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FORAGING BEHAVIOR OF THE BLACK-CAPPED
CHICKADEE AND TUFTED TITMOUSE IN
RELATION TO COMPETITION AND COEXISTENCE IN MICHIGAN

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By

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ABSTRACT

FORAGING BEHAVIOR OF THE BLACK-CAPPED CHICKADEE AND TUFTED TITMOUSE IN RELATION TO COMPETITION AND COEXISTENCE IN MICHIGAN

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Comparative foraging behavior of the Black-capped chickadee (*Parus atricapillus*) and the Tufted Titmouse (*P. bicolor*) were studied in an oak hickory woodlot, in Livingston County, Michigan, during the summer of 1976. Vertical and horizontal feeding positions and methods of obtaining food were examined. A time-budget analysis was conducted, and aggressive encounters were noted. Significant differences were found to exist in vertical foraging position, foraging rate, utilization of tree species, selection of dead versus live substrate and foraging in an upright versus inverted stance. Museum specimens were used to test for character displacement. Culmen length, bill width and depth, and wing length were measured and compared both geographically and temporally. Results indicate that character displacement has not occurred in these parameters. This study demonstrated differences in foraging behavior and microhabitat utilization for the two species, revealing possible mechanisms for coexistence.

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

INTRODUCTION

It has been difficult to demonstrate that competition actually exists in natural communities because if two or more species compete with one another for some feature of the environment which normally limits population growth, the less efficient competitor may be excluded and therefore competition is not observable. Alternatively, the actual process of competition or interspecific interaction may be unobservable because the species in question may have already evolved strategies to minimize contact. Since a habitat can be more efficiently utilized by species with differing ecological niches, natural selection should tend to favor those communities composed of species with slightly different preferences or specializations (Klopfer and Hailman 1965). Therefore, in areas where two or more congeneric or confamilial species occur, one might expect that mechanisms will have developed which reduce competition and increase niche divergence.

Members of the genus Parus are of particular interest when the ornithologist is considering the problem of interspecific competition, because many of the species are morphologically and/or behaviorally similar. Both American and British workers have studied various aspects of Parid ecology including: foraging behavior and resource partitioning (Hartley 1953, Dixon 1954, Gibb 1954, Betts 1955, Root 1964, Myton and Ficken 1967, Smith 1967, Sturman 1968, Hertz *et al*. 1976), habitat distribution and niche relations (Grinnell 1904, Dixon 1950, 1960, 1961, Tanner 1952, Snow 1954a, Minock 1971) and reproductive behavior (Odum 1941a, b, 1942, Hinde 1952, Pielou 1957, Brewer 1963, Stefanski 1967, Brackbill 1970, McLaren 1975).

North American parids have not developed a high degree of sympatry, but when two or more species overlap in specific areas of their ranges, the opportunity exists to examine mechanisms which permit coexistence. The main purpose of this study was to examine the foraging ecology and microhabitat utilization of the Black-capped Chickadee (*Parus atricapillus*) and the Tufted Titmouse (*P. bicolor*) in relation to competition and coexistence in southern Michigan. Vertical and horizontal foraging positions and methods of obtaining food were examined for each species. The amount of time spent in each activity was recorded, and aggressive encounters were noted. Since 1878, when *P. bicolor* was first noted in Michigan (Wood 1921:594), the species has gradually extended its range to encompass the lower five to six tiers of counties, with numerous scattered observations to the north. A thorough treatment of the species distribution and status of *P. bicolor* in Michigan is given by Pielou (1957). Because the short period of contact between *P. atricapillus* and *P. bicolor* may not be more than 100 years in southern Michigan, I felt it was possible that the two species might not yet have developed the behavioral and ecological adaptions that minimize competition. In order to determine if character displacement had occurred, morphological characters were measured and compared for both species.

STUDY AREA

This study was conducted from 22 June to 1 September 1976 at a single study tract in Livingston County, Michigan. The site is located in Oceola Township, T.3N., R.5E. in part of Sec. 36 at an elevation of about 245 m. Approximately 125 hours were spent in actual field observation. Weather permitting, observations were made daily. Observations were conducted at all times during the day, but most frequently from 0800 to 1200 when the birds appeared to be most active. The area sampled consists of a 16 hectare (40 acres) portion of an oak-hickory woodlot surrounded by old fields on all sides (Figure 1). Shallow kettle ponds are scattered throughout the woodlot and some remain filled with water well into the summer. A small excavated pond is located on the eastern edge and a portion of the woodlot's southern boundary consists of white pine (*Pinus strobus*) plantings.

The primary dominants are northern red oak (*Quercus rubra* var. *borealis*), white oak (*Q. alba*), pignut hickory *Carya glabra*), and shagbark hickory (*C. ovata*). Bur oak (*Q. macrocarpa*), black oak (*Q. velutina*), swamp white oak (*Q. bicolor*) and bitternut hickory (*C. cordiformes*) are also numerous. Sugar maple (*Acer saccharum*), red maple (*A.*

rubrum) and wild black cherry (Prunus serotina) occur less frequently. The dense understory consists of many oak, hickory and wild black cherry saplings, hawthorne (Crataegus sp.) and cherry (Prunus sp.) shrubs and much herbaceous vegetation. Dense patches of brambles (Rubus sp.) made portions of the woodlot inaccessible. Previous logging has left numerous stumps throughout the woodlot.

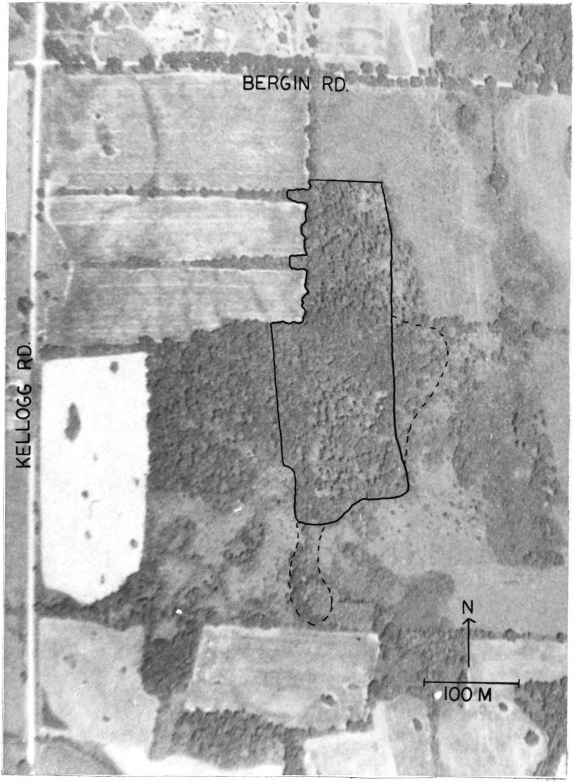

Figure 1. Aerial photograph of study area.

