

THE IMPORTANCE AND CONSEQUENCES OF TEMPORAL VARIATION IN AVIAN FORAGING BEHAVIOR

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Abstract. Monthly and yearly differences in foraging technique, substrate use, and tree species use were examined for three bird species from desert scrub and oak woodland habitats of southeastern Arizona from 1981 to 1983; all species displayed significant variation. Birds in desert scrub showed a strong temporal variation in their foraging behaviors, whereas species from the oak woodland appeared to be relatively temporally invariant. The strongest shifts in behavior appeared to be for choice of foraging site within a plant (substrate) and the differential use of particular plants within a season. Such variation within a season and among years suggests that caution is necessary in drawing inferences about species interactions, community organization, and resource partitioning that are based on data from a single year or data pooled over several years.

Key Words: Foraging behavior; temporal variation; seasonality; yearly variation; desert scrub; oak woodland.

Recent insights into community processes, whether determined directly by dietary variation or indirectly by differences in foraging behaviors, are commonly derived from single sample surveys or a pooled sample from long term studies (e.g., Holmes et al. 1979b; Alatalo 1982; Robinson and Holmes 1982, 1984; Airola and Barrett 1985; Holmes and Recher 1986a). Unfortunately, few studies have examined temporal variation in avian foraging behavior (Ulfstrand 1976, 1977; Smith et al. 1978; Alatalo 1980; Saether 1982; Morrison and With 1987), so that its importance has been uncertain. Furthermore, few data are available regarding the changes in community parameters (e.g., niche overlap and niche breadth) as a consequence of variation in foraging behavior within and among years as well as among seasons. The presence of seasonal or yearly variation may have a significant effect on the confidence we place in the estimates of habitat use, niche breadth and overlap, and consequently on the subsequent inferences drawn about species interactions.

In this study, I examined temporal variation in foraging behaviors of foliage-gleaning passerine birds from two habitats during three breeding seasons. Several questions are pertinent to quantifying avian foraging behavior and to more general problems in avian ecology. First, at what level are temporal fluctuations likely to be detected? Second, are there habitat-related differences in the seasonal patterns of resource use? As a corollary, are these patterns related to fluctuations in abiotic environmental factors that birds use as proximate cues? Third, are temporal fluctuations in foraging behaviors more prominent in particular guilds? Fourth, which aspects of a bird's foraging repertoire are most likely to exhibit seasonal variation? That is, do birds alter

the locations that they forage rather than the particular feeding technique?

STUDY AREA AND METHODS

Study area. The foraging patterns of foliage-gleaning birds were studied at two locations in southeastern Arizona: Saguaro National Monument (Tucson Mountain Unit) and Madera Canyon, Santa Rita Mountains. Data were recorded during the breeding season (May–August) for 3 years (1981–1983). The vegetation of the former site consisted primarily of the scrub trees, ironwood (*Olneya tesota*), and foothill paloverde (*Cercidium microphyllum*) with a variety of cacti (principally the saguaro [*Carnegiea gigantea*] and several species of cholla [*Opuntia* spp.]) and bursage (*Ambrosia deltoidea*). The Madera Canyon site was characterized by open oak woodland, which contained an admixture of Mexican blue oak (*Quercus oblongifolia*), emory oak (*Q. emoryi*), Arizona white oak (*Q. arizonica*) and alligator juniper (*Juniperus deppeana*).

Bird observations. Three 1000-m-long transects were established in each locality; each had ten sampling stations spaced approximately 100 m apart. Observations were recorded throughout the morning until midday. The statistical analyses of foraging behavior data tend to exhibit serial dependencies among the observations (see Morrison 1984a; Hejl et al., this volume; Raphael, this volume). Therefore I employed the following sampling protocol. Upon sighting a foraging bird, I dropped the first foraging observation and recorded the second and subsequent observations every 15 s for 2 min. I visited each sampling station once per day and remained for 15–20 min to avoid repeated sampling of individuals. For every bird that was observed to capture or attack a prey item, I quantified foraging technique, substrates, and the plant species. I collected data for all passerine species and classified foraging behavior as glean, hover, probe, or hawk. I also recognized six foraging substrates: leaves, flowers and fruits, twigs, branches, trunks and ground, including litter. I analyzed seasonal shifts in only the most commonly used species of plant.

