitat; however, they exhibit divergence in bill size and shape apparently functioning for the partitioning of food resources. In addition, only in the zone of overlap do they display a marked difference in the facial stripe which Vaurie has suggested may have a recognition value serving as a reproductive isolating mechanism. It should be mentioned that after re-examining the available data Grant (1972) has suggested that the size difference in sympatric *S. neumaer* and *S. tephronota* may be attributed to a geographical variation in body size in relation to climate (i.e., Bergmann's and Allen's rules) and not to character displacement. Grant does not consider the facial stripe in his discussion. An in-depth study is needed to clarify these points.

Where a competitive equilibrium is established and interbreeding occurs with high frequency it can be concluded that premating reproductive isolating mechanisms have not developed sufficiently (of course, at this point it is ambiguous to say that a competitive equilibrium is reached since the difference between interspecific competition and intraspecific competition is tenuous). Continued interbreeding with high success will result in a zone of intergradation. It is anticipated that introgression (successful gene flow due to hybridization) in this case might eventually cause the gene pools to merge uniting the two species (outcome 6). At some point in time, perhaps, two such forms could be regarded as conspecifics related at the subspecies level. Possible examples of this line of evolution would be the relationship between the titmice, *Parus atricristatus* and *P. bicolor* (Dixon, 1955), the grosbeaks, *Pheucticus ludovicianus* and *P. melanocephalus* (West, 1962)

and the buntings, *Passer cyanea* and *P. amoena* (Sibley and Short, 1959).

If a competitive equilibrium is reached and interbreeding occurs with high frequency but with low success, it is reasonable to assume that only postmating reproductive isolating mechanisms are operative. This situation is comparable to the relationship demonstrated by *P. atricapillus* and *P. carolinensis* where the ranges meet. If competition is chiefly for food, ethological or temporal isolation would have to be achieved as well as displacement of feeding requirements for coexistence to occur (outcome 7). This outcome seems unlikely for the chickadees since premating reproductive isolating mechanisms apparently have not developed to a point where they can be selected for. If competition is for habitat (i.e., breeding territory) as I have suggested for *P. atricapillus* and *P. carolinensis*, there are at least two possible evolutionary routes that would reduce both interspecific competition and wasted reproductive energy. These are the displacement of habitat (outcome 8) which would lead to coexistence or dispersal away from the range interface (outcome 9) which would result in the formation of a gap between the ranges (the latter mechanism I have termed "migratory separation").

The problem remains: Why should migratory separation be selected for instead of habitat displacement? Orians and Willson (1964) have pointed out that the presence of other sympatric species might inhibit the ability of one species to diverge from a competitor. They contend that the presence of many species of North American warblers (*Parulidae*) and vireos (*Vireonidae*) which share the canopy for food and other resources may restrict the evolutionary possibilities for the North

American parids. This could indeed explain why displacement of habitat for *P. atricapillus* and *P. carolinensis* is not selected for.

#### Evolution of the Gap

How then did selective pressures operate to form the gap? Brewer (1963) has offered one line of speculation suggesting that individuals of parental species dispersing into the hybrid zone at the range interface would be selected against unless they returned before the time of mating; thus selection would be for sedentariness at the fringes of either range. Since the population in the hybrid zone would have a low reproductive rate and because few individuals would disperse into it, the population would tend to die off and produce the gap.

My work in Indiana has led me to a new hypothesis which I believe accounts for the formation and evolution of the gap. During my analysis of spring distributions (Figure 16) I found that *P. atricapillus* occupying wood lots in Elkhart County, as far as 80 km north of the range interface at North Manchester, Wabash County, had withdrawn from the area. For the most part, the only chickadees remaining were those left in optimal river bottom forest habitats; even these habitats did not seem to support high densities. In Kalamazoo, Michigan some 175 km north of the range interface, *P. atricapillus* commonly breeds and winters in both wood lots and river bottom forests (personal observation). It seems, then, that the effect of the withdrawal by *P. atricapillus* extends to a point somewhere between 80 and 175 km north of the range interface. Thus, the gap appears to be formed by a migratory withdrawal over an area more widespread than originally expected.