METHODS

Detailed observations on the following parameters were recorded in order to ascertain any differences in resource utilization between *P. atricapillus* and *P. bicolor*.

FORAGING BEHAVIOR

1. *Tree type*. Both the species and the size (large vs. small) were recorded. Small trees were classified as being less than 7 meters in height.

2. *Foraging position*. Prior to the commencement of field work, an Abney level was used to gain experience in visually estimating the height of feeding. At various times throughout the study, the accuracy of feeding height estimates was checked with the Abney level. The forest profile was divided into 3-m intervals. Maximum error in visual estimation was determined to be 1 m for all heights. Relative horizontal position while foraging was quantified by dividing the limb or branch into base, middle and terminal zones.

3. *Substrate type*. The surface on which the bird perched or on which foraging occurred was classified as trunk, limb, branch, twig, foliage, log, ground, and whether it was dead or alive. Since I felt that relative size was sufficient to reflect any differences in utilization, the

absolute size of the various substrates was not recorded, as was the case in the work by Sturman (1968).

4. Foraging style. The method of searching and obtaining food was classified as gleaning (picking objects from the vegetation while perched), peering (apparent searching), hovering (picking objects from the vegetation while momentarily hovering), or pecking, hammering and tearing (obtaining food by vigorous use of the bill). Whether an individual bird secured food by standing upright or hanging upside down was also recorded. During an apparent foraging bout (active food seeking), an individual was classified as to whether or not it was successful in obtaining a prey item. These methods are similar to that used by Sturman (1968).

The amount of time spent foraging was recorded with the aid of a signal emitted at 5 sec. intervals by a cassette tape recorder. In recording data, position and behavior were symbolized and a vertical slash was made for every 5 second "beep". A clipboard suspended from the neck by straps and positioned perpendicular to the body allowed for efficient data collection. In this way, continuous visual observations were made without interruption. Unlike the "one tree-one record" method of Hartley (1953), in which he recorded a single observation, as long as a bird remained in the same tree, the recording of successive foraging stations of an individual gives a more accurate representation of the foraging repertoire. The observer is less likely to bias the data by disproportionately sampling individuals in the more visible portions of the habitat. This technique was especially important for this study since observations were made during the season of densest foliage. No limit was put on the amount of time spent observing each individual since continuous observations lasting more than three minutes were rare due to the dense vegetation. When a flock was encountered, I attempted to observe as many birds as possible in order to account for individual variability.

MORPHOLOGICAL VARIATION

Data for this portion of the study were obtained by examining 177 specimens of *P. atricapillus* and 62 specimens of *P. bicolor* from the collection of the University of Michigan Museum of Zoology. The localities from which specimens were examined have been categorized for treatment into three sample areas: The Southern Lower Peninsula, Northern Lower Peninsula and Upper Peninsula (Figure 2). Both temporal and geographical parameters were examined in order to determine variations within the populations of the two species. Since *P. bicolor* was not common to Michigan until ca. 1910 (Barrows 1912), specimens of both species taken from before and from after this date were compared to test for character displacement. Northern allopatric populations of *P. atricapillus* were compared to southern populations where the species is sympatric with *P. bicolor*.

Several morphological characteristics were measured as follows: Culmen length, from the base of the feathers adjacent to the naso-frontal hinge to the tip of the bill; bill width, from one tomium to the other; and bill depth, from the culmen to the lower edges of the rami. Measurements for width and depth were taken at a position where a plane drawn perpendicular to the bill passes through the anterior margin of the nostril. Wing length was measured as the chord from the wrist to the tip of the longest primary. All measurements were taken with vernier calipers and recorded to 0.01 mm.

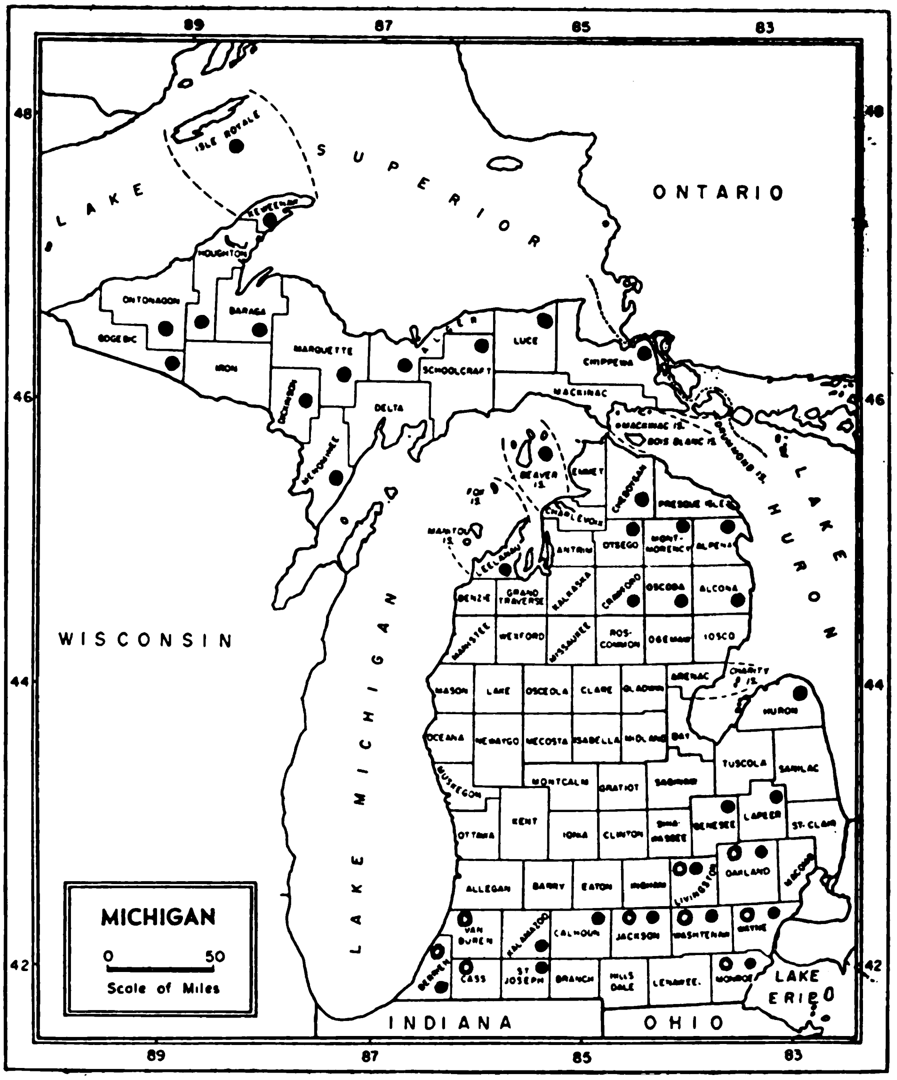

Figure 2. Distribution of specimens of P. atricapillus (•) and P. bicolor (o) in Michigan. Each dot represents one or more specimens examined in the study.

