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TEMPORAL VARIATION IN RESOURCE USE BY BLACK-THROATED GRAY WARBLERS[1]

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Abstract. We studied foraging behavior and habitat use of male and female Black-throated Gray Warblers (*Dendroica nigrescens*) to quantify the effects of temporal variation on interpretations of avian resource use. Overall, both sexes primarily foraged by gleaning in single-leaf pinyon pine (*Pinus monophyla*); however, within-season and between-year variation in behavior and habitat use were found for both sexes. Warblers increased use of shrubs from May to mid-June, and decreased use of shrubs and increased use of pinyon pine from mid-June through August, during each year. Use of sagebrush (*Artemisia tridentata*) and Utah juniper (*Juniper osteosperma*) varied between years. Sex differences were found in proportional use of foraging maneuvers. Within-season shifts in plant species and habitat use corresponded to changes in arthropod numbers on the plant species used by the warblers, but between-year shifts in behavior did not correspond as closely with changes in arthropod numbers. Temporal variation in microhabitat use resulted from shifts within seasons in the plant species used for foraging, which was associated with temporal changes in food abundance. Our results also demonstrate the importance of considering the effects of temporal scale in studies of bird-resource interactions.

Key words: Black-throated Gray Warbler, Dendroica nigrescens, *foraging behavior, habitat use, Neotropical migrant, resource use, temporal variation.*

INTRODUCTION

Data from studies of avian resource use have been used widely to describe the structure and composition of bird assemblages (MacArthur 1958, Holmes et al. 1979, Rotenberry 1985), and have been used in the development of species-habitat models designed for management applications (Verner et al. 1986). Wiens (1986), however, showed that interpretations of assemblage structure can be influenced by inherent temporal and spatial variation. Rice et al. (1986) and Rotenberry (1986) demonstrated that the accuracy and predictability of species-habitat models can vary depending upon the temporal and spatial scales over which they are developed and applied. Thus, temporal and spatial variation at various scales need to be described and considered because they can influence the results of ecological investigations and any subsequent management applications (O'Neill et al. 1986, Block and Brennan 1993).

Studies of avian resource use have demonstrated variation on daily (Hutto 1981b), intraseasonal (Sakai and Noon 1990), interseasonal (Hutto 1981a), and annual (Szaro et al. 1990) time scales as well as on local (Collins 1981) and regional (Wiens and Rotenberry 1981) spatial scales. Furthermore, variation can result from intersexual differences and factors such as age and reproductive status (Holmes 1986, Grubb and Woodrey 1990). Few researchers, however, have attempted to address the potentially interactive effects of between-sex, within-season, and between-year variation in resource use patterns on bird-centered habitat measurements (Kelly and Wood 1996).

The distribution and abundance of food is a primary factor affecting the resource use patterns of birds (Lack 1966, Martin 1987). For insectivorous birds, changes in arthropod distribution and abundance may correspond to changes in bird resource use patterns at different temporal and spatial scales. For example, Brush and Styles (1986) found that changes in bird abundance between pine- and oak-dominated vegetation types corresponded to changes in arthropod biomass. Similarly, seasonal variation in the sizes and species of trees used by bark foraging birds in western North American forests is associated with variation in prey distribution and abundance (Morrison et al. 1985, Lundquist and Manuwal 1990).

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Our objective was to study the resource use patterns of Black-throated Gray Warblers (*Dendroica nigrescens*) during the breeding season. We investigated within-season, between-year, and between-sex variation, and their interactions, in foraging behavior and the habitat characteristics of foraging sites. Additionally, we measured arthropod abundances on the plant species used by the warblers to determine whether variation in warbler foraging behavior and habitat relationships corresponded to changes in arthropod abundances.

METHODS

STUDY AREA

We worked from late April to August of 1989 and 1990 in the White and Inyo Mountains, Inyo County, California (37°50′N, 118°10′W). The White and Inyo Mountains range in elevation from 1,220 to 4,345 m and each forms half of a fault block extending approximately 170 km north to south (Nelson et al. 1991). Climate is typically one of cold, snowy winters and warm, dry summers with summer precipitation occurring from thunderstorms (Powell and Klieforth 1991).

