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## Winter Microhabitat Foraging Preferences of Sympatric Boreal and Black-capped chickadees in Michigan's Upper Peninsula

Zach G. Gayk<sup>1,2,3</sup> and Alec R. Lindsay<sup>1</sup>

**ABSTRACT.**—We examined differences in microhabitat use between Boreal (*Poecile hudsonicus*) and Black-capped chickadees (*P. atricapillus*) where they co-occur near Marquette, Michigan, USA. Twenty-four Boreal and 37 Black-capped chickadees were followed during 60 hrs of field observation. Boreal Chickadees foraged only in three conifer species, 76% of which were black spruce (*Picea mariana*), while Black-capped Chickadees foraged widely across six coniferous and three deciduous tree species. Analysis of foraging data categorized by zones within conifer trees indicated high niche overlap (0.676) between Boreal and Black-capped chickadees across all foraging zones. Individual comparisons on a zone-by-zone basis revealed a significant difference in foraging occupancy in the medial portion of the crowns of conifer trees ( $P = 0.0002$ ). Our results indicate exclusive use by Boreal Chickadees of dense medial foliage within the top 3 m of conifer crowns. Received 22 March 2012. Accepted 31 July 2012.

Niche partitioning in birds has been widely reported between species with similar morphological features, body sizes, and diets (MacArthur 1958, Reynolds and Meslow 1984), or between males and females of the same species that have divergent foraging strategies (Williams 1980, Radford and du Plessis 2003). Two congeneric species, Black-capped and Boreal chickadees (*Poecile* spp.), often forage together in mixed-species flocks within boreal forests of Upper Michigan during winter. Black-capped Chickadees (*P. atricapillus*) are abundant winter residents across a wide spectrum of forested and scrub habitats, but Boreal Chickadees (*P. hudsonicus*) are rare residents within 160 km of their southern range boundary; they occur in lowland black spruce (*Picea mariana*) forests which are localized within the predominantly deciduous forest matrix of this region (Binford 2006). All members of the genus *Poecile* have similar food habits and body sizes, and forage for arboreal insect larvae and seeds. Dhondt (1989) concluded that non-overlapping distributions of North American chickadees indicated either range replacement (allopatry) or habitat partitioning, to

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avoid competition with closely related species. Similar conclusions were noted by Alatalo et al. (1987) in Finland, based on elimination experiments in winter flocks.

Niche partitioning between Boreal and Black-capped chickadees has not been studied during winter, a period in which both species are in greatest contact. Descriptive (Stewart and Aldrich 1952) or summer accounts (Vassallo and Rice 1982) suggest Black-capped Chickadees more frequently occupy deciduous and less dense forests, usually at lower heights within trees, while Boreal Chickadees exploit regions of dense conifer foliage most commonly in spruce crowns.

We investigated microhabitat partitioning in mixed-species chickadee flocks within boreal forests at a McCormick Wilderness Area study site in western Marquette County, Michigan, USA in January–March 2011. We predicted the more abundant Black-capped Chickadee might restrict rarer Boreal Chickadees to confined regions of microhabitats.

#### METHODS

*Study Area.*—Five primary study locations near the McCormick Wilderness Area (centered at 46° 38' 39.04" N, 88° 02' 40.87" W) were identified as quality Boreal Chickadee habitat based on habitat descriptions from Evers (1991) and Hickman (2011), and secondarily through analysis of aerial photographs. Black-capped Chickadees also occur in this area and regularly use these habitats for nesting and foraging. The habitat consisted of mature boreal forest patches ranging from 1.7 km<sup>2</sup> in size to smaller, narrow belts of 0.35 km<sup>2</sup>, and isolated boreal islands that were only 0.1 km<sup>2</sup> in size within a maple-yellow birch (*Acer* spp.-*Betula alleghaniensis*) matrix. All boreal forest patches were close to the Peshekee River or to Baraga Creek, often forming narrow bands of boreal habitat along streams. Tree species in the boreal patches in decreasing order of estimated dominance were: black spruce, white spruce (*Picea glauca*), tamarack (*Larix laricina*), balsam fir (*Abies balsamea*), white birch (*Betula papyrifera*), white pine (*Pinus strobus*), red maple (*Acer rubrum*), quaking aspen (*Populus tremuloides*), white cedar (*Thuja occidentalis*), and jack pine (*Pinus banksiana*).