RESULTS

Selection of Foraging Microhabitat

The data on foraging position and behavior for *P. atricapillus* and *P. bicolor* are graphically presented in Figures 3 through 6 and in Table 1. The histograms constructed for each category depict the actual amount of time spent foraging. For some graphs, the number of observations for each category have also been plotted. In most instances there is a strong correlation between the degree of utilization and the actual number of observations. G-tests (Sokal and Rohlf 1969) were performed and Chi-square values were obtained to determine statistical significance.

Foraging Position and Tree Species Utilization

Although there is a degree of overlap in vertical foraging position, Figure 3 shows that the two species tend to concentrate their foraging activities in different levels. *P. atricapillus* feeds most frequently at heights below 9 m, while *P. bicolor* is most often found in the 9 to 15 m zone. Pooled data shows there is a significant difference in height utilization by the two species at all levels ($X^2 = 20.29$, $P<0.005$). At heights below 9 m, the data also indicate a significant difference in the degree of utilization of small trees (<7 m) and shrubs versus large trees

($X^2 = 7.88$, $P<0.005$). P. atricapillus spends a proportionately larger amount of time foraging in small trees than does P. bicolor; the frequency distribution of total time spent foraging being 37.3 percent and 4.7 percent respectively (Figure 3). P. atricapillus seems to utilize tree species more evenly than P. bicolor (Table 1). The latter species forages over 90 percent of the time in Quercus and Carya species, while P. atricapillus spends less than 56 percent of its time in these species, utilizing Crataegus shrubs and saplings of Acer and Prunus serotina to a greater extent. The difference in tree species utilization was

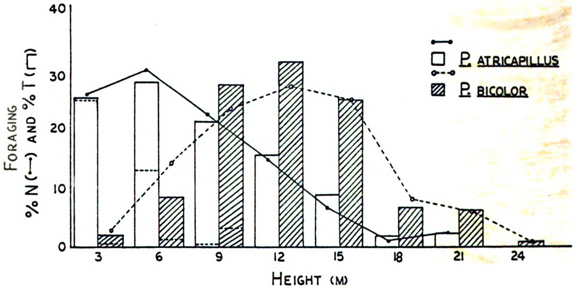

Figure 3. Percentage foraging frequency and time in relation to height for P. atricapillus (N = 330, T = 178.0 min.) and P. bicolor (N = 196, T = 113.4 min.) in oak-hickory woods. Dashed lines within columns indicate percent foraging done in small trees.

found to be significant ($X^2 = 16.75$, $P<0.005$). In relation to horizontal position within the tree, Figure 4 shows that both species utilize the terminal foliage zone to the greatest extent. *P. atricapillus* feeds closer to the trunk more frequently than *P. bicolor*. However, the differences are not statistically significant ($X^2 = 1.39$, $P>0.5$).

Substrate Preference

This category measures the degree of utilization of the surface on which the bird was perched or on which foraging occurred. Because of the strong relation between perch site and foraging site, these data were not analyzed separately. There is a high degree of similarity in selection of foraging site as depicted in Figure 5. Both species prefer to forage on or from branches and in the foliage. *P. atricapillus* feeds more frequently on the trunk than *P. bicolor*. There is no significant difference in substrate preference ($X^2 = 1.69$, $P>0.975$). The data were also analyzed to determine preferential utilization of dead versus live substrate. *P. bicolor* utilizes dead surfaces to a lesser extent than *P. atricapillus*, the percent utilization being 3.9 and 16.0 respectively (Figure 5). These differences were found to be significant ($X^2 = 7.88$, $P<0.005$).

Table 1. Time frequency distribution in relation to utilization of tree species.

	P. atricapillus		*P. bicolor*	
Species	% Time	N	% Time	N
Quercus sp.	36.47	108	46.54	86
Carya sp.	19.29	66	44.41	79
Acer sp.	10.95	31	2.06	9
Prunus serotina	12.17	46	1.98	9
Crataegus sp.	5.66	18	0.07	1
other	15.46	61	4.94	12

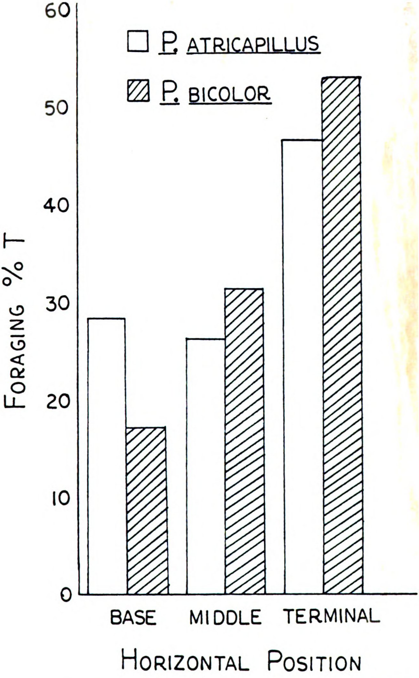

Figure 4. Time frequency distribution for relative foraging distance from central axis of tree for P. atricapillus (T = 104.6 min.) and P. bicolor (T = 99.0 min.).

Figure 5. Percent foraging frequency and time in relation to foraging surface for *P. atricapillus* (N = 725, T = 19.1 min.) and *P. bicolor* (N = 384, T = 108.7 min.). Foraging stance and percent dead surface are also depicted.