I compiled monthly and yearly estimates of the foraging repertoire of the species from each habitat. Following the recommendations of Morrison (1984) I retained only those bird species that had at least 40 observations/month/year. Three species from each habitat fulfilled this criterion: Verdin (*Auriparus flaviceps*), Cactus Wren (*Campylorhynchus brunneicapillus*) and Black-tailed Gnatcatcher (*Poliophtila melanura*) from the desert habitat; and Bridled Titmouse (*Parus wollweberi*), Bewick's Wren (*Thryomanes bewickii*), and Black-throated Gray Warbler (*Dendroica nigrescens*) from the oak woodland habitat.

Statistical analyses. The categorical behavior data were tabulated into frequencies for use in subsequent analyses. I determined whether species in the desert habitats exhibited significant temporal variation in their foraging behavior through a log-linear analysis of multiway contingency tables (Bishop et al. 1975; Fienberg 1977; Hejl and Verner, this volume). I tested for monthly and yearly heterogeneity in the use of each category of foraging variable. I used PROC CATMOD (SAS 1985) to calculate the main effects and interaction (month, year) terms for the models pertaining to each foraging variable.

Two foraging variables, technique and substrate, were crosstabulated and the month and year estimates of each category for all six bird species were used to calculate a similarity matrix. Out of a total of 24 possible combinations among the foraging categories, only 14 were used by the species. I estimated the similarity in foraging behavior between and within-species using the percent similarity coefficient:

$$PS_{ij} = 1 - 0.5 \sum |p_{ik} - p_{jk}|,$$

where p_{ij} represents the percent use of the j th foraging category for the i th species. The similarity matrix was used as a basis to cluster species using the unweighted pair group average (UPGMA) method. Because both habitats exhibited similar patterns of seasonality, I present the results from the oak woodland habitat.

I calculated estimates of niche overlap and breadth for each species. Niche breadth was estimated using the Shannon-Wiener index:

$$H' = - \sum p_i \ln p_i,$$

where p_i is the proportionate use of the i th category. The change in niche breadth between months and years was individually calculated for each foraging category. Estimates of the variance of H' were calculated using formulae given in Poole (1974:393). Niche overlap with other species combined was derived from the percent similarity index described above.

RESULTS

SEASONALITY OF DESERT HABITATS

Total yearly rainfall is bimodally distributed with the majority of precipitation occurring in late summer (Fig. 1). Two distinct seasons are evident: an early period of drought, lasting from late April through late June to early July, followed by the summer rains, which occur largely as convective thunderstorms. Their onset and amount is temporally and spatially variable. This

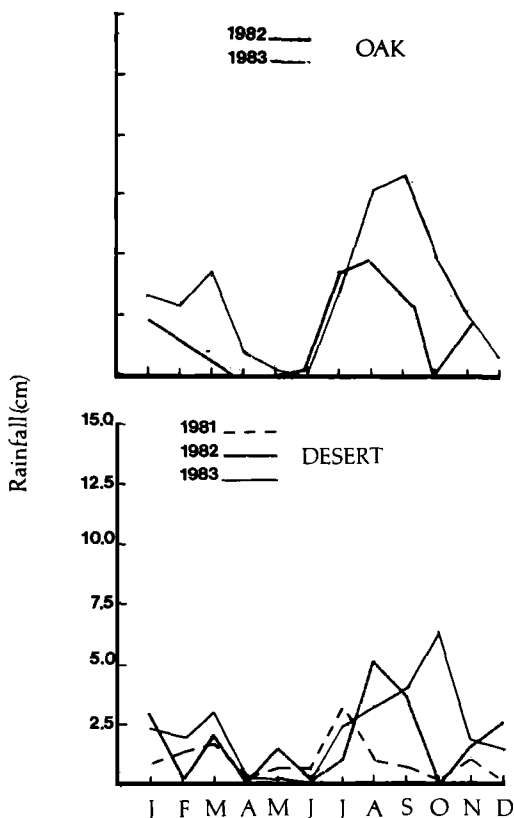


FIGURE 1. Yearly patterns of rainfall in two desert study sites. Data are from 1981–1983 for the desert scrub habitat, and 1982–1983 for the oak woodland habitat.

pattern of rainfall has a profound effect on the vegetation structure and resource base of each habitat. Several species of plants flower throughout the period of drought especially in the desert scrub habitat, where species such as ironwood, foothill paloverde, saguaro, and mesquite (*Prosopis juliflora*) produce flowers from late April through early June. Associated with this period of flowering is an increase in the abundance of arthropods.

