

Substrate use, foraging behavior, & micro
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**SUBSTRATE USE, FORAGING BEHAVIOR, AND MICROHABITAT
DISTRIBUTION: NICHE PARTITIONING BY FOUR BARK-FORAGING BIRD
SPECIES IN A PONDEROSA PINE FOREST**

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Abstract

Sympatric bird species have often been studied by ecologists to gain understanding of how interspecific competition affects foraging success, and how birds reduce competition by partitioning food resources. The Black-capped chickadee (*Parus atricapillus*), Mountain chickadee (*Parus gambeli*), White-breasted nuthatch (*Sitta carolinensis*), and Brown Creeper (*Certhia Americana*) are four insectivore species living sympatrically in a Colorado Ponderosa Pine (*Pinus ponderosa*) forest in the fall. These species' substrate use, foraging behavior, and microhabitat distribution were observed and the results statistically analyzed to endeavor to replicate foraging patterns shown in previous niche partitioning studies of the species. Additionally, microhabitat distribution was analyzed to demonstrate the resource partitioning assumption of MacArthur (1958), which proposed that species might divide up the food resources of a community, so that species can use the *same* resources in *different* places as a mechanism for coexistence in light of the Lotka-Volterra principle. Generally, the results from this study matched the results of previous studies, and MacArthur's (1958) assumption was supported. Species found to be in the same foraging guild, because they used the same tree resources, were shown generally not to overlap spatially in the study area.

Introduction

Foraging is a critical daily activity to birds as they expend energy at a very high rate due to their small size and high metabolism (Gill 1995). The availability of constant food resources is therefore extremely important to birds, and is a significant density-dependent limiting factor to population maintenance or growth (Newton 1998). Environmental factors can limit the quantity or quality of food supplies available to birds at different times throughout the year. For example, annual food shortages may be related to seasonal weather,

periodic shortages related to extreme weather events, or drought. Food quality often varies throughout the year, as well, depending on plant and invertebrate lifecycles.

Interspecific competition also limits food resources. The Lotka-Volterra equation predicts that when two species use the same resource each will limit the carrying capacity of the resource for the other, and will limit each other's population growth. If one species dominates another, it can stop the other's population growth, or bring about its decline, leading to its eventual exclusion (Smith 2001).

Sympatric bird species have often been studied by ecologists to gain understanding of how interspecific competition affects foraging success, and how birds reduce competition by partitioning food resources. Research that has been undertaken to demonstrate interspecific competition related to food resources, and its effects on bird populations, has examined two main lines of data. First, are the evolutionary and other long-term responses of populations to competition. These include changes in morphology and distribution and are usually inferred by existing patterns and theoretical past patterns of both (e.g. Moss 1974, Dhondt 1989). Second are short-term responses, which include direct observations of competition for resources and the results of competition. Short-term responses to competition include changes in the density of populations over space and time (e.g., Gerstell & Bednarz 1999), and changes in a population's realized niche (e.g. MacArthur 1958, Williams & Batzli 1979).

Four insectivore species are sympatric members of the bark-foraging guild in a Colorado Ponderosa Pine (*Pinus ponderosa*) forest in the fall. These include the Black-capped chickadee (*Parus atricapillus*), Mountain chickadee (*Parus gambeli*), White-breasted nuthatch (*Sitta carolinensis*), and Brown Creeper (*Certhia americana*). Numerous studies, both experimental and observational, have been performed by ecologists to gain insight into the foraging behaviors of these species, and to quantify differences in their realized niches.

The foraging behavior of Black-capped and Mountain chickadees were studied by Hill and Lein (1988) in an area of year-round sympatry. Food competition between the congeners was reduced by significant ecological segregation due to different foraging substrate selection. Furthermore, Black-capped chickadees were found to forage more often in deciduous trees than Mountain chickadees. Observations did not support interference aggression being the cause for this segregation, because the two species were rarely seen together, and when they were no aggression was observed. The mosaic nature of the habitat was suggested as the reason that the two species coexisted in their study area (Hill & Lein 1988).

An earlier study by Sturman (1968) of the foraging ecology of sympatric Black-capped and Chestnut-backed (*Parus rufescens*) chickadees showed similar differences in substrate selection between the two species. Additionally, he showed that they exhibited little spatial overlap and would not often compete for food. Sturman (1968) asked the question: why, if the two species do not often overlap in habitat was there such ecological segregation of their foraging substrate selection? He suggested that their distinct evolutionary histories, which included spatial segregation to different regions in North America, might have caused them to adapt different foraging strategies based on the types of trees they had foraged in formerly.

Morse (1970) studied mixed-species flocks of bark-foraging species and found a system of dominance hierarchy in which subordinate species exhibited a wider fundamental niche size in the number of substrates utilized than the dominants did. He hypothesized that dominance rank and fundamental niche size would be inversely related in bird communities that have high levels of niche overlap. In his study, chickadees, subordinate to nuthatches and woodpeckers, displayed the widest fundamental niche.

Conversely, the Brown creeper has a much more specialized and stereotyped set of foraging behaviors. Generally, Brown creepers stay on tree trunks and move up the trees from a starting position low on the trunk. Brown creepers were shown to select trunks more than twice as often as branches for foraging substrate. This may be due to the fact that trunk bark surface is generally rougher and contains more crevices than branch surfaces, and therefore provides more habitat for invertebrate prey (Franzreb 1985). Brown creepers have relatively longer beaks than other bark-foraging birds, and this morphological difference allows them to reach into these crevices.

In a lab study, White-breasted nuthatches were found to utilize tree substrates at a frequency proportional to the substrate's area. In other words, larger diameter substrates were utilized more often than smaller diameter substrates by the species (Pierce & Grubb 1981). Carolina Chickadees (*Parus carolinensis*), also observed in this study, had no similar size-proportional use of substrates. Pierce and Grubb (1981) suggested that this might be due to the fact that larger substrates have the greatest portion of available surface area for foraging and also tend to have greater abundance, as well as depth of bark crevices. White-breasted nuthatches, like Brown creepers, have relatively long beaks that allow them to reach into bark crevices.