All fieldwork was conducted in pinyon-juniper woodland between 1,970–2,875 m elevation. Woodland overstory was composed of singleleaf pinyon pine (*Pinus monophyla*) and Utah juniper (*Juniperus osteosperma*). Antelope bitterbrush (*Purshia tridentata*) and big sagebrush (*Artemisia tridentata*) were the dominant components of the understory. Other shrubs present with localized distributions included Parry rabbitbrush (*Chrysothamnus parryi*) and cliffrose (*Cowania mexicana*). The herbaceous layer was poorly developed and consisted of grasses and forbs including eriogonum (*Eriogonum* spp.) and penstemon (*Penstemon* spp.). Spira (1991) provides further descriptions of plant assemblages in the White and Inyo Mountains.

ACTIVITY BUDGETS

Data collection. We sampled activity behaviors of Black-throated Gray Warblers within a 100-m band on either side of 10 transect lines. Transect lines were 4.2 km long, about 0.5 km apart, and located to span the elevational distribution of the pinyon-juniper woodland (see Morrison et al. 1993 for further details). Four observers collected data during the study. All observers were trained to standardize data collection. Observers moved along transect lines to avoid repeated observations of the same bird. When a warbler was detected, the observer watched the bird for 5 sec without recording data. This period was used to minimize bias to the most conspicuous activities. The observer then recorded all activities and locations where the activities occurred over the next 15 sec. Only observations where the bird was in full view for the 15 sec were included for analysis. Variables recorded were: sex of the bird, time of day, plant species where the activities occurred, height of the bird, frequency of use of foraging maneuvers (glean, hover-glean [= sally-hover], flycatch [= sally-strike to aerial prey], flush-chase [= flutter-chase], fly-glean [= sally-strike at stationary substrate], probe, peck, as described by Remsen and Robinson 1990), and substrate where each activity occurred (foliage, twig [< 1 cm diam.], small branch [1–10 cm diam.], medium branch [11–30 cm diam.], large branch [> 30 cm diam.], trunk, air, ground, and flower). All measurements were visually estimated. All foraging locations were flagged for later habitat analysis.

Data analysis. We split the data for each year into two periods for analysis. Early summer was defined as occurring from late April to 10 June, and late summer as 11 June to late August. We justified this cut-point date biologically because it corresponded with observed plant phenological patterns. Bitterbrush flowered primarily from late April through mid-June. These periods also broadly overlapped with changes in warbler breeding phenology (Keane, unpubl. data). Nest building was observed in late May and nests with eggs were located from late May through mid-June. Nests with young were found from mid-June through early July. Thus early summer broadly overlapped with the territory establishment, nest building, and incubation phases of the nesting cycle, and late summer broadly overlapped with the nestling, fledgling, and post-breeding phases, although overlap undoubtedly occurred as a result of renesting attempts.

The raw data for plant species use for each foraging observation was transformed from a discrete to a continuous variable by calculating the corresponding number of observation seconds for each plant species per 15-sec sample (Brennan and Morrison 1990). This resulted in a value of percent time use for each variable. We used a multivariate analyses of variance (MANOVA; Green 1978) to investigate the effects of year, period, and sex on plant species use by Black-throated Gray Warblers. Multicollinearity between variables was reduced by eliminating one of a pair of variables with a product moment correlation > 0.70 (Sokal and Rohlf 1981). The variable retained was the one with the higher F-value in the analysis (Morrison et al. 1987). Variables in MANOVA testing of plant species use were percent time use of pinyon, juniper, bitterbrush, and sagebrush. Use of other plant species was ≤ 1% for either sex in any period and therefore was discarded from the analysis. Variables were transformed using the square-root arcsine transformation for percentage data to better satisfy the assumption of normality, although univariate normality does not infer multivariate normality. Box's M statistic was used to test the assumption of homogeneity of variance-covariance matrices (Green 1978). Although the ramifications of failing to meet this assumption are poorly understood, apparently they are of far less concern than performing the analysis with inadequate sample sizes (Williams and Titus 1988).