After the summer rains begin there is a period of vegetative growth, which is mainly attributable to the emergence of annual plants, particularly grasses (Cable 1975; Maurer 1985b; Miles, unpubl. data). This is correlated with an increase in the number of arthropods, which is mainly manifested in a high density of lepidopteran larvae (pers. obs.). Thus, the foraging behaviors of birds in desert habitats, if tracking resource flushes, should vary between the drought and rainy seasons.

TABLE 1. SIGNIFICANCE OF LOG-LINEAR ANALYSIS OF SEASONAL VARIATION IN FORAGING TECHNIQUE, FORAGING SUBSTRATE AND PLANT SPECIES. DATA WERE ANALYZED FOR THREE SPECIES FROM THE DESERT SCRUB AND OAK WOODLAND STUDY LOCALITIES. FORAGING DATA FROM THE BREEDING SEASON FROM THREE YEARS, 1981, 1982 AND 1983, WERE ANALYZED

Species	Temporal component	Foraging*		
		Technique	Substrate	Plant species
Desert Scrub				
Black-tailed Gnatcatcher	Month	ns	P < 0.05	ns
	Year	ns	ns	ns
	Month × Year	ns	ns	ns
Cactus Wren	Month	P < 0.005	P < 0.03	P < 0.001
	Year	P < 0.02	P < 0.05	ns
	Month × Year	ns	ns	ns
Verdin	Month	P < 0.003	P < 0.001	P < 0.001
	Year	P < 0.001	P < 0.001	P < 0.001
	Month × Year	ns	ns	ns
Oak Woodland				
Black-throated Gray Warbler	Month	ns	P < 0.05	ns
	Year	ns	ns	ns
	Month × Year	ns	ns	ns
Bridled Titmouse	Month	ns	ns	P < 0.001
	Year	P < 0.01	ns	ns
	Month × Year	ns	ns	ns
Bewick's Wren	Month	ns	P < 0.05	ns
	Year	ns	ns	P < 0.01
	Month × Year	ns	ns	ns

* ns = not significant.

LOG-LINEAR ANALYSIS OF TEMPORAL VARIATION IN AVIAN FORAGING BEHAVIORS: TESTS OF MONTHLY AND YEARLY EFFECTS

The log-linear analysis of the variation in foraging behavior within a species between months and years and the interaction between month and year yielded heterogeneous results (Table 1). In spite of the divergence in temporal responses, several trends were evident. First, most of the temporal variation seemed attributable to monthly changes in the foraging repertoire. Second, the species rarely showed statistically significant patterns of variation among years in foraging, except for the Verdin and Cactus Wren. Both of these species were generalized in their foraging repertoire (Table 2). Species from the oak woodland habitat showed greater temporal heterogeneity in substrate choice and plant species preference rather than vary their foraging techniques (Table 1). The species showed a complex pattern of changing their choice of foraging substrate as the breeding season progressed as well as showing significant yearly variation in substrate and plant species use. Lastly, the species from the desert scrub habitat exhibited a far larger magnitude in their temporal shifts than the oak woodland species. This may be attributable

to the larger effect summer rains have on desert scrub vegetation than in the oak woodlands.