In ambitious study by Holmes, et al. (1979), researchers collected and performed statistical analysis on 27 foraging characteristics of 22 forest bird species, including the White-breasted nuthatch and Black-capped chickadee. The study showed a separation of forest species into several different guilds based on food exploitation behaviors. The White-breasted nuthatch and the Black-capped chickadee were separated based on the fact that the former forage mainly on bark, and the latter forage more frequently on foliage and branches. Furthermore, as in the study by Morse (1970), the Black-capped chickadee was shown to have a wider niche breadth and to sometimes exploit more than one foraging guild.

This study will contribute by attempting to replicate the foraging patterns shown in the previous studies with a study of these same species found in a Colorado Ponderosa Pine forest. Toward that purpose, I make several hypotheses:

- 1.) Black-capped and Mountain chickadees will have significant ecological segregation due to different foraging substrate selection,
- 2.) Black-capped and Mountain chickadees will have significant ecological segregation due to different tree species selection,
- 3.) White-breasted nuthatches and Brown creepers will forage mainly on bark on the trunks of trees, while Black-capped chickadees and Mountain chickadees will forage more frequently on foliage and branches, and finally,
- 4.) because White-breasted nuthatches and Brown creepers are in the same foraging guild, and Black-capped and Mountain chickadees are in the same foraging guild, in order to satisfy the principal of competitive exclusion, and to demonstrate the resource partitioning assumption of MacArthur (1958), the pairs of species in each foraging guild will show spatial separation into different microhabitats within the study area.

Methods

Study Area

Focal surveys were conducted between October 12th and October 30th, 2004 in a 21-hectare area of Ponderosa Pine forest in the foothills at the Chatauqua Park Open Space, (39.99463 N., -105.28116 W.) Boulder, Colorado, U.S.A. Chatauqua Park is located at the Rocky Mountain foothills-urban interface and has been preserved as city open space since 1898. The study area encompasses a mountain foothills forest habitat between 1,743 and 1,817 meters in elevation along the Enchanted Mesa trail system. It includes a closed canopy deciduous forest located along riparian drainage, an open canopy mixed Ponderosa Pine

forest along northern slopes and the top of the mesa, and xeric mountain shrubs, grass and forbs along south facing slopes (Figure 1).

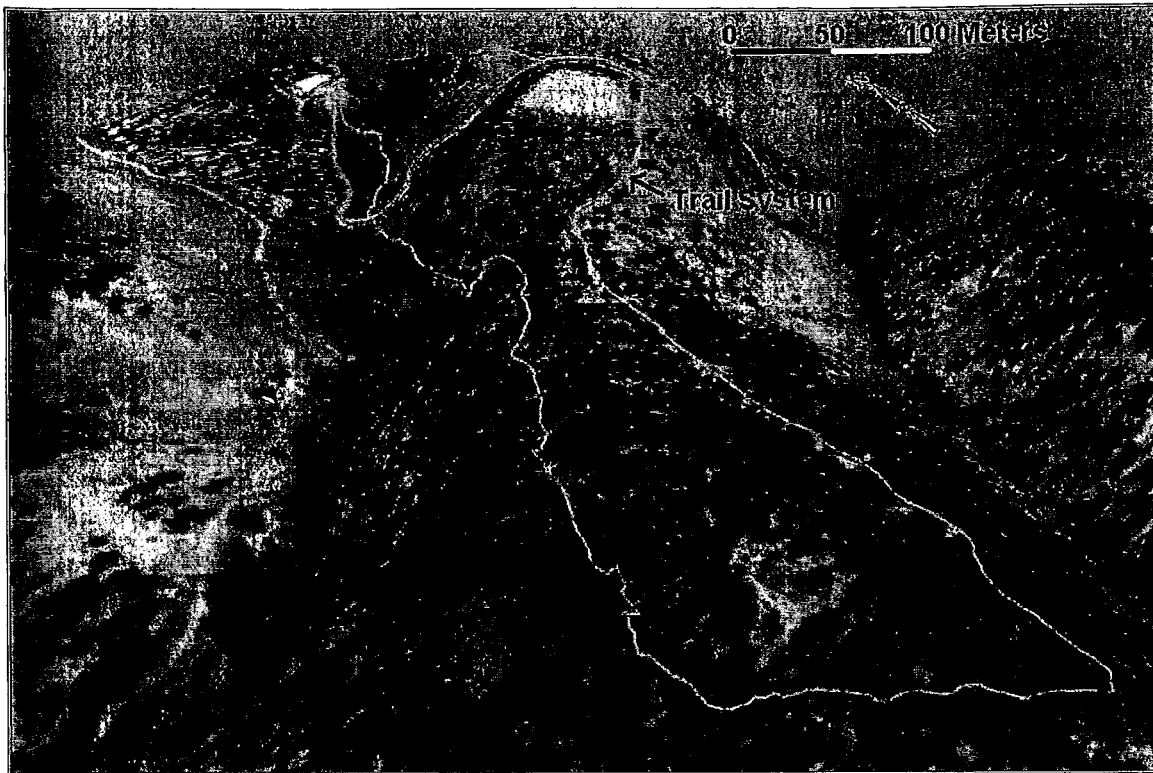


Figure 1. Study area. Gray area at top of map is urbanized area.

The typical climate of the area is hot and dry summers with cold winters. Annual precipitation is less than 49 centimeters. Typical October temperatures range from 4° Celsius to 19° Celsius and mean precipitation is 3.2 centimeters.

Materials and Procedures

Focal surveys were made of any Black-capped chickadee, Mountain chickadee, White-breasted nuthatch, or Brown creeper individual located by sight or call that could be watched while it was foraging using binoculars from either on the trail, or a short distance off of it. Surveying times during the study period were as follows: 0800 to 1100 on a total of two days, 1430 to 1730 on a total of three days, and 1100 to 1400 on a total of two days for a total of 21 hours of survey time. An additional three hours was spent assessing the study area trails

and habitat before beginning the actual survey. The direction of walking the trail was rotated each time period sampled to avoid potential over sampling of any one area.