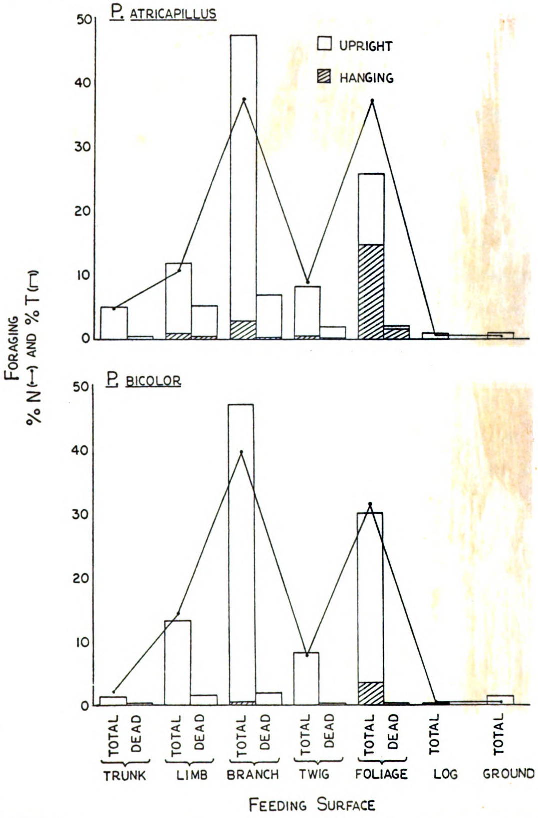
P. ATRICAPILLUS
UPRIGHT
HANGING
P. BICOLOR
0
10
20
30
40
50
FORAGING
% N (•—•) AND % T (⊓)
TOTAL
DEAD
TRUNK
LIMB
BRANCH
TWIG
FOLIAGE
LOG
GROUND
FEEDING SURFACE

Figure 5.

Foraging Style

The two species utilize a variety of methods in order to obtain food, but gleaning and peering seem to be the predominant forms (Figure 6). Peering accounts for 66.5 percent and 85.2 percent of total foraging methods in *P. atricapillus* and *P. bicolor*, respectively. This shows that *P. bicolor* spends a proportionately greater amount of time in searching for prey items. If peering behavior is categorized into successful and unsuccessful attempts, the results show that for the total amount of time engaged in peering *P. atricapillus* is unsuccessful 18.3 percent while *P. bicolor* is 38.1 percent unsuccessful. This would seem to indicate that although *P. bicolor* spends more time searching for food, it encounters or selects fewer prey items than *P. atricapillus*. Possible explanations for these differences will be discussed later. The data also show that *P. atricapillus* hovers more frequently and utilizes pecking, hammering and tearing methods to a greater extent than *P. bicolor* (Figure 6). There is a significant difference in the foraging methods of these two species ($X^2 = 18.55$, $P < 0.005$). In addition to foraging method the species were also categorized as to whether they obtained their food in an upright or hanging position. There is a significant difference ($X^2 = 7.88$, $P < 0.005$) with *P. atricapillus* obtaining food more frequently by hanging upside down than *P. bicolor* (Figure 5). When foraging in the foliage, *P. atricapillus* utilizes this inverted method about 60 percent of

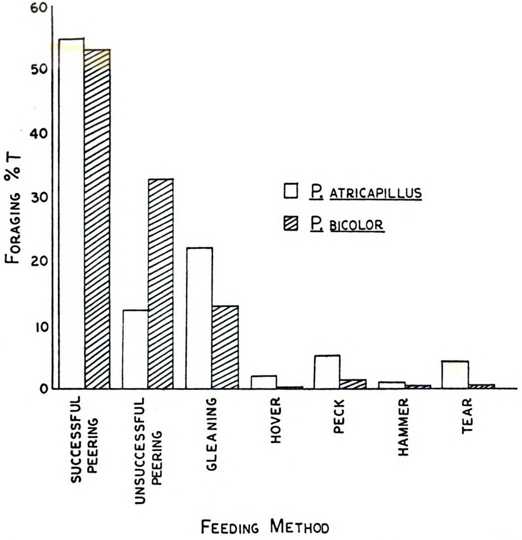

Figure 6. Time frequency distribution for foraging methods of *P. atricapillus* (T = 172.6 min.) and *P. bicolor* (T = 110.6 min.).

the time. It was observed on several occasions that when P. bicolor attempted to obtain food in the terminal foliage zone by hanging upside down, the twigs or branches were unable to support the bird's weight and the foraging attempt was unsuccessful.

Aggressive Encounters

During the study physical contact between the two species was never observed. They appeared to be quite compatible, often occurring in association with each other. On numerous occasions the species were found foraging in the same vicinity often within 10 m of one another. If the species were foraging in the same tree or adjacent trees, P. bicolor usually foraged a bit higher than P. atricapillus. However, on two occasions the two species were found foraging at the same level, once in bushes below 2 m, and once at 8 m within 1 m of each other on the same branch. In both instances, no overt aggression was observed. Individuals of each species appeared to be oblivious to one another. The two species often answered each other with their "dee-dee" calls, and in many instances if I located one species by call, the other would soon appear. On several occasions after locating a vocal foraging P. bicolor, it would often cease calling and feeding if P. atricapillus entered the area. The same was true for P. atricapillus but this behavior was observed less frequently. It almost seemed that in these instances the species entering the area was inhibiting the species already present. Possibly the two species are competing through indirect interference, but no definite conclusions can be drawn. Only on a single occasion did _P. bicolor_ appear to be upset by the presence of _P. atricapillus_. Both birds were foraging in the same tree and when the latter species moved to a position 2 m below _P. bicolor_, _P. bicolor_ began to jump around erratically on the branch, uttering an aggressive "dee-dee" call with an additional vireo-like trill at the end. Twice, an attempt was made at foraging upside down from a leaf. As soon as _P. atricapillus_ moved to a lower position the "dee-dee trill" call stopped but _P. bicolor_ continued to jump erratically, giving its normal "dee-dee" call. During this encounter _P. atricapillus_ continually foraged. The dee-trill call was heard on a second occasion when the two species were within 7 m of each other in adjacent trees. However, _P. bicolor_ was not plainly visible so no other behavior was observed. The call stopped when _P. atricapillus_ left the area.

Morphological Variation

Even though the two species are morphologically dissimilar in both body weight and bill dimensions, with _P. bicolor_ being almost twice as heavy and having a more massive bill, several morphological characteristics were examined in order to gain additional information on possible competitive relations. Since _P. bicolor_ was not common to

Michigan until around 1910, specimens of both species from before and after this date were compared to test for character displacement. P. bicolor occurs regularly in the southern portion of the state while P. atricapillus is found throughout Michigan. Northern allopatric populations of P. atricapillus were compared to southern populations where the species is sympatric with P. bicolor. Results are shown in Figure 7 and Table 2. A t-test analysis is given in Table 3.