We used nonparametric log-linear analyses to examine the effects of year, period, and sex on the use of foraging maneuvers and substrate use separately (Bishop et al. 1975). The initial maneuver and the substrate at which it was directed for each individual observation were used in the analyses (Bell et al. 1990). Because expected values within cells should be > 1 and no more than 20% of the cells should have expected values < 5 (Cochran 1954), it was necessary to pool infrequently used maneuvers and substrates. This resulted in three categories for foraging maneuvers (glean, hover-glean, aerial). Aerial included flycatch (54% of pooled category), flush-chase (26%), and other (20%). Three categories also were used for substrates (foliage, air, other). The "other" category included twigs and branches (41% of pooled category), flowers (26%), terminal buds (19%), and other substrates (14%). We used step-wise procedures to remove interaction terms not significantly different from zero and selected the simplest models that best fit the data ($P > 0.05$).

MICROHABITAT USE

Data collection. We measured habitat variables at 50 randomly chosen activity locations per sex per period per year for a total of 400 habitat plots. The activity location of the bird served as the center of a 15-m radius plot. Within each plot we counted the number of pinyon and juniper trees within three height classes (1.5–3 m, > 3–6 m, > 6 m). We established a 30-m line transect bisecting the plot along a random compass bearing. We measured the presence of pinyon, juniper, bitterbrush, and sagebrush in four height classes (< 1 m, 1.1–3 m, 3.1–6 m, > 6 m) along a vertical line at 1-m intervals along the transect line. These data were used to calculate a measure of percent cover of bitterbrush and sagebrush and to develop pinyon and juniper foliage indices. Foliage indices were defined as the total number of height classes that contained pinyon or juniper foliage. At 5-m intervals along the transect line, for a total of 6 points per transect, we used a meter stick and measured the height and crown diameter to the nearest 0.1 m of the nearest bitterbrush and sagebrush along the compass bearing of the transect line.

Data analysis. We used a MANOVA to investigate year, period, and sex effects on the series of habitat variables, as described above for foraging data.

ARTHROPOD ABUNDANCES

Data collection. Sampling the arthropods available to birds is not a trivial problem (Smith and Rotenberry 1990). It is difficult to determine precisely from which spectrum of the available arthropods a bird is selecting prey (Hutto 1990). Furthermore, each arthropod sampling method is biased toward that spectrum of the arthropod assemblage it effectively samples (Cooper and Whitmore 1990). Because Black-throated Gray Warblers have been described as foliage gleaners (Grinnell and Miller 1944), we used branch-clipping to provide a measure of relative arthropod abundances in the primary locations and on the plant species used by foraging warblers (Cooper and Whitmore 1990). However, not all food items used by the warblers were adequately sampled using this technique.

We sampled arthropods over a 2-day period at approximately 2–3 week intervals throughout the breeding period to provide measures of relative changes in abundance on the primary plant species used by the warblers across time. Each day was divided into morning (06:00–11:00) and afternoon (14:00–19:00) sampling periods. We sampled 25 each of pinyon and juniper in the morning and 30 each of bitterbrush and sagebrush in the afternoon of the first day. This procedure was repeated on the second day in reverse order (i.e., shrubs in morning and trees in afternoon) to account for within-day variation in arthropod numbers between plant species.

We sampled plants beginning from a randomly selected sampling point along a randomly selected transect line. At five sample points located at 75-m intervals along the chosen transect line, we sampled five each of pinyon and juniper trees or six each of bitterbrush and sagebrush. We chose the closest five trees or six shrubs of each species > 10 m from the center of the sampling point by selecting the first tree or shrub closest to a compass bearing due north and sampling subsequent trees or shrubs located at approximately 60–70° angles in a circle around the sampling point. We collected four samples from each tree at approximately 2 m in height in the four cardinal compass directions. We placed a wire-rimmed, canvas insect net over approximately 0.5 m of terminal foliage and clipped the branch into the net. Branches were vigorously shaken to dislodge arthropods, which were collected in a plastic cup in the bottom of the net. The cup was then quickly sealed, the branch placed in a plastic bag, and both labeled. Shrubs were sampled in a similar fashion along six points located at 75-m intervals. Only one clipping was collected per shrub. Arthropod samples were frozen at the end of each day and branch clippings were weighed to the nearest 0.5 g. Arthropod samples were subsequently sorted and all arthropods picked out.