CLUSTER ANALYSIS OF AVIAN FORAGING BEHAVIORS

I present the results for the oak woodland species, although a similar pattern was found for the desert scrub species. Four clusters are apparent from the dendrogram (Fig. 2). The first cluster consisted of observations on the Black-throated Gray Warbler and Bridled Titmouse, mainly during May and June, the period of low rainfall. At this time the birds foraged primarily by gleaning leaves (Table 3). A second cluster includes the same species, but the samples were taken in July–August, after the beginning of the summer rains. At this time the birds spent more time gleaning from small and large twigs (Table 4). The third and fourth clusters describe monthly variation in Bewick's Wren, which presumably reflects a response to changes in the vegetation related to rainfall. The former cluster represents the foraging behavior of the wren during the early summer (May and June) and the latter represents the late summer (July). This species foraged in the lower strata of the vegetation and often would glean or probe at leaves on the ground (Tables

TABLE 2. CHANGES IN THE PROPORTION OF FORAGING TECHNIQUES EMPLOYED BY BIRDS OF THE DESERT HABITAT SITE BY MONTH IN 1981, 1982, AND 1983

Technique	1981			1982			1983		
	June	July	August	May	June	July	May	June	July
Black-tailed Gnatcatcher									
Hawk	0.0	2.0	2.7	1.5	0.0	0.0	3.7	0.0	0.0
Glean	86.7	91.8	83.8	87.9	95.8	98.1	81.5	80.0	88.9
Hover	0.0	2.0	8.1	6.1	4.2	0.0	14.8	10.0	11.1
Probe	0.0	2.0	2.7	3.0	0.0	0.0	0.0	0.0	0.0
Other	13.3	2.0	2.7	1.5	0.0	1.9	0.0	10.0	0.0
Cactus Wren									
Hawk	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Glean	100.0	38.7	17.9	41.2	20.8	25.4	35.0	14.3	13.3
Hover	0.0	0.0	7.1	0.0	0.0	0.0	0.0	0.0	0.0
Probe	0.0	48.4	53.6	47.1	79.2	73.0	65.0	85.7	86.7
Other	0.0	12.9	21.4	11.8	0.0	1.6	0.0	0.0	0.0
Verdin									
Hawk	0.0	0.9	0.0	0.6	0.0	0.0	0.0	0.0	0.0
Glean	93.8	96.4	97.7	96.2	73.0	68.0	95.4	88.5	97.9
Hover	0.0	2.7	0.0	1.9	0.0	0.4	0.9	1.6	2.1
Probe	6.3	0.0	2.3	0.6	27.0	30.2	3.7	9.8	0.0
Other	0.0	0.0	0.0	0.6	0.0	1.5	0.0	0.0	0.0

3, 4). Thus, it is likely that the Bewick's Wren would show a greater response to the flush of annual plants that follows the summer rains.

CONSEQUENCES OF TEMPORAL VARIATION IN FORAGING BEHAVIOR

Changes in niche breadth

As shown for the Black-tailed Gnatcatcher, the diversity of foraging techniques changes both between the dry and rainy seasons and between years (Fig. 3). Prior to the onset of summer rains the species displays a high niche breadth, utilizing a number of foraging maneuvers. During the rainy season the gnatcatcher tends to specialize on gleaning at foliage. For example, during 1981, which was characterized by a relatively dry summer, the range of foraging techniques increased during the latter part of the breeding season. However, the difference was not statistically significant. Estimates of niche breadth were not significantly different between years for the months of May or June. There were significant differences between years when comparing the niche breadth estimates for July (1981–1982, $t = 2.05$, $P < 0.05$, $df = 46$; 1982–1983, $t = 2.16$, $P < 0.05$, $df = 68$). Thus the gnatcatcher had a significantly narrower niche breadth during July 1982 than in either 1981 or 1983. This was also the driest July among the three years, suggesting that the gnatcatcher was specializing on gleaning maneuvers, mainly at leaves and fine substrates

(Table 2). A comparison of the estimates of niche breadth for each month during the 1982 breeding season showed that June and July significantly differed from May ($t = 2.24$, $P < 0.05$, $df = 77$; and $t = 2.87$, $P < 0.05$, $df = 91$). Estimates for June and July were not significantly different. There were no differences in the estimates of niche breadth between months for 1981 and 1983.