The results show that the morphological dimensions of P. atricapillus from the Lower Lower Peninsula (LLP) and Upper Lower Peninsula (ULP) are very similar and are not significantly different. However, both LLP and ULP populations differ significantly from populations in the Upper Peninsula (UP) in a number of characteristics, the most notable being bill width as shown in Table 3. When LLP populations before and after 1910 were compared, there was no significant difference in any of the bill dimensions. Wing length was significantly different for males at the 0.05 level. Overall this would seem to indicate that character displacement has not occurred in the dimensions that were measured for the LLP population of P. atricapillus. This conclusion is supported by evidence that the adjacent allopatric ULP population shows similar results. The only dimension which shows a significant temporal difference is bill width for males, although the low sample size for the before 1910 population leaves some doubt as to the real

Figure 7. Morphological variation in *P. atricapillus* and *P. bicolor* in Michigan. Given are range, mean, ± 2 S.D. (outer block), and ± 2 S.E. (inner block) for characters as described in text. LLP (Lower Lower Peninsula), ULP (Upper Lower Peninsula), UP (Upper Peninsula). Due to damaged specimens, sample size varies, these numbers being placed above the particular dimension.

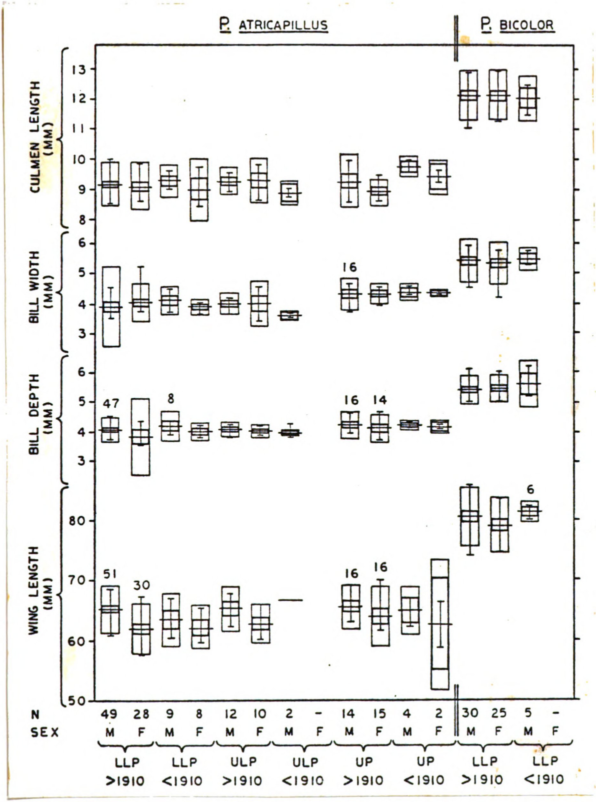
P. ATRICAPILLUS
P. BICOLOR
CULMEN LENGTH (MM)
BILL WIDTH (MM)
BILL DEPTH (MM)
WING LENGTH (MM)
13
12
11
10
9
8
6
5
4
3
6
5
4
3
80
70
60
50
16
47
8
16
14
6
51
30
16
16
N
SEX
49 28 9 8 12 10 2 - 14 15 4 2 30 25 5 -
M F M F M F M F M F M F M F M F
LLP >1910
LLP <1910
ULP >1910
ULP <1910
UP >1910
UP <1910
LLP >1910
LLP <1910

Figure 7.

Table 2. Mean ($\bar{X}$) and variance (S^2) for several morphological characters in *P. atricapillus* and *P. bicolor*.

Population		Sex	Culmen length $\bar{X}$	Culmen length S^2	Bill width $\bar{X}$	Bill width S^2	Bill depth $\bar{X}$	Bill depth S^2	Wing length $\bar{X}$	Wing length S^2
P. atricapillus										
LLP	>1910	M	9.18	.13	3.92	.37	4.06	.04	65.24	3.69
	<1910		9.31	.07	4.14	.05	4.19	.06	63.59	4.78
	>1910	F	9.09	.15	4.06	.09	3.85	.39	62.07	4.54
	<1910		9.00	.26	3.90	.02	4.01	.02	62.24	3.30
ULP	>1910	M	9.27	.05	4.02	.03	4.09	.01	65.41	3.49
	<1910		8.90	.04	3.62	.01	3.98	.00	66.70	0.00
	>1910	F	9.31	.13	4.02	.14	4.03	.01	62.91	2.61
	<1910		-	-	-	-	-	-	-	-
UP	>1910	M	9.28	.19	4.33	.07	4.23	.05	65.72	3.13
	<1910		9.76	.03	4.39	.02	4.21	.01	65.08	3.84
	>1910	F	8.96	.06	4.34	.03	4.12	.05	64.16	6.18
	<1910		9.42	.08	4.36	.00	4.17	.01	62.76	29.11
P. bicolor										
LLP	>1910	M	12.12	.16	5.43	.12	5.40	.06	80.61	5.89
	<1910		12.04	.16	5.49	.04	5.60	.15	81.46	0.72
	>1910	F	12.12	.17	5.36	.12	5.46	.05	79.19	4.96
	<1910		-	-	-	-	-	-	-	-

significance. Populations of _P_. _bicolor_ before and after 1910 were compared and again there is no significant difference in culmen length, bill width, bill depth or wing length indicating lack of character displacement in these dimensions. Except for the UP population of _P_. _atricapillus_, both species are fairly uniform both temporally and spatially.

Mechanisms of Prey Selection

In order to achieve ecological compatibility two species occupying the same habitat should make adjustments so as not to utilize the same resources. By developing a distinct set of morphological features and associated behavioral responses, competition may be minimized. Lack (1944) suggested that there is a correlation between bill size and selection of a prey item. In Great Britain, Betts (1955) has shown that differences in bill dimensions of certain sympatric parids allow for selection of different size and type of prey. Schoener (1965) was able to show theoretically that sympatric congeneric species of nearly the same body weight or bill length would feed on similar sized prey in different microhabitats. Species with greater differences in bill length and body size were capable of coexistence in the same microhabitat through selection of different prey items. Schoener compared the ratios of character difference (larger culmen compared to smaller culmen length) for groups of species in numerous families and postulated

Table 3. Summary of t-test for morphological dimensions.