Data analysis. We used a series of ANOVA (Sokal and Rohlf 1981) to investigate the effect of date on the number of arthropods per 100 g of foliage for each of the plant species in each of the years. The four samples from each tree were averaged to provide a single measure for that individual tree. Data were transformed with the log(x + 1) transformation to better satisfy the assumptions of normality and homogeneity of variances, as measured by visual inspection of residual plots and Cochran's C, respectively. Significant differences ($P < 0.05$) between the number of arthropods within each year and on each plant species were determined by multiple comparisons using Scheffe's test (SPSS 1986).

RESULTS

ACTIVITY BUDGETS

Plant species use. Warbler use of plant species differed between periods ($F_{1,897} = 14.83$, $P < 0.001$, MANOVA) and years ($F_{1,897} = 7.42$, $P < 0.001$), and between periods within years ($F_{1,897} = 7.45$, $P < 0.001$). Overall, warblers primarily used pinyon pine in all years and periods, with use varying between 62.5% and 88.9% (Table 1). Use of pinyon was greater in late summer of each year ($F_{1,897} = 30.36$, $P < 0.001$, ANOVA) and differed between periods between years ($F_{1,897} = 6.39$, $P < 0.01$). Use of bitterbrush was greater in early summer of each year ($F_{1,897} = 16.64$, $P < 0.001$), ranging from 6.3% to 14.8% in early summer versus 0.7% to 4.6% in late summer. Use of sagebrush was greater in early summer of each year ($F_{1,897} = 36.97$, $P < 0.001$), greater in 1990 ($F_{1,897} = 23.03$, $P < 0.001$), and differed between periods between years ($F_{1,897} = 23.45$, $P < 0.001$), ranging from 2.3% to 22.6% in early summer versus 0% to 2.0% in late summer. Use of juniper was greater in 1989 versus 1990 ($F_{1,897} = 7.03$, $P < 0.01$, Table 1). Box's M was significant ($P < 0.001$).

Foraging maneuvers. Stepwise log-linear analysis indicated that the best model for warbler use of foraging maneuvers included the period-by-maneuver interaction, and the year and sex main effects ($\chi^2_{16} = 14.95$, $P = 0.53$). Gleaning was the most frequently used foraging maneuver by each sex, ranging from 61% to 80.6% for males and 68.6% to 78.8% for females between periods and years (Table 1). Hover-gleaning was the second most frequently used foraging maneuver by both sexes in all years and periods except for females during period 2 of 1989. Use of hover-gleaning ranged from 12.0% to 20.4% for males and 8.1% to 23.5% for females between periods and years. Use of aerial maneuvers increased in late summer versus early summer of each year for both sexes and ranged from 7.4% to 18.6% for males and 6.1% to 19.4% for females between periods and years. Both sexes decreased use of gleaning in late summer of each year versus early summer. Males increased use of both hover-gleaning and aerial maneuvers in late summer versus early summer of each year. Females use of hover-gleaning was lower and use of aerial maneuvers higher in late summer versus early summer during 1989, whereas in 1990 females use of hover-gleaning was higher and use of aerial maneuvers was approximately equal in proportion in late summer versus early summer (Table 1).

Substrate use. Stepwise log-linear analysis indicated that the best model included the year-by-

TABLE 1. Percent use of plant species, foraging maneuvers, and substrates by Black-throated Gray Warblers in the White and Inyo Mountains, California, during 1989 and 1990.[a]

	1989				1990			
	Early summer		Late summer		Early summer		Late summer	
	male	female	male	female	male	female	male	female
Plant species use								
bitterbrush	6.4	9.8	4.4	4.6	6.3	14.8	0.7	2.2
sagebrush	2.3	4.0	1.4	0.8	22.6	14.0	0.0	2.0
pinyon	76.1	68.2	84.0	77.5	63.4	62.5	88.9	83.1
juniper	15.2	17.6	10.2	16.8	7.5	7.7	10.2	12.3
other	0.0	0.4	0.0	0.3	0.2	1.0	0.2	0.4
Foraging maneuver use								
glean	78.0	75.6	66.0	72.6	80.6	78.8	61.0	68.7
hover-glean	13.6	17.1	19.6	8.1	12.0	15.2	20.4	23.5
aerial	8.5	7.3	14.4	19.4	7.4	6.1	18.6	7.8
Substrate use								
foliage	78.0	71.1	74.5	81.3	77.8	69.7	88.1	90.4
air	5.9	4.8	9.2	14.1	4.6	4.6	1.0	1.9
other	16.1	24.1	16.3	4.6	17.6	25.7	10.9	7.7