After an individual of one of the study species was located, I recorded a unique identification number for the individual on a cassette recorder. Next, I began recording the tree species, foraging substrate, foraging location, and foraging behavior of the bird by speaking into the cassette recorder. I recorded each time the bird moved to a different substrate as a unique observation for a maximum of five different substrate moves before another bird was located to avoid problems of sampling pseudo-replication. If the bird did not complete five different substrate moves before 5 minutes elapsed, I moved on to the next individual. This method is a modified technique of Sturman (1968). Finally, before continuing up the trail in search of the next bird, a Garmin eTREX Legend GPS was used to record the location of the bird for later GIS mapping. Each GPS recording was taken only after WAAS correction minimized location error to ± 30 meters.

The foraging substrates, foraging locations, and foraging behaviors were classified and defined beforehand into several possible characteristics. For foraging substrates these included:

- 1.) Coniferous trees – horizontal substrate: trunk, branch, twig, or needles (Figure 2),
- 2.) Deciduous trees – horizontal substrate: trunk, primary branch, secondary branch, tertiary branch, or leaves, (Figure 3), and
- 3.) Ground

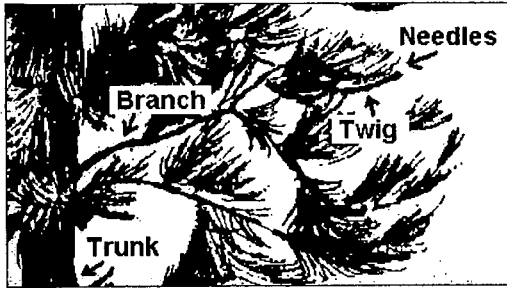


Figure 2. Coniferous tree foraging substrates.

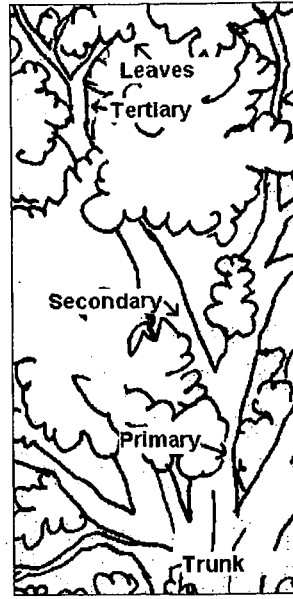


Figure 3. Deciduous tree foraging substrates.

Foraging vertical substrate locations were recorded as distance from the top of the tree in percent ranges. These included the categories: 0-25%, 25-50%, 50-75%, 75-100% and below the canopy for both coniferous and deciduous trees (Figures 4 & 5).

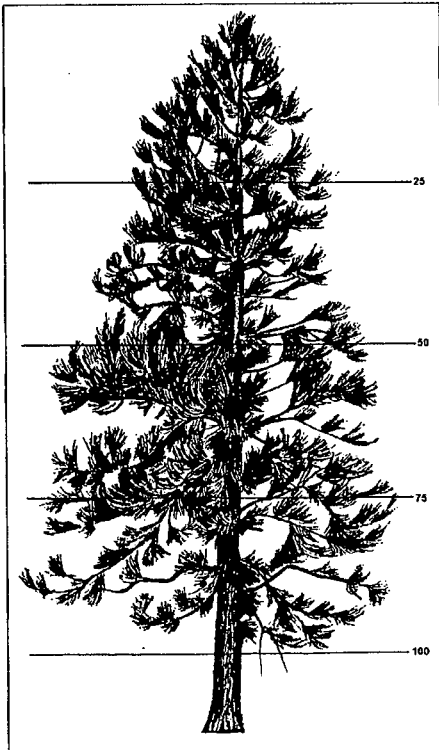


Figure 4. Foraging locations for conifers.

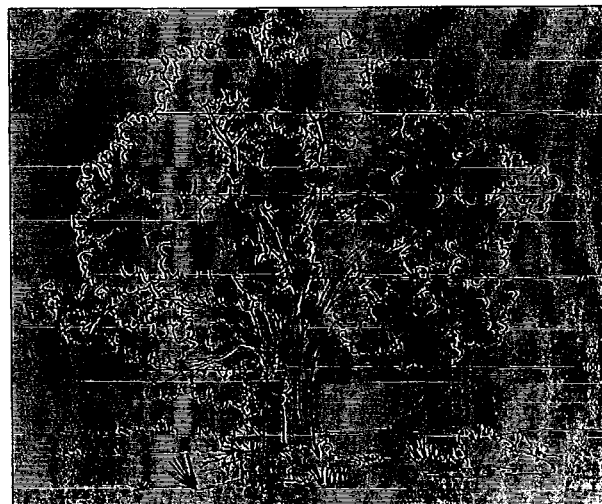


Figure 5. Foraging location for deciduous trees.

Foraging behaviors were both the type of foraging performed and the social environment of foraging. Types of foraging included:

- 1.) Gleaning – standing or hopping bird taking stationary prey item from a substrate (Robinson & Holmes 1982),
- 2.) Hanging – Bird flies to a leaf or twig, hangs from it, then either takes a prey item directly from the substrate or, more often, manipulates it (for example, uncurls the leaf to get at a caterpillar or spider hidden inside the curl) (Robinson & Holmes 1982).
- 3.) Hovering – All attacks in which a food item is taken from a substrate while the bird is flying (Robinson & Holmes 1982),
- 4.) Probing – Maneuvers with the bill when a bird explores for hidden insects (Robinson & Holmes 1982),
- 5.) Pecking – Pick up prey by pecking on the substrate, and
- 6.) Scaling – Removing bits of flaky bark in search of prey underneath.

Social environment foraging characteristics included:

- 1.) Foraging in tree and area alone,
- 2.) foraging with conspecific in the same tree,
- 3.) foraging with another species in the same tree,
- 4.) foraging with conspecific in nearby trees, and
- 5.) foraging with another species in nearby trees.