Similarly, the range of substrates used within a season and between years was characterized by a certain amount of variation (Fig. 4). In 1981 and 1982 the gnatcatcher showed a decrease in the breadth of substrates used over the course of the breeding season. Yet in 1983, which was characterized by the lowest amount of rainfall through the drought months and a late arrival of the summer rains, the gnatcatcher exhibited a contraction of the number of substrates used and specialized on small twigs and leafy substrates entirely. This decrease in niche breadth was statistically significant only during June (1981–1983, $t = 2.06$, $P < 0.05$, $df = 23$; 1982–1983, $t = 2.38$, $P < 0.05$, $df = 33$). There were no significant differences between years for the May or July estimates of niche breadth. There were no differences among months within a year for 1981 and 1982. But significant differences among months were evident for 1983 (May–June, $t = 3.42$, $P < 0.05$, $df = 18$; June–July, $t = 2.83$, $P < 0.05$, $df = 41$; May–July, $P > 0.05$). Thus, only the 1983 estimates of niche breadth showed a

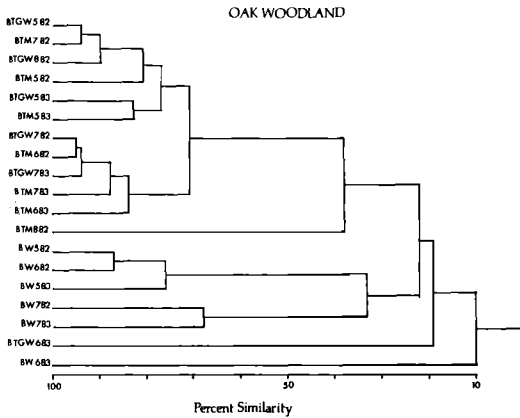


FIGURE 2. Average Linkage Cluster Analysis of the oak woodland species. The analysis was based on the percent similarity coefficient calculated from 14 cross-classified foraging categories. Species codes are BTGW = Black-throated Gray Warbler, BTM = Bridled Titmouse, and BW = Bewick's Wren. The numbers following each code represent the sample month and year: 5 82 = May 1982, 6 82 = June 1982, 7 82 = July 1982, 8 82 = August 1982, 5 83 = May 1983, 6 83 = June 1983, 7 83 = July 1983.

significant decrease within the breeding season suggesting an increase in specialization of substrate use.

Unlike the previous two variables, the temporal change in breadth of use of plant species exhibited a complex pattern (Fig. 5). In two of the years (1981 and 1982), gnatcatchers tended to specialize on a few plant species early in the breeding season, primarily foothill paloverde and ironwood. Later in the breeding season the gnatcatcher broadened the number of plant species it would search for food, primarily by searching saguaro cactus and white-thorn acacia. Comparing months within years supported this pattern and revealed several statistically significant differences for 1981 (June–August, $t = 1.98$, $P < 0.05$, $df = 48$) and 1982 (May–June, $t = 2.24$, $P < 0.05$; June–July, $t = 2.61$, $P < 0.05$, $df = 76$). The decrease between May and June during 1983, which was attributable to relatively high usage of foothill paloverde and ironwood, was not statistically significant. Furthermore, the change in niche breadth was not significant between years.

CHANGES IN NICHE OVERLAP

Mean overlap, which was calculated as the average overlap with each of the other species, fluctuated among months and between years (Fig. 6). Two trends were evident for all species. Low overlap values (i.e., dissimilar foraging behaviors) tended to occur during the dry summer

TABLE 3. CHANGES IN THE PROPORTION OF FORAGING TECHNIQUES EMPLOYED BY BIRDS OF THE OAK WOODLAND SITE BY MONTH IN 1982 AND 1983

Technique	1982			1983		
	May	June	July	May	June	July
Bewick's Wren						
Hawk	3.7	0.0	0.0	5.6	0.0	0.0
Glean	18.5	18.2	54.3	16.7	18.2	64.7
Hover	0.0	4.5	0.0	77.8	0.0	0.0
Probe	77.8	77.3	45.7	0.0	81.8	35.3
Other	0.0	0.0	0.0	0.0	0.0	0.0
Bridled Titmouse						
Hawk	0.0	0.0	0.0	0.0	0.0	0.0
Glean	93.8	92.9	76.4	100.0	82.2	79.2
Hover	4.2	3.6	0.0	0.0	2.2	16.7
Probe	2.1	3.6	0.6	0.0	15.6	4.2
Other	0.0	0.0	0.0	0.0	0.0	0.0
Black-throated Gray Warbler						
Hawk	0.0	0.0	0.0	0.0	0.0	3.7
Glean	95.7	90.9	100.0	89.5	100.0	92.6
Hover	4.3	9.1	0.0	5.3	0.0	3.7
Probe	0.0	0.0	0.0	0.0	0.0	0.0
Other	0.0	0.0	0.0	5.3	0.0	0.0