[a] Sample sizes: 1989—early summer male = 181, female = 118; 1989—late summer male = 131, female = 78; 1990—early summer male = 162, female = 94; 1990—late summer male = 77, female = 64.

period-by-substrate and the period-by-sex-by-substrate interactions ($\chi^2_6 = 4.24$, $P = 0.64$), indicating complex patterns of substrate use by warblers. However, overall warblers used foliage most frequently in all periods, ranging from 69.7% to 90.4% between periods and years (Table 1). Both sexes use of air was higher in late summer compared to early summer in 1989, whereas the opposite pattern occurred in 1990. Males in 1990 and females in both years used "other" substrates less in late summer (Table 1). This in part was due to warbler use of bitterbrush flowers or terminal buds in early summer that were either not available (flowers) or infrequently used (terminal buds) during late summer (Keane 1991). "Other" substrates used in late summer were primarily twigs and branches (Keane 1991).

MICROHABITAT USE

Microhabitat used by warblers differed between periods ($F_{1,392} = 6.96$, $P < 0.001$, MANOVA) and years ($F_{1,392} = 2.64$, $P < 0.01$), and between periods between years ($F_{1,392} = 2.99$, $P < 0.01$). Overall, warbler microhabitat was characterized by a greater shrub component in early summer relative to late summer and a greater tree component in late summer relative to early summer of each year. Warbler microhabitat had significantly greater percent cover of sagebrush ($F_{1,392} = 10.11$, $P < 0.01$, ANOVA) and number of pinyon trees in the > 6-m height class ($F_{1,392} = 2.50$, $P = 0.03$) in 1990 versus 1989. Warbler microhabitat had greater bitterbrush crown diameter ($F_{1,392} = 19.29$, $P < 0.001$) and percent cover sagebrush ($F_{1,392} = 9.57$, $P < 0.01$), and lower numbers of pinyon trees in the > 6-m height class ($F_{1,392} = 21.16$, $P < 0.001$), pinyon foliage index ($F_{1,392} = 23.44$, $P < 0.001$), juniper foliage index ($F_{1,392} = 7.02$, $P < 0.01$), and number of juniper trees in the < 3-m height class ($F_{1,392} = 4.45$, $P = 0.04$) in early summer versus late summer. Microhabitat differed between periods between years in bitterbrush crown diameter ($F_{1,392} = 7.51$, $P < 0.001$), pinyon foliage index ($F_{1,392} = 19.93$, $P < 0.001$), and the number of pinyon trees in the > 6-m height class ($F_{1,392} = 9.05$, $P < 0.01$). Box's M was significant ($P < 0.001$). Further details can be found in Keane (1991).

ARTHROPOD ABUNDANCES

The number of arthropods differed significantly between sampling intervals on bitterbrush ($F_{4,1109} = 20.11$, $P < 0.001$), sagebrush ($F_{4,1109} = 12.63$, $P < 0.001$), pinyon ($F_{4,1109} = 32.61$, $P < 0.001$), and juniper ($F_{4,1109} = 10.61$, $P < 0.001$) in 1989. Similarly, arthropod numbers differed between sampling periods on bitterbrush ($F_{7,1759} = 8.98$, $P < 0.001$), sagebrush ($F_{7,1759} = 3.23$, $P < 0.01$), pinyon ($F_{7,1759} = 9.73$, $P < 0.001$), and juniper ($F_{7,1759} = 6.22$, $P <$

TABLE 2. Arthropods (number/100 g of foliage) sampled on plant species in the White and Inyo Mountains, California, during 1989 and 1990. Values are means ± SD.[a]