Microhabitat vegetation data was obtained for the study area from the Natural Diversity Information Source (NDIS) on-line GIS collection (ndis.nrel.colostate.edu). This dataset contains Landsat Thematic Mapper imagery processed using an unsupervised

classification procedure into a land cover 25-meter grid. This dataset and the locations of the bird observations were loaded into ArcView 3.3 GIS for spatial manipulations that allowed each bird observed to be assigned its vegetation context and elevation. These parameters were used in combination to define the specie's microhabitat in the study area.

Data gathered in the field was entered into Excel after each field survey and was later statistically analyzed in Excel using statistiXL Version 1.4. Two statistical techniques were used, frequency contingency tables and cluster analysis. Several descriptive and graphical techniques were also used to visualize patterns in the data.

Results

A total of 145 foraging observations were made of the study species at 51 locations in the study area (Figure 6). This was a smaller sample size than was hoped, and was due to the low frequencies of birds found on colder study days.

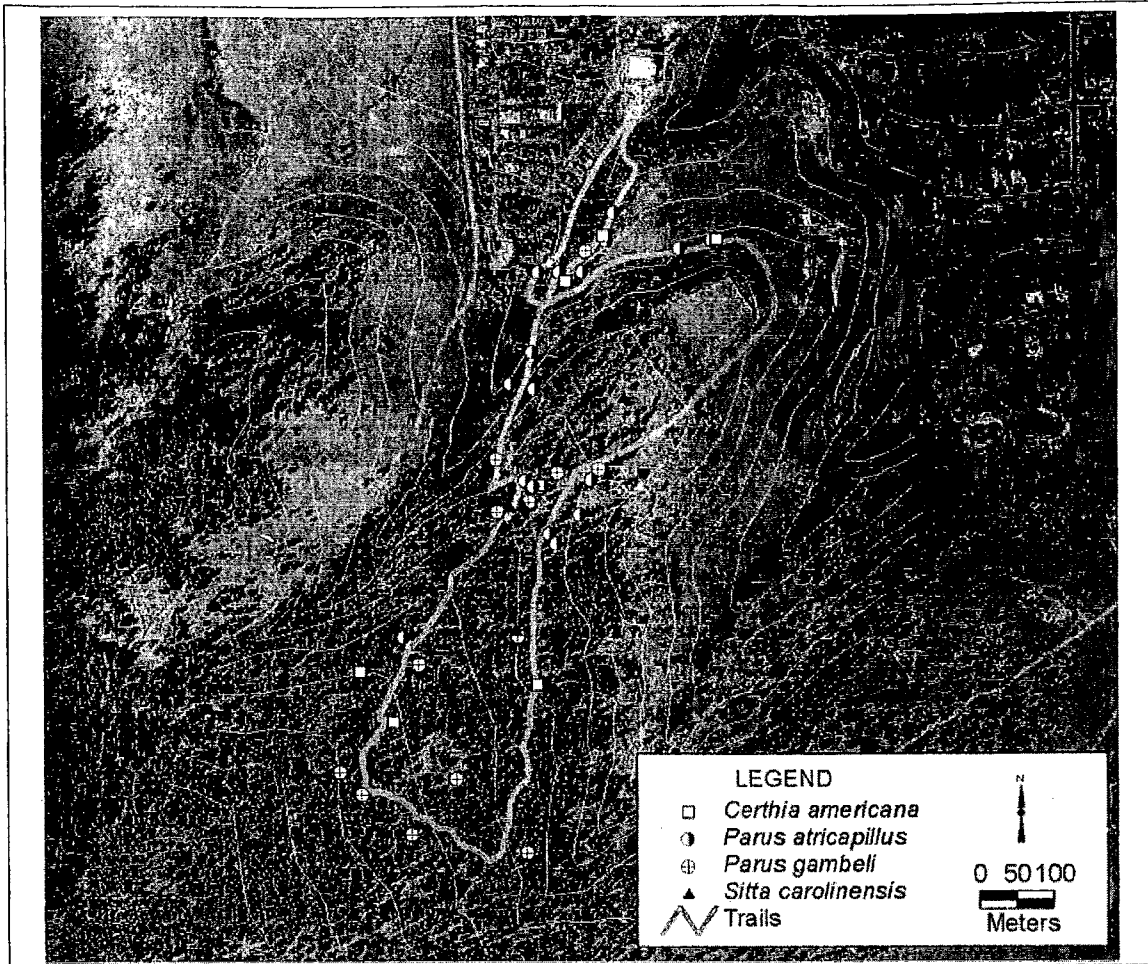


Figure 6. Locations of various species observed in the study area.

Black-capped and Mountain Chickadee Comparisons

Foraging substrate selection for bark-foraging birds can be characterized both vertically and horizontally in trees. Statistically significant differences were found both in vertical and horizontal substrate selection between Black-capped and Mountain Chickadees. Vertical differences showed a chi-square p-value of 0.049 and horizontal differences showed a chi-square p-value of 0.013 (Tables 1 & 2). Horizontal data was reclassified prior to analysis so that the differences in coniferous and deciduous horizontal tree structures were removed, for example, needles and leaves were given the same values on a numerical scale.

Frequency Table				
SPECIES	POS.VPINE	Observed	Expected	Obs - Exp
Parus atricapillus	Ground	3	1.571	1.429
Parus atricapillus	Below Canopy	5	5.238	-0.238
Parus atricapillus	25-50	5	3.667	1.333
Parus atricapillus	50-75	8	10.476	-2.476
Parus atricapillus	0-25	9	13.095	-4.095
Parus atricapillus	75-100	14	9.952	4.048
Parus gambeli	Ground	0	1.429	-1.429
Parus gambeli	Below Canopy	5	4.762	0.238
Parus gambeli	25-50	2	3.333	-1.333
Parus gambeli	50-75	12	9.524	2.476
Parus gambeli	0-25	16	11.905	4.095
Parus gambeli	75-100	5	9.048	-4.048
Test Results				
Statistic	Value	DF	P	
Chi-Square	11.144	5	0.049	
Log-Likelihood	12.527	5	0.028	

Table 1. Frequency contingency table comparing vertical foraging location differences for two species.