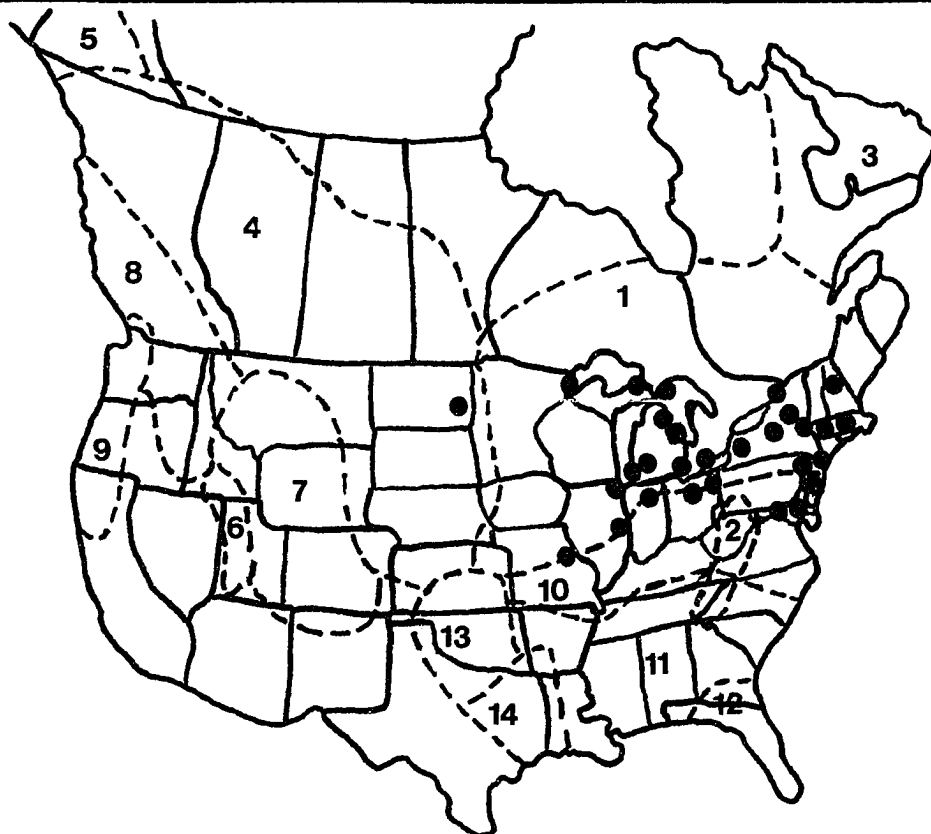
An examination of the literature reveals many records of large scale seasonal migration in *P. atricapillus* (e.g., see Butts, 1931; Bent, 1946; Lawrence, 1958; Wallace, 1941). In Figure 18 I have plotted the location of most of the major accounts of this migration. From their distribution it is apparent that (1) migration is most prevalent in the subspecies, *P. a. atricapillus*, whose range is directly north of the range of *P. carolinensis*, (2) the southernmost records correspond with the approximate location of the range interface between *P. atricapillus* and *P. carolinensis*, and (3) the majority of the records occur east of the hybrid zone in Illinois, where the gap between the ranges is thought to occur.

In view of the accumulated data I propose that the gap has been formed by selective pressures favoring genetically based migration in *P. atricapillus*. These birds migrate north from the range interface in the spring, probably to breed near the northern edge of their range in Canada. Observations by Wood (1914), Baillie (1952), Lawrence (1958), W. E. Saunders in Bent (1946) and Butts (1931, 1931a) indicate that *P. atricapillus* migrates into and from Canada. In the fall, migration is south to their wintering grounds near the range interface. Invading *P. atricapillus* probably fill the available chickadee habitats to carrying capacity as they approach the range interface.

The increased density of chickadees during the fall, winter and spring probably inhibits the northern spread of *P. carolinensis* and the southern spread of resident *P. atricapillus* into the gap. This might be accomplished in several ways. First, the resident chickadees of either



Figure 18. Map of continental United States and Canada showing approximate distributions of *Parus atricapillus* and *P. carolinensis* (based on A.O.U., 1957) and records of migration in *P. atricapillus*. Each dot represents at least one record. Sources for migrational records are as follows: Poor (1946), Thomas (1958), Blake (1952), Griscom (1952), Lawrence (1958), Taver-  
ner and Swales (1908), Van Tyne (1928), Palmer (1885), Bent (1946), Cutler (1933), Butts (1931, 1931a), Bowdish (1938), Baillie (1952), Perkins (1914), Monson (1934), Jones (1915), Lyon (1924), Whittle (1938), Wallace (1941), Odum (1942), Kelly (1976), Wood (1914, 1951), Simon (1959), Widmann (1907), Green and Janssen (1975), Pinkowski (1976) and personal ob-  
servation.