	Plant species			
	Bitterbush	Sagebrush	Pinyon	Juniper
1989				
18–19 May	8.3 ± 0.9A	18.8 ± 2.9A	0.6 ± 0.2A	0.4 ± 0.1A
9–10 June	5.4 ± 0.7AB	22.5 ± 4.0A	0.6 ± 0.1A	0.5 ± 0.1A
1–2 July	2.2 ± 0.3C	5.4 ± 1.2B	1.3 ± 0.1B	0.6 ± 0.1AB
18–19 July	2.9 ± 0.3BC	4.5 ± 0.7B	4.2 ± 0.6C	1.0 ± 0.1C
15–16 August	1.7 ± 0.3C	2.7 ± 0.4B	1.0 ± 0.1AB	0.8 ± 0.1BC
1990				
24–25 April	1.2 ± 0.2A	3.6 ± 0.6AB	0.2 ± 0.1A	0.3 ± 0.1A
16–17 May	5.8 ± 0.2D	3.4 ± 0.5ABC	0.5 ± 0.1AB	0.4 ± 0.1AB
30–31 May	11.1 ± 1.4E	10.6 ± 1.6EF	0.9 ± 0.2BC	0.6 ± 0.1B
14–15 June	2.7 ± 0.3ABCD	11.7 ± 2.1DEF	0.8 ± 0.1BC	0.6 ± 0.1B
1–2 July	3.3 ± 0.4BCD	13.0 ± 3.4F	1.0 ± 0.1BCD	0.5 ± 0.1AB
15–16 July	3.7 ± 0.6CD	6.2 ± 0.8CDEF	1.2 ± 0.2CD	0.4 ± 0.1AB
6–7 August	2.7 ± 0.3ABCD	4.2 ± 0.5BCD	1.4 ± 0.2DE	0.5 ± 0.1AB
20–21 August	3.3 ± 0.4BCD	1.2 ± 0.2A	1.7 ± 0.1E	0.5 ± 0.1B

[a] Within each plant species and year, values with the same letter are not significantly different ($P < 0.05$).

0.001) in 1990. Arthropod numbers on bitterbrush were greatest during May and early June of both years (Table 2). Arthropod numbers were greatest on sagebrush in May and June of each year. Arthropod numbers on pinyon increased over the sampling period in both years. The large increase in the sample for 19 July 1989 was due to a large number of hemipteran nymphs (Keane 1991). Arthropod numbers on juniper increased in July and August of 1989 but remained fairly constant throughout the season in 1990. Sagebrush always had higher arthropod numbers than pinyon or juniper, and usually had substantially higher numbers than bitterbrush. In 1990, although numbers on sagebrush were lower than in May and early June 1989, they were still about 70% higher than bitterbrush (vs. 300% higher in 1989).

DISCUSSION

Our results show within and between season variation in foraging behavior and habitat use patterns by Black-throated Gray Warblers. Greater use of shrubs in early summer of each year corresponded with greater relative abundances of arthropods on both bitterbrush and sagebrush during the early part of the breeding season. The greater number of arthropods on bitterbrush was associated with its early season flowering phenology. Although sagebrush did not flower until late summer-early fall, arthropod numbers also were greater during the early part of the breeding season. Greater use of pinyon in late summer of each year corresponded with both increases in the number of arthropods sampled on pinyon and declines in arthropod numbers on bitterbrush and sagebrush.

The patterns in plant species use and at least some substrate use (e.g., use of flowers in early summer) observed in our study are similar to results from other studies of within-season variation in resource use by birds that have demonstrated variation associated with changes in plant phenology and/or prey availability (Root 1967, Hejl and Verner 1990, Miles 1990). For example, Hejl and Verner (1990) reported that both Bushtits (*Psaltriparus minimus*) and Oak Titmice (*Baeolophus inornatus*) used buckbrush (*Ceanothus cuneatus*) more frequently during March and increased use of blue oak (*Quercus douglasii*) during April in a California oak woodland. Increased use of buckbrush corresponded to its flowering phenology and both species of bird increased use of flowers as foraging substrates, whereas increased use of blue oak corresponded to its leafing out period. Similarly, Root (1967) demonstrated that seasonal changes in Blue-gray Gnatcatcher (*Polioptila caerula*) foraging behavior and prey availability were associated with changes in plant phenology.