Frequency Table				
SPECIES	POS.HORZ	Observed	Expected	Obs - Exp
Parus atricapillus	1	3	1.571	1.429
Parus atricapillus	2	6	4.190	1.810
Parus atricapillus	4	9	7.333	1.667
Parus atricapillus	3	20	18.333	1.667
Parus atricapillus	5	6	12.571	-6.571
Parus gambeli	1	0	1.429	-1.429
Parus gambeli	2	2	3.810	-1.810
Parus gambeli	4	5	6.667	-1.667
Parus gambeli	3	15	16.667	-1.667
Parus gambeli	5	18	11.429	6.571
Test Results				
Statistic	Value	DF	P	
Chi-Square	12.695	4	0.013	
Log-Likelihood	14.216	4	0.007	

Table 2. Frequency contingency table comparing horizontal foraging location differences for two species. 1=Ground, 2=Trunk, 3=Branch and Primary branches, 4=Twigs, Secondary and Tertiary Branches, and 5=Needles and Leaves.

The chi-square analyses shown in these tables, however, must be considered with some caution as the data violated sample size assumptions for the chi-square test.

Examination of the particular differences in vertical substrate selection showed that Mountain chickadees tended to forage higher in trees, while Black-capped chickadees foraged lower and were observed to forage on the ground occasionally (Figure 7).

Assessment of horizontal foraging observations showed that Mountain chickadees selected needles most often, while Black-capped chickadees selected primary branches most often (Figure 8).

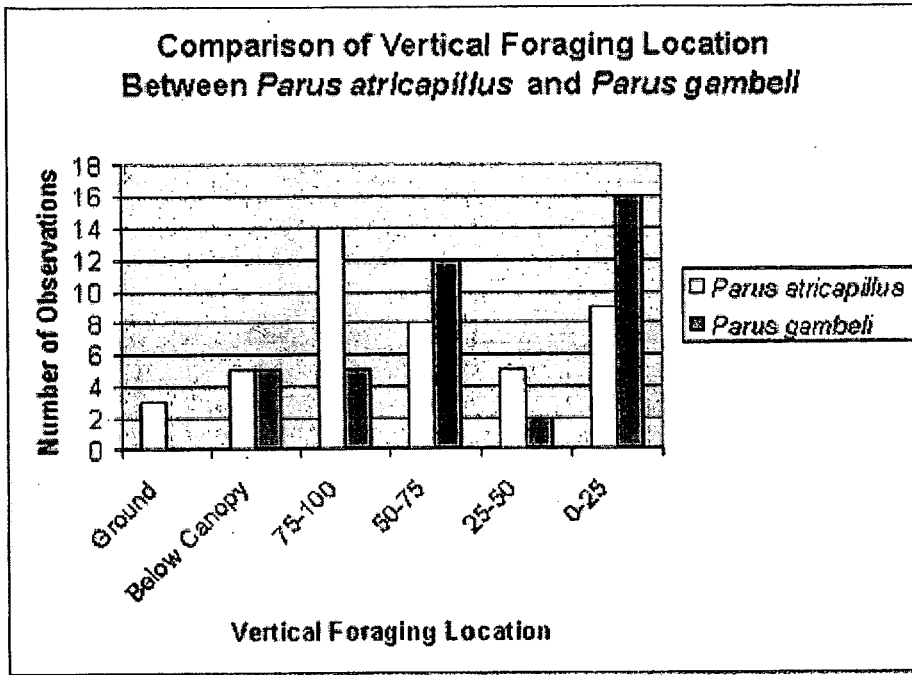


Figure 7. Categorical distribution of vertical foraging location observations.

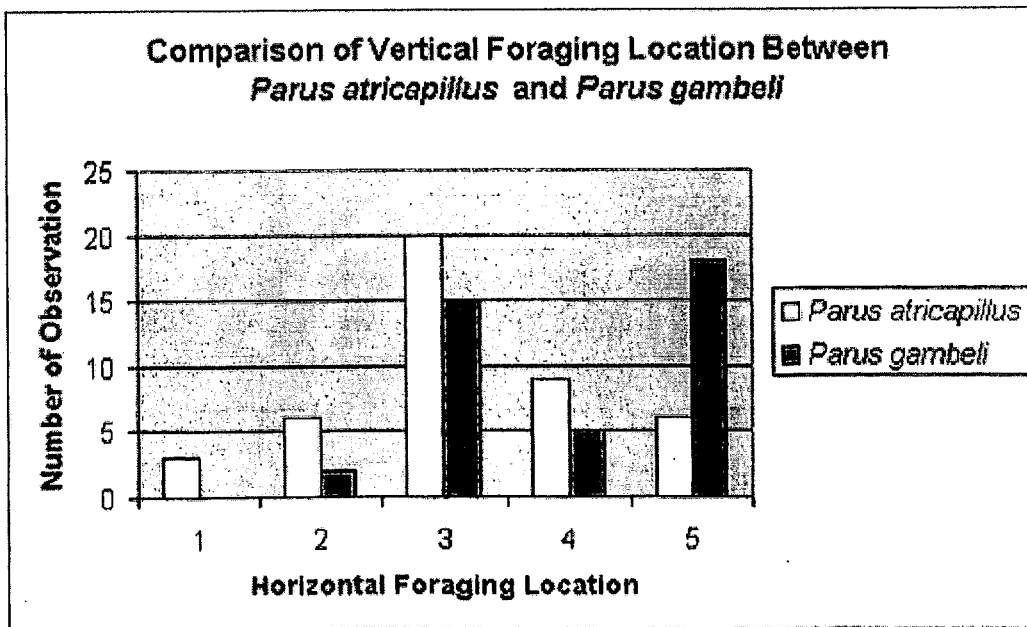


Figure 8. Categorical distribution of horizontal foraging location observations. 1=Ground, 2=Trunk, 3=Branch and Primary branches, 4=Twigs, Secondary and Tertiary Branches, and 5=Needles and Leaves.