months and high overlap values in the wetter summer months. The two foliage-gleaning species—Black-tailed Gnatcatcher and Verdin—showed almost coincident patterns of niche overlap. On the other hand, the Cactus Wren was characterized by low overlap values; peak overlap occurred at the onset of summer rains, but low overlap values were found both in early summer and late summer.

DISCUSSION

I found significant differences in bird foraging behaviors between early and late summer months and among years. Several generalizations emerged from these results. First, the response to environmental fluctuations appeared to be greater in the desert scrub. This result follows the pattern found by Smith et al. (1978) for *Geospiza* finches in the Galapagos. Significant differences were found in the foraging behavior and diet of the finches between the wet season and dry season. Second, species in both habitats responded similarly to the environmental variation, mainly by moving to new foraging locations and plant species, rather than adjusting their foraging behaviors. The seasonal shifts in foraging behavior tended to be consistent among years. Third, the cluster analysis of foraging behaviors failed to reveal a strong within-species grouping, which is similar to the findings of Rotenberry (1980a). Thus, foliage-gleaning birds exhibited similar be-

TABLE 4. PERCENT USE OF THE 14 CROSS-TABULATED FORAGING CATEGORIES BY THE BIRDS OF THE OAK WOODLAND STUDY AREA. DATA ARE PRESENTED FOR THE BREEDING SEASON IN 1982 AND 1983. SPECIES CODES ARE: BTGW = BLACK-THROATED GRAY WARBLER, BTM = BRIDLED TITMOUSE, BW = BEWICK'S WREN. CODES FOR FORAGING CATEGORIES ARE: GLST = GLEAN AT SMALL TWIGS (5 CM < IN DIAMETER), GLBT = GLEAN AT BIG TWIGS (5 CM >), GLBR = GLEAN AT BRANCHES, GLTR = GLEAN AT TRUNK, GLGR = GLEAN AT GROUND, GLLF = GLEAN LEAVES, HVBR = HOVER AT BRANCH, HVLF = HOVER AT LEAVES, PRBT = PROBE BIG TWIGS, PRBR = PROBE BRANCH, PRTR = PROBE TRUNK, PRGR = PROBE GROUND, PRFDWD = PROBE FALLEN DEADWOOD.