Annual shifts in the relative use of plant species did not correspond as closely to changes in arthropod numbers as did the within-season shifts. Greater use of juniper in 1989 versus 1990 corresponded with higher arthropod numbers during July and August of 1989 versus 1990. However, arthropod numbers on sagebrush were lower during May through mid-June in 1990 versus 1989, although warblers used sagebrush more during this period in 1990 versus 1989. Sagebrush had the highest numbers of arthropods during most sampling periods, and these numbers were substantially higher in 1989 than 1990. Use of sagebrush by the birds was, however, higher during 1990, although use averaged only about 8% higher for males and females combined (Keane 1991). Correspondingly, warbler microhabitat had greater percent cover of sagebrush in 1990. Because sagebrush and bitterbrush are interspersed throughout the pinyon-juniper region, and because sagebrush is more abundant than bitterbrush (Keane 1991), we think our annual results were mostly a reflection of relatively minor variations in plant species use by the birds, and likely small differences in our sampling locations along transects between years.

Male and female warblers did not differ in their proportional use of plant species, although they did differ in their relative use of foraging maneuvers and substrates. In addition, males had greater activity heights than females in early summer, although these differences were reduced in late summer (Keane 1991). Differences between the sexes may be a result of intersexual competition (Petit et al. 1990, Kelly and Woods 1996). However, males and females did not differ in plant species nor microhabitat use, predominantly foraged by gleaning, and had more similar activity heights in late summer, suggesting that the sex differences we found were generally consistent with the proposal that reproductive activities influence foraging and activity patterns of birds, rather than direct resource partitioning between sexes (Holmes 1986, Kelly and Woods 1996).

Black-throated Gray Warblers in our study area exhibited within-season and annual variation in plant species and substrate use. Black-throated Gray Warblers are distributed throughout a number of forest and woodland vegetation types in western North America (Bent 1938). Miles (1990) investigated monthly and annual variation in foraging behavior of breeding Black-throated Gray Warblers in Arizona oak woodlands and reported significant monthly variation in substrate use, but no monthly nor annual differences in use of plant species and foraging maneuvers. Warblers gleaned ≥ 90% of the time during each month of both years of the study (Miles 1990). Morrison (1982) also reported that male (82%) and female (88.2%) Black-throated Gray Warblers foraged predominately by gleaning throughout the breeding season in oak-conifer forests in Oregon. Gleaning also was the predominant foraging maneuver used by warblers in the pinyon-juniper woodland within our study area, although we found significant within-season, annual, and intersexual variation in the proportion of maneuvers used. Miles (1990) observed that although use of plant species did not differ between months or years, use of substrates varied monthly, with warblers using leaves relatively more early in the breeding season and twigs and small branches more frequently later in the breeding season.

Black-throated Gray Warblers are able to exploit a number of vegetation types throughout western North America. Holmes and Schultz (1988) proposed that food availability for forest birds is a function of: (1) the types and abundances of prey present, which varies among plant species, (2) the foliage structure and characteristics of the plants, which influence prey detectability and accessibility, and (3) the morphological and behavioral abilities of a species to perceive and capture those prey. Although Black-throated Gray Warblers forage predominately by gleaning from foliage in a number of these vegetation types, our results indicate that they can exhibit significant temporal variation in foraging behaviors. Furthermore, the specific behaviors that vary and the magnitude of these differences differ between vegetation types. These observations suggest that this species is morphologically and behaviorally adapted to exploit a number of forest and woodland vegetation types and that differences in foraging behaviors between vegetation types is a result of unique responses to the particular vegetation structure and prey availability specific to each vegetation type (Holmes and Schultz 1988).

We propose that temporal variation in foraging behavior and microhabitat use by Black-throated Gray Warblers in our study resulted from shifts within seasons in the plant species used for foraging, which in turn was associated with temporal changes in food abundance. These results indicate that intraseasonal, interseasonal, and sexual differences in resource use can be significant sources of variation in studies of bird foraging behavior and habitat use. Thus, future studies should address sources of temporal variation in order to improve understanding of avian foraging behavior and habitat relationships.

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