Differences in tree species selection by Black-capped and Mountain Chickadees was found to be statistically significant with a chi-square p-value of 0.002 (Table 3). Cautions previously noted regarding chi-square calculations and low sample size apply here as well. During the 44 observations made of Black-capped chickadees, they utilized all types of substrate species, however, the 40 Mountain chickadees observed used only Ponderosa Pine trees.

Frequency Table				
SPECIES	FOR-SITE	Observed	Expected	Obs - Exp
Parus atricapillus	Ground	3	1.571	1.429
Parus atricapillus	Ppine	27	35.095	-8.095
Parus atricapillus	Bcottonwood	4	2.095	1.905
Parus atricapillus	UShrub	3	1.571	1.429
Parus atricapillus	UDecidous	6	3.143	2.857
Parus atricapillus	Shrub oak	1	0.524	0.476
Parus gambeli	Ground	0	1.429	-1.429
Parus gambeli	Ppine	40	31.905	8.095
Parus gambeli	Bcottonwood	0	1.905	-1.905
Parus gambeli	UShrub	0	1.429	-1.429
Parus gambeli	UDecidous	0	2.857	-2.857
Parus gambeli	Shrub oak	0	0.476	-0.476
Test Results				
Statistic	Value	DF	P	
Chi-Square	19.376	5	0.002	
Log-Likelihood	25.915	5	0.000	

Table 3. Frequency contingency table comparing tree species selection differences for two species.

Functional Niche Comparisons of Chickadees and White-breasted Nuthatches

Observations of foraging behaviors and foraging substrates were independently compared statistically between both species of chickadees and White-breasted nuthatches. Foraging behavior differences were significant with a chi-square p-value of 0.00000861. Differences are shown in Figure 9. All three species used gleaning the most. White-breasted nuthatches using pecking and scaling much more than the chickadee species, while only the Black-capped chickadees used hanging, but not frequently.

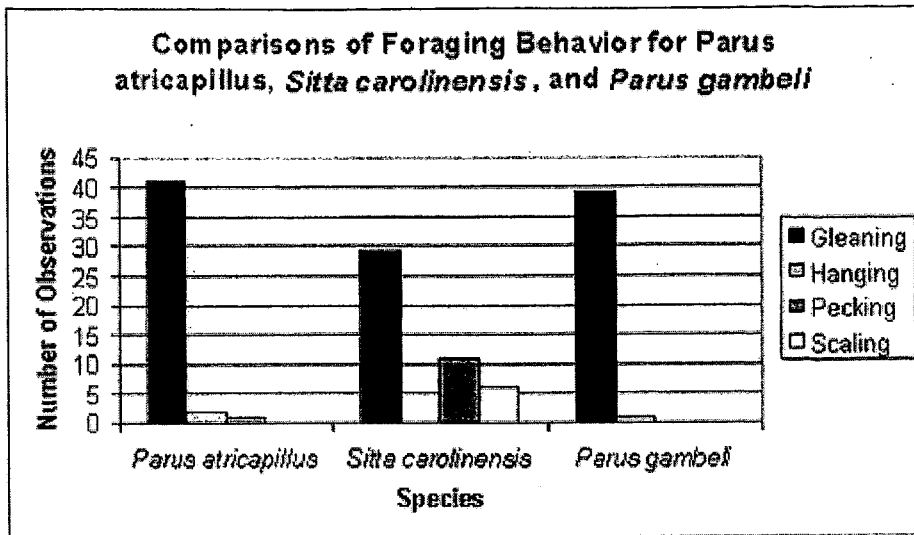


Figure 9. Categorical distribution of foraging behavior observations.

Comparisons of foraging substrate observations between the chickadee species and White-breasted nuthatch showed that for vertical foraging substrates, Black-capped chickadees had the largest collection of locations, with 6 locations used, as well as the most even partitioning in the use of these substrates. However, the Mountain chickadee and White-breasted nuthatch, both with 5 vertical foraging locations, had nearly as many. Evenness in selection by these two species was somewhat lower (Table 4).

	<i>Parus atricapillus</i>	<i>Sitta carolinensis</i>	<i>Parus gambeli</i>
Total number of observations	44	46	40
Foraging Richness (S)	6	5	5
Foraging Evenness (H/ln S)	0.94	0.87	0.87
Shannon Diversity (H)	0.73	0.61	0.61

Table 4. Diversity and evenness of vertical substrate selection by Black-capped chickadee, White-breasted nuthatch, and Mountain chickadee.

Comparisons of horizontal foraging substrate observations between the chickadee species and the White-breasted nuthatch showed that the Black-capped chickadee had the most horizontal substrate locations, while the White-breasted nuthatch had the least.

Evenness for the chickadee species was nearly the same, while evenness for the White-breasted nuthatch was significantly lower (Table 5).

	<i>Parus atricapillus</i>	<i>Sitta carolinensis</i>	<i>Parus gambeli</i>
Total number of observations	44	46.00	40.00
Foraging Richness (S)	5	3	4
Foraging Evenness (H/ln S)	0.88	0.67	0.82
Shannon Diversity (H)	0.61	0.32	0.49

Table 5. Diversity and evenness of horizontal substrate selection by Black-capped chickadee, White-breasted nuthatch, and Mountain chickadee.

Foraging Guilds and Microhabitat Separation

A cluster diagram of Euclidean distances represents the positions of the four species with regard to their observed selections of horizontal foraging position (Figure 10). In this diagram, the species are quantitatively separated into groupings that can be considered to be guilds. The first guild consists of the chickadee species, which were observed utilizing branches and needles most often. The second guild consists of the White-breasted nuthatch and the Brown creeper, which were observed using trunks most often (Table 6). Furthermore, Cluster analysis of vertical foraging location selection showed the same guild separation groupings.