	Culmen length			Bill width			Bill depth			Wing length		
Population	N/N	t_α	Pop.[1]	N/N	t_α	Pop.	N/N	t_α	Pop.	N/N	t_α	Pop.
P. atricapillus												
LLP M/F	--[2]	--	--	--	--	--	--	--	--	49/28	.01	>1910
ULP	--	--	--	--	--	--	--	--	--	12/10	.01	>1910
UP	14/15	.01	>1910	--	--	--	--	--	--	--	--	--
LLP >1910/<1910	--	--	--	--	--	--	--	--	--	49/9	.05	M
ULP	--	--	--	12/2	.05	M	--	--	--	--	--	--
UP	14/4	.01	M	--	--	--	--	--	--	--	--	--
	15/2	.05	F									
UP/LLP >1910	--	--	--	16/49	.01	M	16/47	.01	M			
				15/28	.01	F				16/30	.01	F
UP/ULP	15/10	.05	F	16/12	.01	M	--	--	--	--	--	--
				15/10	.05	F						
LLP/ULP	--	--	--	--	--	--	--	--	--	--	--	--
UP/LLP <1910	4/9	.05	M	2/8	.01	F	--	--	--	--	--	--
UP/ULP	4/2	.05	M	4/2	.01	M	4/2	.05	M	--	--	--
LLP/ULP	--	--	--	9/2	.05	M	--	--	--	--	--	--
P. bicolor												
LLP M/F	--	--	--	--	--	--	--	--	--	30/25	.05	>1910
>1910/<1910	--	--	--	--	--	--	--	--	--	--	--	--

[1] Date or sex with significant population difference.
[2] No significant difference

that two species exhibiting a ratio less than 1.14 would partition by microhabitat, while above 1.14 indicated partitioning by food size. Beaver and Baldwin (1975) found food and microhabitat partitioning to be consistent with theory for several tyrannid flycatchers.

Ratios for character difference in bill length, width and depth, wing length and body weight were calculated according to Schoener's method and are presented in Table 4. All ratios are above the critical value indicating that when _P_. _atricapillus_ and _P_. _bicolor_ occur sympatrically, they may occupy the same microhabitat due to differences in prey selection.

Table 4. The ratios (R) of larger to smaller dimensions of bill, wing length and body weights of *P. atricapillus* and *P. bicolor*.

	Sex	Culmen length x (mm)	R	Bill width x (mm)	R	Bill depth x (mm)	R	Wing length x (mm)	R	Body weight[1] x (g)	R
P. atricapillus	adult male	9.26 (90)[2]	1.31	4.08 (92)	1.33	4.13 (89)	1.31	65.39 (94)	1.24	12.5	1.8
P. bicolor		12.11 (35)		5.44 (35)		5.43 (35)		80.75 (36)		22.5	
P. atricapillus	adult female	9.13 (63)	1.33	4.13 (63)	1.30	4.04 (62)	1.35	62.99 (67)	1.25		
P. bicolor		12.11 (26)		5.37 (26)		5.46 (26)		79.08 (26)			

[1] Measurements obtained from Poole (1938). Sex and N not designated.

[2] N - sample size varies because of damaged specimens.

DISCUSSION

Competition for space may take place at three levels: 1) geographic range, 2) different types of community within a geographic range, and 3) microhabitat within a community (Hespenheide 1964). North American parids are divided into two subgenera, the *Poecile* (chickadee) and *Baeolophus* (titmouse) groups (Snow 1954b). While there may be widespread sympatry between the two groups, subcongeneric members are usually ecologically isolated from one another because of differences in geographic range (Dixon 1961). In those areas where subcongeneric species ranges overlap, there is isolation because of difference in habitat utilization. Where *P. atricapillus* and the Boreal Chickadee (*P. hudsonicus*) occur sympatrically, they prefer open upland forest and moist, shaded coniferous forest respectively (Dixon 1961). In the southern Appalachians *P. atricapillus* and the Carolina Chickadee (*P. carolinensis*) are marginally in contact but altitudinally segregated (Tanner 1952). If two or more species occur in the same microhabitat, they may be segregating by feeding on different size or type of food (Beaver and Baldwin 1975), by utilizing different vertical and horizontal feeding positions (MacArthur 1958, Root 1964, Crowell 1968, Sturman 1968, Hertz *et al.* 1976), or by utilizing different foliage densities leading to spatial distribution (Hespenheide 1971a).

Microhabitat Utilization

P. atricapillus and *P. bicolor* are potential competitors because they occupy the same microhabitat, are primarily insectivorous, and utilize similar methods to obtain their prey. My results suggest that differential utilization of the microhabitat both in foraging position and behavior allow for coexistence. There is a significant difference in vertical separation of foraging niches, with *P. bicolor* preferring higher foraging positions. Horizontal partitioning of the microhabitat was not observed. It is possible that vertical separation and/or other factors are sufficient to minimize contact between the two species. A further segregation of the microhabitat is achieved by preferential utilization of different tree species. *P. bicolor* fed almost exclusively on *Quercus* and *Carya* spp., while *P. atricapillus* utilized different tree species more evenly, often feeding in *Prunus* and *Crataegus* shrubs. Utilization of lower vertical foraging positions allows *P. atricapillus* to encounter a wider variety of tree species more frequently than *P. bicolor* which concentrates its activities in the non-shrub profile. Root (1964) has observed a similar relationship in the Plain Titmouse (*P. inornatus*) and the Brown-backed Chickadee (*P. rufescens*) with the latter species being more diversified in its utilization of tree species.

Unlike *P. bicolor*, data on foraging height for *P. atricapillus* indicate that the majority of feeding done at low levels is concentrated in small trees and shrubs. This utilization of denser foliage has also been noted by Aldrich (1943) who suggested that even though *P. bicolor* and *P. atricapillus* occupy the same habitat, the latter species seems to have a greater tolerance for shrubby growth. Differences in foraging height might thus be compounded by this preference. Both species utilize foraging surfaces to the same extent, preferring to forage on or from branches and in the foliage. Again, selection of different foraging perches may not be necessary due to vertical separation of the forest profile. However, there was a significant difference noted in utilization of dead versus live substrate, with *P. atricapillus* foraging on dead branches, twigs and leaves to a greater extent. It is not known whether this preference is associated with a particular food type. The two species also differed significantly in their method of obtaining food. The smaller size of *P. atricapillus* allows it to frequently forage in an inverted position, often examining the terminal foliage zone which offers little support. A similar behavioral difference has been observed in *P. rufescens* when compared to the larger *P. inornatus* (Root 1964). Another difference was observed in the amount of time spent locating a food item, with *P. atricapillus* foraging at a faster rate than *P. bicolor*. Even though the latter species spends a proportionately greater amount of time in searching for food, it encounters or selects fewer prey items than *P. atricapillus*. Root (1964) observed that *P. rufescens* had a faster foraging rate than *P. inornatus*. The relation of this behavior to weight difference and metabolic efficiencies will be discussed in a later section.