*Data Collection.*—Observers systematically searched the study sites for chickadee flocks on 6 days between 24 January and 13 March 2011. Flock size, species composition, general flock

location, and time of observation were recorded once a flock with chickadees was located. Individual observers focused on one individual chickadee of either species for as long as possible (but <10 min) for each flock. The tree species in which a bird was foraging and estimated height of tree were recorded. Observers visually divided each tree used for foraging into zones by estimating 3-m vertical areas (e.g., 21-m tree = 7 zones) that each contained three horizontal zones (basal, medial, distal) per 3-m vertical zone. Observers recorded the number of seconds using stop-watches that a focal chickadee foraged in different zones of the tree. Shifts to new zone positions and trees were recorded as discrete observations. Timing stopped when the focal chickadee stopped foraging. The number of foraging observations within zones was recorded per individual chickadee followed to ascertain each bird's contribution to the data set. Zones used to segregate chickadee foraging to a specific location within trees were numbered from tree crowns to the tree base following MacArthur (1958). Trees were numbered from the top so those of varying height could be compared on a zone-by-zone basis while retaining as much similarity in vegetation structure. Chickadees foraging in trees <10 m in height were not used in the data analysis.

*Statistical Analysis.*—We analyzed differences between Boreal and Black-capped chickadee foraging time in nine tree species where chickadees were observed foraging. Chickadee foraging time in each tree species was scaled to the total number of seconds chickadees were observed foraging by species throughout the study, and the total number of individuals observed. The number of individual chickadees observed per species was estimated from detailed records of flock locations. Totals were based on the maximum number of each species recorded each day plus addition of individuals recorded on subsequent days that were >8 km from previous observations.

Differences in foraging zone occupancy between Boreal and Black-capped chickadees within trees in each of 21 zones were evaluated (unpaired *t*-tests) with Bonferroni correction of the *alpha*-value to account for repeated tests (Cabin and Mitchell 2000). We calculated niche overlap between Boreal and Black-capped chickadees based on foraging zone data using EcoSim 7.0 (Gotelli and Entsminger 2001) to evaluate the likelihood of niche overlap. Each null model calculated niche overlap with different assumptions about the specialization of the species compared based on Pianka's index (Pianka

1974). The software generates upper and lower  $P$ -values based on the number of observed niche overlaps greater or less than the mean niche overlap generated by random simulations. Model RA2 relaxes niche breadth from observed niche overlap by assigning a random number for use, but retains the resource states where use was zero. Model RA3 retains the exact use in the original data, but reshuffles the distribution of zeros. We also analyzed foraging data using model RA4, which retains both the use and zero distributions as in the original data. Model RA4 reshuffles only the distribution of each use within cells. This model has the most stringent assumptions to satisfy and may cause Type II error (Gotelli and Entsminger 2001). We reanalyzed evidence for niche overlap by combining all horizontal zones using EcoSim to simulate niche overlap and eliminate arbitrary distinctions imposed by the zoning system.

## RESULTS

We observed chickadees on 6 days between 24 January and 13 March, totaling 60 hrs of field observation time. This amounted to 1,875 and 1,074 seconds of timing foraging of Boreal and Black-capped chickadee zone use, respectively. Foraging zone data were recorded for 24 Boreal and 37 Black-capped chickadees that were in 20 different flocks containing Black-capped Chickadees and 15 flocks containing Boreal Chickadees. This resulted in 72 (56.2%) Boreal and 56 (43.8%) Black-capped chickadee zone observations. Data were drawn from eight observations and 178 sec of individual chickadees within Boreal Chickadee flocks, 28 observations and 484 sec within Black-capped Chickadee flocks, and 92 observations and 2,293 sec within mixed flocks containing both species.

*Microhabitat Use.*—Boreal Chickadees foraged in only three conifer tree species with 76% of total foraging in black spruce. Black-capped Chickadees foraged widely across six conifer and three deciduous tree species. Boreal Chickadees spent 36.5% of the total observation time in the top vertical zone (zone 1) of trees when foraging, while Black-capped Chickadees spent only 4.5% of the observation time in this vertical zone (Table 1). There was no significant difference in foraging time between species in zone 1 when  $\alpha$  values were Bonferroni-corrected ( $P = 0.04$ ,  $\alpha = 0.0045$ ). Neither Black-capped (4.1% occupancy) nor Boreal (1.6% occupancy) chickadees spent much time in the zones nearest the ground (zones 5–6) (Table 1). Boreal and

Black-capped chickadee foraging time was similar in zone 2 ( $P = 0.19$ ) for 34.36 and 38.05% of total observation time, respectively, largely in the medial horizontal zone (2 medial). Foraging time was similar for both species in horizontal zones with Boreal Chickadees spending less time in the basal zone. Differences in foraging time between chickadee species were significant only in the medial portion of zone 1 ( $P = 0.0002$ ).