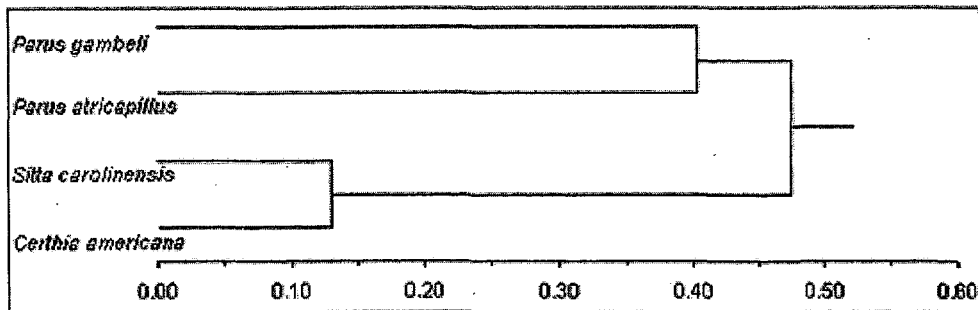


Figure 10. Cluster analysis dendrogram of horizontal foraging selection for four species. Cophenetic Correlation p-value = 0.02.

	Ground	Trunk	Branch	Primary	Secondary	Tertiary	Twig	Needles	Leaves
<i>Parus atricapillus</i>	0.07	0.14	0.30	0.16	0.02	0.07	0.11	0.11	0.02
<i>Certhia americana</i>	0.07	0.53	0.40	0.00	0.00	0.00	0.00	0.00	0.00
<i>Parus gambeli</i>	0.00	0.05	0.38	0.00	0.00	0.00	0.13	0.45	0.00
<i>Sitta carolinensis</i>	0.00	0.63	0.35	0.00	0.00	0.00	0.02	0.00	0.00

Table 6. Percent use of various horizontal foraging substrates by four species. The highest percent value is in bold for each species.

Land cover values found in the study area are shown in Table 7. Each of 51 observed bird locations were spatially associated using GIS with one of these values (Table 8). Cluster analysis was then performed to determine separation by land cover microhabitat (Figure 11). Additionally, each bird location was assigned an elevation range using GIS and was analyzed by cluster analysis (Figure 12). Both parameters show clear separation of microhabitat selection pairing the White-breasted nuthatch with the Mountain chickadee, and the Brown creeper with the Black-capped chickadee.

TYPE	DESCRIPTION
Ponderosa Pine/Mtn. Shrub Mix	Codominant Ponderosa Pine forest and mountain shrubland.
Ponderosa Pine	Coniferous forest dominated by PIPQ.
Riparian	Cottonwood, willow, sedges along waterways.
Ponderosa Pine/Aspen Mix	Mixed forest codominated by PIPQ and Aspen.
Mesic Mountain Shrub Mix	Oak dominant with sagebrush, snowberry, grass.
Xeric Mountain Shrub Mix	Deciduous woodland (or tall shrubland) dominated by Mtn. Mahogany.
Grass/Forb Mix	Rangeland codominated by grasses and forbs.
Ponderosa Pine/Douglas Fir Mix	Mixed forest codominated by PIPQ and PSME.

Table 7. Land cover values in the study area.

	Ponderosa Pine/Mtn. Shrub Mix	Ponderosa Pine	Riparian	Ponderosa Pine/Aspen Mix	Mesic Mountain Shrub Mix	Xeric Mountain Shrub Mix	Grass & Forb Mix	Ponderosa Pine/Douglas Fir Mix
<i>Parus gambeli</i>	0.54	0.15	0.00	0.08	0.08	0.15	0.00	0.00
<i>Parus atricapillus</i>	0.17	0.00	0.33	0.11	0.11	0.22	0.08	0.00
<i>Sitta carolinensis</i>	0.46	0.08	0.00	0.00	0.23	0.00	0.15	0.08
<i>Certhia americana</i>	0.14	0.14	0.29	0.14	0.00	0.29	0.00	0.00

Table 8. Percent of observations of the four species in various land cover areas. The highest percent value is in bold for each species.

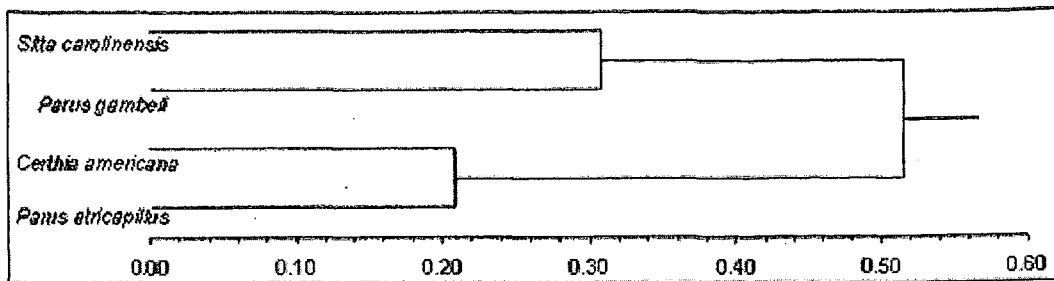


Figure 11. Cluster analysis of land cover microhabitat for four species. Cophenetic Correlation p-value = 0.001.

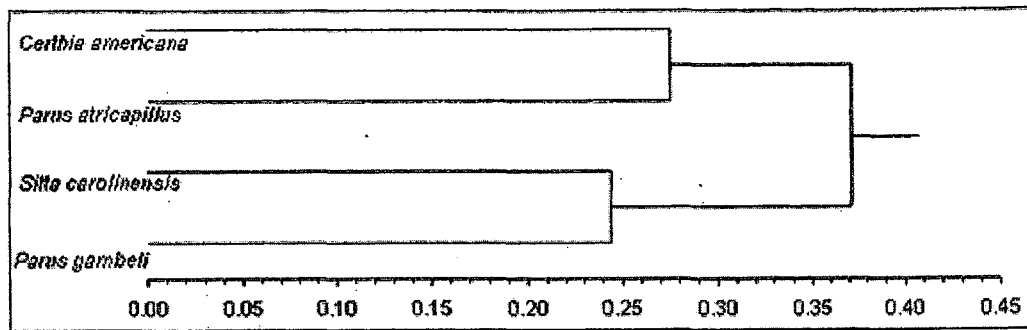


Figure 12. Cluster analysis of elevation range microhabitat for four species. Cophenetic Correlation p-value = 0.021.