Species	Hawk	Foraging category																
		GLST	GLBT	GLBR	GLTR	GLGR	GLLF	HVBR	HVLF	PRBT	PRBR	PRTR	PRGR	PRFDWD				
BTGW	5/82	0.0	13.0	4.3	0.0	0.0	0.0	0.0	0.0	0.0	73.9	0.0	4.3	0.0	0.0	0.0	0.0	0.0
	6/82	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	90.9	0.0	9.1	0.0	0.0	0.0	0.0	0.0
	7/82	0.0	20.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	80.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
BTM	5/82	0.0	0.0	0.0	0.0	4.2	0.0	0.0	0.0	0.0	89.6	0.0	4.2	0.0	2.1	0.0	0.0	0.0
	6/82	0.0	7.1	14.3	0.0	0.0	0.0	0.0	0.0	0.0	71.4	0.0	3.6	3.6	0.0	0.0	0.0	0.0
	7/82	0.6	15.9	4.0	0.0	2.3	0.0	0.0	0.0	0.0	76.7	0.0	0.0	0.6	0.0	0.0	0.0	0.0
	8/82	0.9	25.5	0.0	0.0	0.9	0.0	0.0	0.0	0.0	50.0	0.0	0.9	17.3	0.0	0.0	0.0	0.0
BW	5/82	0.0	0.0	18.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	33.3	33.3	3.7	3.4
	6/82	0.0	0.0	0.0	0.0	13.6	0.0	0.0	0.0	0.0	4.5	4.5	0.0	0.0	45.5	27.3	4.5	0.0
	7/82	0.0	2.9	2.9	5.7	11.4	5.7	25.7	0.0	0.0	5.7	0.0	0.0	2.9	28.6	5.7	8.6	0.0
BTGW	5/83	5.3	0.0	0.0	0.0	15.8	0.0	0.0	0.0	0.0	73.7	5.3	0.0	0.0	0.0	0.0	0.0	0.0
	6/83	0.0	0.0	0.0	0.0	85.7	0.0	0.0	0.0	0.0	14.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	7/83	3.7	0.0	11.1	0.0	0.0	0.0	3.7	0.0	0.0	77.8	0.0	3.7	0.0	0.0	0.0	0.0	0.0
BTM	5/83	0.0	11.1	0.0	0.0	22.3	0.0	0.0	0.0	0.0	66.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	6/83	0.0	2.2	20.0	0.0	8.9	0.0	0.0	0.0	0.0	51.1	0.0	2.2	0.0	15.6	0.0	0.0	0.0
	7/83	0.0	0.0	20.8	0.0	0.0	0.0	4.2	0.0	0.0	54.2	0.0	16.7	4.2	0.0	0.0	0.0	0.0
BW	5/83	5.6	0.0	0.0	5.6	11.1	5.6	0.0	0.0	0.0	0.0	0.0	0.0	5.6	27.8	38.9	0.0	5.6
	6/83	0.0	4.5	0.0	0.0	9.1	0.0	0.0	0.0	0.0	4.5	0.0	0.0	0.0	31.8	0.0	50.0	0.0
	7/83	0.0	0.0	5.9	0.0	5.9	0.0	47.1	0.0	0.0	5.9	0.0	0.0	0.0	23.5	5.9	0.0	0.0

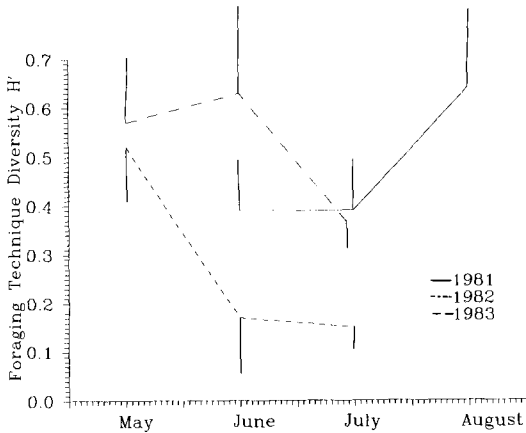


FIGURE 3. Temporal variation in the diversity of foraging techniques, as estimated by the Shannon-Wiener Diversity statistic (H'), by Black-tailed Gnatcatchers at the desert scrub locality in each month in 1981, 1982, and 1983. Vertical lines represent 1 SE.

haviors within a particular season, suggesting an opportunistic pattern of foraging behavior. The species that demonstrated the largest shifts in foraging behaviors also tended to be those that concentrated on exploiting leafy substrates (e.g., Black-throated Gray Warbler). Resident species showed more temporally flexible foraging repertoires, perhaps in response to the seasonal unpredictability of food resources and the spatial variation in availability of such resources. Yet, several studies have shown that migrants vary their foraging behaviors between the breeding and wintering sites (e.g., Greenberg 1987b). Re-

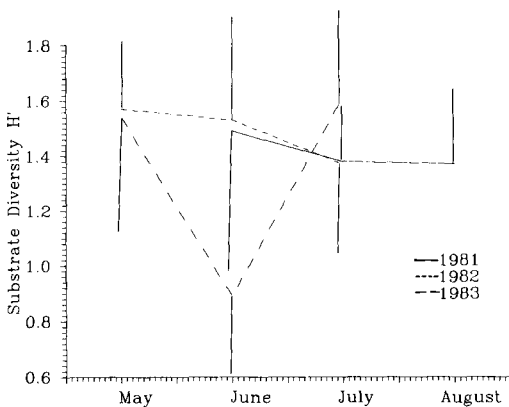


FIGURE 4. Changes in the range of foraging substrates as shown by variation in the Shannon-Wiener Diversity statistic (H') by Black-tailed Gnatcatchers during the breeding season in 1981, 1982, 1983. Vertical lines represent 1 SE.