Even though partial overlap in microhabitat utilization occurs, results indicate there is minimal contact between two species. This appears to be contradictory to Schoener's hypothesis which predicts coexistence because of differences in food utilization. Instead, I found the two species coexisting in homogenous woodland but spatial segregation limited their contact. Are they partitioning the microhabitat because bill dimensions are insufficient to minimize competition, or are other factors responsible? An attempt will be made to answer these questions.

Competition and Mechanisms of Prey Selection

Since closely related species are likely to draw on the same food resources, a good test of ecological compatibility would be to observe interspecific relationships during the winter and breeding season when conditions are more stressful due to limited resources (Dixon 1961). Since this study was conducted during the summer months when insects (potential food) are most plentiful, the question arises as to whether food is a limiting factor. Evans (1964) found no evidence for differences in food utilization in several coexisting sparrows and concluded the species could breed sympatrically because of abundant food resources. Allaire and Fisher (1975) observed that during summer, the Field Sparrow (Spizella pusilla) and Chipping Sparrow (S. passerina) fed on similar seeds, but during the winter greater differences in food utilization occurred. Betts (1955) has shown that British tits take a negligible proportion of the larva present in oak-woods during the summer. It has also been observed by Hartley (1953) that during the summer and autumn, ecological separation disappears between different English parids due to a temporarily abundant supply of food. In a similar study Gibb (1954) found competition to be most severe during the winter and least severe in the summer, when he observed that all species foraged together even though partial segregation still existed. All these studies indicate that competition for food is reduced during the summer months and may even be eliminated if food is super-abundant. Although an analysis of insect abundance was not conducted during this study, the previous studies strongly suggest that food is not a limiting factor during the summer.

As noted by Betts (1955) a study of the type presented in this paper can only give information regarding foraging locations but not the type of food taken. Early works on the economic importance of certain bird species to agriculture indicate that P. atricapillus and P. bicolor select similar proportions of animal and plant matter. In stomach analyses of P. atricapillus, Forbush (1929) found that food consisted of 68 percent animal matter and 32 percent plant matter. Beal _et al_. (1916) examined stomachs of _P_. _bicolor_ and discovered 66.57 and 33.43 percent animal and plant matter respectively. These studies show that the two species utilize similar proportions of animal and plant foods. The results do not indicate the size of the prey item, species of prey, or foraging sites. No conclusions can be drawn as to possible competitive relations.

Since Betts (1955) has shown that length and shape of bill are related to the size of food items taken by British tits a similar relationship may be expected in North American parids. Myton and Ficken (1967) have shown that _P_. _bicolor_ always prefers larger seeds, while _P_. _carolinensis_ feeds more efficiently on smaller seeds. Cody (1974) suggests that body size may be a better predictor of prey size selection than bill size. Both Hespenheide (1971b) and Johnston (1971) have used body size as an indicator of prey size in the Tyrannidae. Based on these studies and differences in bill dimensions, wing length and weight, evidence suggests that _P_. _bicolor_ is probably selecting larger prey items. Since larger species have a lower surface to volume ratio they require less energy per body weight than smaller organisms. This is metabolically advantageous because larger birds can afford to search more deliberately for larger prey items (Salt 1957). In British tits, Gibb (1954) found the proportion of time spent foraging varied inversely with body weight. The larger size of P. bicolor probably allows it to forage at a slower rate than P. atricapillus, permitting the former species to select larger prey in terms of energy yield per effort expended than the latter species. This difference in food utilization tends to support Schoener's prediction. If this is true, then the species segregate not only by foraging position but by food as well.

According to MacArthur (1972), foliage gleaning insectivorous birds spend the majority of time in searching for a prey item, but relatively little time in actual pursuit. No predator should refuse any prey item it encounters unless it expects to catch a better item during the time required to capture and ingest the first item. A productive environment offers a lower mean search time per prey item than a food sparse area and in this type of situation, the predator can afford to select food which is most beneficial. Based on this concept, the rate of foraging may also be associated with food abundance. The differences in foraging rate may not be a result of competition but relate instead to the energy requirements of the species and maximum efficiency in utilization of available food.

A comparison of morphological variation in allopatric and sympatric populations can be used to test the presence of competition. Presumably greater differences will occur between congeners in areas of sympatry, with competition being reduced by niche divergence (Brown and Wilson 1956). Temporal and spatial comparisons of some morphological dimensions in *P. atricapillus* and *P. bicolor* indicate character displacement has not occurred in these dimensions, suggesting that the species are not competing for food. Other studies indicate that competition for nesting sites does not occur (Trautman 1940, Williams 1947). The mean nest height of *P. bicolor* was found to be about 13 m (Pielou 1957) while nests of *P. atricapillus* were found almost exclusively below 5 m (Odum 1941b). *P. bicolor* utilizes preexisting holes and natural crevices while *P. atricapillus* often excavates its own nest (Bent 1946). Palmer (1949) has stated that nest site selection does not reflect interspecific pressure since *P. atricapillus* is found nesting in similar heights in allopatric areas.

Except for one instance, aggressive encounters between the two species were never observed. This would seem to suggest that competition for a resource is not presently occurring either because resources are not limiting and/or because the species have already evolved distinct preferences.

Range Extension and Spatial Segregation

If we assume that food is not a limiting factor and that differences in bill size and body weight favor selection of different size prey, it would appear that the species are probably not competing for food. Lack of character displacement suggests that competition probably did not occur during the period of range extension either. Why then is spatial segregation of the microhabitat still maintained?

The explanation seems to lie in the evolutionary relation of the two species. Prior to range extension, P. bicolor and P. atricapillus occurred sympatrically in the southern bordering states. These areas are physiographically and floristically similar (Pielou 1957) and support similar avian species. It would appear that P. bicolor had already made the ecological adjustments and evolved a distinct foraging repertoire prior to range extension, thus permitting coexistence and successful colonization of similar habitats in Michigan.