Discussion

As with any study based on field observations, many confounding variables could have been present to influence the data. One such variable, weather, has already been noted as the probable cause for low numbers of foraging observations on certain days during the study. Additional confounding variables could include: the loss of leaves on deciduous trees during the study period, predators that were observed or heard, and the sex and age of study individuals.

Post-hoc power analysis of the sample size of the study indicated the results should be interpreted with some caution. Confidence in the significance of results could be greatly improved with more observations. However, many of the results do support the patterns of previous studies and several tests performed were found to be statistically significant.

Examination of foraging substrate selection differences between Black-capped and Mountain chickadees showed that Mountain chickadees only utilized Ponderosa pine trees,

and in these tended to forage higher in the trees and in the needles. Black-capped chickadees, however, utilized several different tree species, foraged on the ground occasionally, and foraged lower and tended to select primary branches most often. Significant foraging substrate and tree selection segregation between the chickadee species, as hypotheses 1.) and 2.) predicted, was supported by this study. Black-capped and Mountain chickadees generally do not overlap in range in Colorado (Andrews & Righter 1992), and it may be that as with Hill and Lein's (1988) conclusions, the diverse nature of the habitat facilitates the overlapping of the two species in the study area. The study area does in fact straddle several known avian habitat types: foothill riparian forest, foothill shrub land, and Ponderosa pine forest (Andrews & Righter 1992).

Comparisons of foraging behavior, showed that both the Black-capped chickadee and White-breasted nuthatch used a variety of foraging behaviors, with gleaning being the most common for both. The Mountain chickadee used one less technique than the others, but this could be due simply to small sample size. Diversity and evenness measures of vertical and horizontal foraging substrates showed that Black-capped chickadees utilized the most foraging substrates, and utilized them most uniformly out of all three species. Horizontal substrate selection was where the White-breasted nuthatch showed the most difference from the chickadees. Mountain chickadees had nearly as much horizontal diversity as the Black-capped chickadees and nearly the same evenness for horizontal substrate selection, but lower evenness for vertical substrate selection.

Mixed species foraging flocks of chickadees and nuthatches were not observed during the study period. However, they are known to exist (Gill 1994, Morse 1970). Morse (1970), hypothesized that in mixed-species communities with high levels of niche overlap, fundamental niche size would be larger for subordinate species. Contrary to Morse's (1970) study, I was not prepared to analyze fundamental niche size from my observations, because

the term "fundamental" implies all the potential resources that could be used by the species. Diet preferences, feeding morphologies, and complete predator/competitor relationships would need to be better understood, and controlled for, in order to describe and quantify each species' fundamental niche. Instead, realized niche can be measured from observations. In this study, both chickadee species rejected the null hypothesis, as predicted by hypothesis 3.), and displayed a wider realized niche than the White-breasted nuthatch. However, contrary to Morse's (1970) study area, high levels of niche overlap didn't seem to exist in this study area. On average only 12% of the time were congeners found to be foraging near each other. It may be that the chickadee's wider niche breadth was determined previously by genetics and evolutionary history, as Sturman (1968) suggested was the case for the chickadees he studied.

Foraging guilds can be defined quantitatively using cluster analysis to sort foraging characteristics and group those species that are most alike (Holmes, et al. 1979). The results of this study show that White-breasted nuthatches and Brown Creepers are in one foraging guild, while Black-capped and Mountain chickadees are in another. It should be noted that these guilds are defined at the fine scale of foraging location in the tree, whereas, it is possible to define coarser-scale guilds, such as bark-foraging guilds. Scale variability is a characteristic of the guild concept. Though I have demonstrated that there are significant differences between the chickadee species with regard to foraging location and tree selection, when compared to White-breasted nuthatches and Brown creepers for foraging location, they are in the same guild. Furthermore, the fact that they are in the same guild means that there is at least a potential for interspecific competition. Likewise, Brown creepers and White-breasted nuthatches utilized the trunks of trees and large branches most often, and are potential competitors. I proposed in hypothesis 4.), that because of this potential for competition, spatial segregation of species in the same guilds should be seen.

Spatial segregation was calculated by performing cluster analysis on the four species with regard to observations of them in various habitat types and elevations. Habitat types can be used to assign the species into different "preferred" microhabitats based on the frequency with which the species occurred in each habitat. It should be noted that the true preference of species for certain habitat types, or elevations, can not be precisely calculated without including data on the area of each habitat type potentially available to the species. However, since I was looking at relative comparisons of habitat use by different species, including area dimensions was not critical to my analysis.

Again using cluster analysis, elevation was used to calculate spatial segregation of the species. Elevation choice by species is likely correlated with different microclimate variables, such as wind speed, temperature, and precipitation. These parameters have been studied by others (Grubb & Dolby 1999), but couldn't be examined during this study. This is an area for future research in the study area.

The hypothesized spatial segregation of the White-breasted nuthatch from the Brown creeper and two chickadee species from each other was demonstrated in the cluster analysis. This helps to demonstrate the resource partitioning assumption of MacArthur (1958), which proposed that, as a mechanism for coexistence in light of the Lotka-Volterra principle, species might divide up the food resources of a community so that species can use the *same* resources in *different* places.

This study does not conclude that the species in each foraging guild never overlap spatially in the study area. Additionally, it is not know if resources were limited, or were abundant, during the study period. Species distribution likely changes throughout the year in response to changes in prey abundance, composition, and quality. It may be that the study species overlap spatially more in different seasons. Further research in the study area on seasonal changes in invertebrate prey species abundance and quality would be informative.

The bark-foraging Black-capped chickadee, Mountain chickadee, White-breasted nuthatch and Brown creeper observed in the study area were found to have foraging patterns similar to those studied in other locations. This research has contributed by providing additional support for these patterns, as well as providing specific information on the substrate use, foraging behavior and microhabitat distribution of the species in a diverse Colorado mountain park foothills habitat.

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