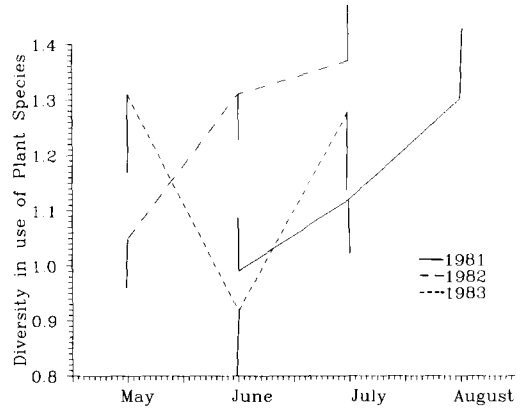


FIGURE 5. Monthly change in the diversity of plant species used by the Black-tailed Gnatcatcher in the breeding season in 1981, 1982, 1983. Vertical lines represent 1 SE.

gardless of these additional factors, this study demonstrated that temporal variation in avian foraging behaviors is a factor that should be incorporated in many community-level or guild analyses. Lastly, species whose foraging repertoire tends to be more flexible exhibit the strongest temporal effects. Species that are specialized in foraging behavior tend to vary in substrate choice or plant species preference rather than modify their search patterns or feeding techniques.

Evidence of temporal variation in foraging method or choice of foraging substrate has important consequences in the interpretation of resource exploitation patterns in terrestrial communities. Most studies determine levels of niche overlap among species or degree of generalization or specialization within species by exami-

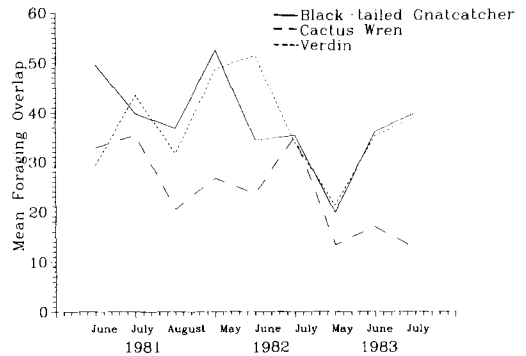


FIGURE 6. Change in niche overlap among three species of birds, Black-tailed Gnatcatcher, Cactus Wren, and Verdin, from the desert scrub in each of three months in three years, 1981, 1982, 1983.

nation of foraging data gathered over a number of seasons or years or both. As this study demonstrated, estimates of niche breadth and overlap are not temporally invariant. That is, these indices may not tend to some yearly average value. Therefore, the conclusions drawn by an investigator regarding intensity of competition or degree of resource specialization will vary depending on the season or even year. Depending on the date that foraging observations are collected on the desert species, the interpretations about species interaction would be quite different. Estimates of niche overlap calculated from June 1981 would suggest that the Verdin and gnatcatcher were not competing. Yet, if the overlap coefficients were calculated based on data from May 1982, the conclusion could be that the gnatcatcher and Verdin were competitors.

Several studies have demonstrated significant temporal variation in the foraging behaviors of birds. Alatalo (1980) found seasonal variation in foraging posture and tree species use in a number of foliage-gleaning species. Similarly, Ulfstrand (1976, 1977) demonstrated seasonal shifts in the manner in which species exploit the habitat in

coniferous forest species. Several other studies have shown that seasonal changes in foraging behavior of birds are common (Wagner 1981b; Hutto 1981b; Morrison and With 1987; Wiens et al. 1987b; Hejl and Verner, this volume; Szaro et al., this volume; Ford and Bell, this volume; Sakai and Noon, this volume). Thus, future studies of community organization, guild structure, and resource partitioning must incorporate a temporal component to their analyses. The use of seasonal or yearly estimates of niche breadth and overlap or patterns of resource partitioning may then reveal convincing evidence about factors structuring communities and affecting a species' use of a habitat.

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