Of interest is the similar situation which exists between P. rufescens and P. inornatus in California. Studies on competition and coexistence between these two species have lead to similar conclusions. In the original study, Dixon (1954) observed that the extension of P. rufescens into the range of P. inornatus was successful because the two species exhibited interspecific territoriality and were essentially isolated from one another. However, a later study by Root (1964) showed extensive overlap of territories. Coexistence was achieved by differences in utilization of the foraging microhabitat. Root suggested that an "open chickadee niche" existed in the area prior to range extension thus permitting successful colonization by P. rufescens. Since the two species occur sympatrically in other areas, P. rufescens had already evolved the competitive adjustments necessary for coexistence. The disparity between these two studies may reflect the type of habitat occupied by the two species. Hertz et al. (1976) suggested that successful invasion by *P. rufescens* depends on the degree of structural heterogeneity of the woodland. In the habitat studied by Dixon, there was less structural diversity than in Root's study site; therefore, segregation of the foraging niche did not occur. It is also possible that further ecological isolation occurs with time. In examining a woodland similar to that studied by Dixon, and where invasion by *P. rufescens* was not a recent phenomenon, Rowlett (1972) found a lack of interspecific territoriality between the two species. This temporal factor is also a possibility for my study. Ecological isolation may have occurred after *P. atricapillus* invaded Michigan (even though this is not supported by character displacement). Studies of presently expanding titmouse populations should be conducted in order to determine the possible competitive relation between the two species.

It is not presently clear why *P. bicolor* has not become successfully established in the Northern Lower Peninsula, or what factors originally stimulated its range extension. The availability of suitable nest sites, food, predators, potential competitors, vegetation structure and climate are all factors affecting extension of the range. Although there is no evidence to support this conjecture, it is possible that *P. bicolor*, being of southern origin, may not be physiologically adapted to cold Michigan winters. Natural selection may act slowly in producing fit individuals and as a result, dispersal, induced by surplus populations, may take a long time. This may also be why *P. bicolor* did not become a common resident of Michigan until the early 1900's. Pielou (1957) suggests that _P_. _bicolor_ is limited to the Southern Lower Peninsula because of its dependence on deciduous trees as nesting sites. Supposedly, the ecotonal coniferous-deciduous zone of the Northern Lower Peninsula does not have abundant nest sites since "woodpecker holes and decayed knotholes are usually not found in conifers". He fails to note that deciduous forests are abundant and that large tracts of cedar swamps are located in northern Michigan, providing numerous dead trees and offering excellent nesting sites. Since climate affects insect distribution and availability, food may be scarcer in northern regions and competition may be more severe, thus decreasing the potential for successful invasion. It is also possible that due to lumbering operations and agricultural exploitation of the habitat, the present vegetation structure may be more suitable for _P_. _bicolor_ than pre-existing habitat.

Although evolutionary relations may be responsible for promoting spatial segregation, other possibilities exist. Since the foraging ecology and competitive relations of other members of the foliage gleaning guild were not examined, it is not known if these potential competitors are influencing height distribution. Since some insects are associated with a certain species of tree and/or height distribution, it is also possible that _P_. _bicolor_ is keying in on a particular type of food which is more abundant in the canopy. This seems unlikely though since food availability varies through the season and the diets of many birds appear to be determined by the availability of prey (Brewer 1963). However, since a food analysis was not conducted this possibility can not be overlooked.

Because of its larger wing size, foraging maneuverability and efficiency of *P. bicolor* may be increased in the more open canopy layer than the dense understory occupied by *P. atricapillus*. It should also be kept in mind that although food may be abundant during the summer, potential for competition increases in the spring when food may be limiting. At this time of year it may be very necessary to segregate by height as well as by food. It is also possible that feeding habits and diet may be more similar in the spring, and spatial segregation the sole mechanism for reducing competition. Even if competition does not occur, for some reason *P. bicolor* may respond to certain "unknown" cues during times of food abundance. For example, foraging height preference might be correlated with similar nest height preferences. Williamson (1971) has observed a bimodal distribution in utilization of the vertical foliage profile by male and female Red-eyed Vireos (*Vireo olivaceous*). Males forage close to their singing perches, while females forage close to the nest. This behavior seems to be the most energetically efficient method of exploiting the available resources. A similar relationship was observed by Morse (1968) in *Dendroica* warblers.

SUMMARY

Since 1878, when the Tufted Titmouse (*P. bicolor*) was first sighted in Michigan, the species has extended its range northward so that presently it is a permanent resident and occurs sympatrically with the Black-capped Chickadee (*P. atricapillus*) in southern Michigan. These two species are potential competitors and this study was conducted in order to investigate their ecological compatibility in relation to foraging behavior.

Significant differences were found to exist both in foraging position and method of obtaining food. *P. atricapillus* prefers to forage in the understory, often obtaining food in an inverted position. *P. bicolor* concentrates its feeding at higher levels and seems to be more deliberate in its movements, taking a longer time to select prey. It is suggested that differences in foraging rate are related to the species weight and metabolic requirements. Evidence from other works suggests that the species may be selecting different size prey because of differences in bill dimensions. Further segregation of the foraging niche is achieved by utilization of different tree species, with *P. atricapillus* having a more even utilization. No significant differences were observed in horizontal position or utilization of a foraging surface. Spatial and temporal comparisons of several morphological dimensions indicate that character displacement has not occurred in the parameters measured, suggesting that *P. bicolor* had already evolved competitive adaptations prior to its range extension. Based on differences in bill size, weight, and evidence presented in other studies, it is suggested that food is not a limiting factor during the time of this study and that other parameters are responsible for spatial segregation of the microhabitat.

SUGGESTIONS FOR FUTURE RESEARCH

1. Actual determination of the type and size of food utilized by these two species is essential. Behavior and foraging position may be correlated with the food obtained by observing the birds for a period of time before capture.
2. Examination of foraging ecology could be conducted in an area where the two species have had a longer period of contact in order to determine if their foraging behavior is similar to this study.
3. As *P. bicolor* continues its northward range extension, its behavior should be monitored in order to determine if any changes in feeding repertoire occurs through time. This might provide empirical evidence for the "open niche" hypothesis.
4. Allopatric populations of *P. atricapillus* should be studied to determine if there are any differences in the foraging repertoire. This might indicate whether *P. bicolor* has any effect on the foraging efficiency of *P. atricapillus*.
5. A study of the ecological relationship of the two species throughout the entire year might reveal seasonal changes in foraging repertoires in relation to food abundance.

6. Comparative foraging behavior in a completely different floristic habitat would be interesting in order to determine if the relationship of the two species is similar in different areas.
7. The relationship of the two species to other potential competitors should be determined.

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