Key to subspecies distributions

- |   |                                       |
|---|---------------------------------------|
| 1) <i>Parus atricapillus atricapillus</i> | 8) <i>P. a. fortuitus</i>             |
| 2) <i>P. a. praticus*</i>                 | 9) <i>P. a. occidentalis</i>          |
| 3) <i>P. a. bartletti</i>                 | 10) <i>Parus carolinensis extimus</i> |
| 4) <i>P. a. septentrionalis</i>           | 11) <i>P. c. carolinensis</i>         |
| 5) <i>P. a. turneri</i>                   | 12) <i>P. c. impiger</i>              |
| 6) <i>P. a. nevadensis</i>                | 13) <i>P. c. atricapilliodes</i>      |
| 7) <i>P. a. garrinus</i>                  | 14) <i>P. c. agilis</i>               |

\*geographically isolated from *P. carolinensis* by altitude

species may attempt to pair with the migratory individuals. Since there is no obvious courtship between the sexes of either chickadee species (Odum, 1941; Brewer, 1961; Smith, 1972), the time of pair formation is unclear; however, Brewer (1961) concluded that pair formation probably begins in the winter flock. It appears, then, that resident birds could attempt to form pair bonds with migratory birds and be left without mates at the time of migration and reproduction. Second, since high densities of migrating individuals invade the wintering grounds of the sedentary chickadees, intraspecific competition for food may become severe during cold winter months. Assuming both migratory and sedentary birds are equal competitors, additional competition from the influx of *P. atricapillus* might have the effect of decreasing the winter survival rate of resident individuals near the range interface.

The lack of the gap's presence along the range interface west of the hybrid zone in Illinois could be for several reasons. As suggested by Brewer (1963) the northward dispersal of *P. carolinensis* and the replacement of *P. atricapillus* may still be occurring. In this situation the competitive pressures applied by *P. carolinensis* might be sufficient to prevent the gap from forming. Probably more important, though, as the range interface is traced westward from Illinois through Missouri and Kansas, the abundance of wooded areas diminishes owing to climatic factors. It is possible that along this portion of the range interface the migratory birds are not able to concentrate themselves in an area where they can effectively form a gap when they leave. During pre-settlement times the prairie and prairie peninsula was probably an effective barrier between these species along the western portion of the

range interface.

The available records (see Figure 18) suggest that seasonal migration in *P. atricapillus* is erratic. This may indeed be so; however, it seems that several factors could mask the observation of a regular migration. If chickadees traveled chiefly at night, they would be relatively inconspicuous; but there is little evidence to support a nocturnal migration. If the chickadees moved along from day to day without passing in conspicuous waves, the migration would be difficult to detect. Quite possibly migration is light some years and goes unnoticed by ornithologists who observe resident chickadees throughout the year anyway. If this is the case, it might be expected that the gap would tend to narrow during years of light migration and widen during years of heavy migration.

It is unclear whether *P. carolinensis* is migratory at the range interface. My data suggest some withdrawal but most authors consider this species to be sedentary (Bent, 1946; A.O.U., 1957) and no large scale migrations have been reported in the literature. If the proposed hypothesis for migration is correct, it seems unlikely that pressures selecting for migration in *P. atricapillus* could operate effectively on *P. carolinensis*, since the result would be reverse migration against the north-south climatological gradient.

Selection for migration as I have suggested would favor the reduction of competition between *P. atricapillus* and *P. carolinensis* and cause a gap to form between the ranges providing an efficient reproductive isolating mechanism. The treatise by Cox (1968) evaluating the role of competition in the evolution of migration supports my hypothesis.

Cox's findings indicate that migration occurs most frequently in groups having problems attaining ecological isolation; as pointed out by Orians and Willson (1964), this seems to be the case with *P. atricapillus* and *P. carolinensis*. The gap probably originated during an interglacial period as suggested by Brewer (1963), where the ranges first came into secondary contact. As *P. carolinensis* replaced *P. atricapillus* with the retreat of the glacier the genetic mechanism necessary to form the gap was retained by the populations of *P. a. praticus* isolated in the Appalachian Mountains. This would explain why the altitudinal gap observed by Tanner (1952) on Mt. LeConte formed so similarly to the gap observed in Indiana.