*Niche Breadth Analysis.*—The observed niche overlap was larger than expected (simulated) in all three models assessed (Table 2). The observed mean niche overlap was significantly greater than expected by chance and observed niche breadth was greater than simulated niche breadth in all trials when foraging occupancy was reanalyzed with broader zone use.

## DISCUSSION

Use of black spruce, white spruce, and tamarack (in decreasing order) suggests Boreal Chickadees may prefer the highest quality boreal habitats of the region (Evers 1991). This minimizes competition with Black-capped Chickadees which preferentially use the more common deciduous and mixed forests (Grubb and Bronson 2001, Foote et al. 2010). A more open branch structure and dispersed tree-spacing in deciduous forests appears to offer Boreal Chickadees less-desirable habitat. Few data exist on interspecific interactions between Boreal and Black-capped chickadees, but Black-capped Chickadees may be socially dominant to Boreal Chickadees in congeneric winter flocks and limit Boreal Chickadee foraging outside of high-density conifer regions.

Minimal differences in foraging microhabitat (1 of 21 zones) are shown in the medial region of dense foliage within the top 0 to 3 m of conifer crowns. The upper regions of spruce trees often contain the densest foliage, cone crop, and branch structure on the entire tree, which Black-capped Chickadees may be less able to exploit (Ficken et al. 1996). This small spatial area within conifer crowns may be the region where Boreal Chickadees have a competitive advantage. Boreal Chickadees in Alaska and Newfoundland, where their habitat is far more common, apparently forage in a wider range of tree heights, suggesting ecological release (Haftorn 1972, Vasallo and Rice 1982).

The null model analysis of Boreal and Black-capped chickadee zone use indicates high niche overlap (0.676), which is greater than the overlap predicted to occur by chance alone. Pianka (1974) and Glasser and Price (1988) provide explanations

TABLE 1. Boreal and Black-capped chickadee foraging time in 21 distinct vertical and horizontal zones corresponding to spatial foraging position in trees.

Percent time per zone							
Black-capped Chickadee				Boreal Chickadee			
Vertical zones	Basal	Medial	Terminal	Vertical zones	Basal	Medial	Terminal
1	2.42	0.74	1.30	1	0.80	16.44	19.26
2	1.77	28.65	7.63	2	5.50	22.20	6.67
3	10.88	6.51	13.30	3	1.49	12.97	0.27
4	2.51	20.19	0.00	4	0.00	11.21	1.60
5	0.00	0.00	0.37	5	0.00	0.27	1.33
6	2.79	0.93	0.00	6	0.00	0.00	0.00
7	0.00	0.00	0.00	7	0.00	0.00	0.00

why these species may have more overlap than predicted by chance: (1) Boreal and Black-capped chickadees use resources that are in sufficient abundance and each species can overlap spatially without competing, or (2) these two species are currently competing for food resources. Both species appear to have similar diets, foraging heavily (>50%) in winter for dormant caterpillars (heterocampids), pupae, and insect eggs (Bent 1946, Haftorn 1974, Oatman 1985, Smith 1991). Similar foraging strategies (Moreno 1990, Ficken et al. 1996), and the general microhabitat used for foraging support Boreal and Black-capped chickadees' apparent overlap in use of food resources in winter.

Higher niche overlap was found in our study than in that conducted on Boreal and Black-capped chickadee partitioning during summer (Vassallo and Rice 1982). This may indicate foraging behavior and extent of niche overlap varies seasonally.

We conclude niche overlap between Boreal and Black-capped chickadees as indicated by random models is likely high. However, the macroscale region within Black-capped Chickadee habitats where niche overlap occurs is small as indicated by: (1) Boreal Chickadees use of localized boreal

forest regions, and (2) foraging overlap with Black-capped Chickadees in only three conifer species. Boreal Chickadees used the dense medially-located foliage of conifer crowns significantly more than Black-capped Chickadees. This may indicate differential resource use, but further research is needed.

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TABLE 2. Observed versus expected mean niche overlap based on three null randomization algorithms which use Pianka's index. Lower and upper probabilities indicate the observed niche overlap is either less than or greater than expected by chance (in the null model), respectively.

Model	Mean niche overlap		Probability	
	Observed	Expected	Lower	Upper
RA2	0.676	0.617	0.719	0.281
RA3	0.676	0.306	0.978	0.022
RA4	0.676	0.379	0.964	0.036

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