## CHAPTER IX

### SUMMARY

*Parus atricapillus* and *P. carolinensis* are two closely related species of chickadees whose ranges meet in a variety of situations. The geographical range relationship of these species was studied in northern Indiana from the fall of 1975 through the summer of 1976. Chickadees were trapped, banded and observed at six locations along a north-south line transecting the range interface and song responses were solicited from chickadees by broadcasting pre-recorded tapes in surrounding areas.

The winter ranges of the two species were found to overlap by about 30 km near North Manchester, Wabash County. Based on body measurements, feather coloration and vocal responses little, if any, evidence of hybridization was found. During the last two weeks of March most *P. atricapillus* withdrew from the range interface creating a gap of about 30 km between the ranges at the time of reproduction. Some withdrawal by *P. carolinensis* was detected in early April.

Possible explanations for the presence of the gap are discussed. It is concluded that where the ranges of these two species come together a competitive equilibrium has been established and the gap has evolved as a reproductive isolating mechanism. It is proposed that selective pressures have favored migration in *P. atricapillus* at the range interface to reduce interspecific competition and unsuccessful interbreeding. These birds probably migrate to the north edge of their range in Canada

to breed.

A model for the evolution of geographical range relationships in bird species is offered. In the model, I have attempted to inter-relate both the reproductive and competitive aspects of secondary contact.

## APPENDIX

## Appendix 1

Location and ownership of trapping stations in northern Indiana.

Trapping Station	Location	Owner
1	SE 1/4 of SW 1/4 of sec. 30 T. 33N, R.6E, Plain Twp. Kosciusko Co.; woods is at NW corner of 300N and 150 W.	Fae O. Rosbrugh
2	NW 1/4 of sec. 2 T. 31N, R.7E, Monroe Twp. Kosciusko Co.; access off of 400 S.	Beulah L. Brygider
3	SE 1/4 of SE 1/4 of sec. 2 T. 29N, R.6E, Pleasant Twp. Wabash Co.; access off of IND 13.	Samuel Blocker
4	NE 1/4 of SW 1/4 of sec. 35 T. 28N, R.6E, Paw Paw Twp. Wabash Co.; access off of 200 W.	Robert L. Miller
5	NW 1/4 of SW 1/4 of sec. 1 T. 27N, R.7E, Legro Twp. Wabash Co.; woods is at end of fireland #5 in Salamonie River Forest.	State of Indiana Dept. of Conservation
6	SE 1/4 of NE 1/4 of sec. 4 T.25N, R.6E, Pleasant Twp. Grant Co.; access at N. end of 300 W.	USA, managed by the State of Indiana Dept. of Conservation



## Appendix 2

Trapping dates and number of hours spent trapping at each station.

Trapping Station	Date	Time Spent Trapping		Total Time Trapping	
		Hours	Minutes	Hours	Minutes
1	12/27/75	7	3	25	14
	1/09/76	6	35		
	3/07/76	6	5		
	3/20/76	5	31		
2	1/02/76	6	23	24	57
	1/13/76	2	50		
	1/20/76	4	50		
	3/11/76	5	9		
	4/03/76	5	45		
3	12/24/75	7	25	26	46
	1/08/76	6	31		
	2/24/76	7	38		
	3/23/76	5	12		
4	1/17/76	8	0	26	42
	1/22/76	6	55		
	2/28/76	5	45		
	3/27/76	2	0		
	3/28/76	4	2		
5	1/03/76	6	16	25	1
	1/18/76	7	0		
	3/06/76	5	15		
	4/04/76	6	30		
6	12/31/75	7	7	25	53
	1/15/76	6	38		
	3/14/76	4	38		
	4/01/76	7	30		

## Appendix 3

Body measurements (mm), weight (g) and observations on edgings of secondary wing and lateral tail feathers (ATR-"*atricapillus* like," CAR-"*carolinensis* like," INT-intermediate) for *Parus atricapillus* banded; body measurements to nearest 0.5 mm, weights to nearest 0.1 g.

Individual	Wing Chord	Tail	Culmen	Tarus	Body Weight	Edgings
<u>Trapping Station 1</u>						
B-5	64.0	60.5	7.5	17.0	11.2	ATR
B-24	65.5	63.0	7.5	17.0	12.1	"
B-25	63.0	60.5	7.0	16.0	11.0	"
B-26	63.0	60.0	7.0	16.0	10.3	"
B-27	67.0	64.0	7.5	17.0	12.2	"
B-28	64.5	61.0	7.5	16.0	11.3	"
B-43	63.0	58.0	7.0	16.0	10.0	"
B-44	64.5	62.0	7.5	16.0	11.5	"
B-45	66.0	62.0	7.5	17.0	11.7	INT
B-46	62.5	61.5	7.0	15.5	10.2	ATR
<u>Trapping Station 2</u>						
B-11	63.0	60.5	7.0	16.0	10.7	ATR
B-12	63.0	60.0	7.5	16.5	11.4	"
B-13	65.0	64.5	7.5	17.0	11.6	"
B-35	65.0	62.5	7.5	17.0	12.4	"
B-36	61.5	59.0	7.0	15.0	9.8	INT
B-37	62.0	57.0	7.0	16.0	10.2	"
B-38	61.5	58.5	7.0	15.5	9.8	ATR
B-39	62.5	61.0	7.5	16.0	11.3	"
B-47	61.5	58.5	7.0	16.0	10.2	"
B-48	61.5	60.0	7.0	16.5	11.1	"
B-49	65.0	62.0	7.0	16.0	10.7	"

## Appendix 3 continued

Individual	Wing Chord	Tail	Culmen	Tarus	Body Weight	Edgings
<u>Trapping Station 3</u>						
B-2	64.0	61.0	7.5	17.0	11.7	ATR
B-3	66.0	63.0	7.5	17.5	11.7	"
B-21	63.0	61.0	7.0	16.0	10.9	"
<u>Trapping Station 4</u>						
B-29	63.0	61.0	7.0	16.5	11.5	ATR
B-30	65.5	61.0	7.0	17.0	12.0	"
B-40	63.0	60.0	7.0	16.0	10.6	INT
B-51	63.0	60.0	7.0	16.5	11.3	ATR
B-52	64.0	60.5	6.5	16.0	12.4	"
<u>Trapping Station 5</u>						
B-14	66.0	63.0	7.5	16.5	11.9	ATR

## Appendix 4

Body measurements (mm), weight (g) and observations on edgings of secondary wing and lateral tail feathers (ATR-"*atricapillus* like," CAR-"*carolinensis* like," INT-intermediate) for *Parus carolinensis* banded; body measurements to nearest 0.5 mm, weights to nearest 0.1 g.

Individual	Wing Chord	Tail	Culmen	Tarus	Body Weight	Edgings
<u>Trapping Station 3</u>						
C-1	63.0	54.0	7.0	16.0	10.1	CAR
C-4	65.0	59.0	7.5	17.0	11.4	"
C-20	60.0	53.0	7.5	15.5	10.3	"
C-22	61.0	53.0	7.0	15.5	10.8	"
C-23	64.0	60.0	7.5	16.5	11.3	"
<u>Trapping Station 4</u>						
C-31	58.5	50.5	6.5	15.5	10.4	CAR
C-32	63.0	55.0	7.0	16.0	11.7	"
C-41	61.0	54.0	7.0	16.0	11.7	"
<u>Trapping Station 5</u>						
C-15	63.5	57.0	7.0	16.0	10.3	CAR
C-16	60.0	56.0	7.0	16.0	11.0	INT
C-17	61.0	56.0	7.0	15.5	9.8	"
C-18	61.5	54.0	7.0	15.5	10.6	CAR
C-19	65.0	58.0	7.0	16.0	10.9	INT
C-33	60.0	54.5	6.5	15.5	9.0	CAR
C-34	61.5	52.0	7.0	16.0	10.6	"
C-42	62.0	56.0	7.5	15.5	11.1	INT
<u>Trapping Station 6</u>						
C-6	60.5	53.0	7.0	15.0	9.4	CAR
C-7	67.0	59.0	7.5	17.0	10.7	"
C-8	65.0	58.5	7.0	16.5	11.4	"
C-9	62.0	55.0	7.0	16.0	10.9	"
C-10	63.5	58.0	7.0	15.5	10.4	"
C-50	61.5	53.5	7.0	15.5	10.4	"
C-53	57.5	51.0	6.5	14.5	10.3	"

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