

## AVIAN COMMUNITIES IN TEMPERATE AND TROPICAL ALDER FORESTS

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Patterns of bird species richness have been studied fairly extensively (Lack 1933, Gibb 1954, MacArthur and MacArthur 1961, Diamond and Terborgh 1967, Terborgh 1967, Balda 1969, Orians 1969, Cody 1970, Karr and Roth 1971, Pearson 1971, 1975, 1977, Lovejoy 1975). These patterns have been interpreted in terms of gradients of vegetation structural complexity, elevation, latitude, temporal predictability of resources and climatic severity. Some studies have dealt with temperate-tropical comparisons (MacArthur et al. 1966, Terborgh and Weske 1969, Karr 1971, Cody 1974), or with the concepts of latitudinal gradients (Pianka 1966), but no investigation has compared individual species' patterns of resource utilization in temperate and tropical communities. In this paper I investigate how bird community structure differs in response to different conditions of climatic predictability and degree of seasonality.

Predictability and availability of food are probably the two most important factors that affect the breadth of the feeding dimensions of a bird's niche. Unvarying (relatively constant over time), or at least predictable (values at a recent time enable accurate prediction of future values) weather provides conditions in which food resources for insectivorous birds are usually also predictable or invariable. Some measure of predictability and variability of the weather should, therefore, be a useful index of the relative niche breadths of different species in different places (Cody 1974, Lovejoy 1975). Temperate and tropical communities fall at different places along the continua of these two variables. Among places where weather conditions are the only variables, I expect more species to coexist as climate becomes more predictable and stable. Here, if productivity of the environment remains constant, the number of individuals per species should decrease as the average bird's feeding niche becomes narrower.

I chose two dimensions of a bird's feeding niche to compare temperate and tropical habits: (a) foraging height, and (b) foraging technique, a combination of the foraging guild (Root 1967) and the substrate where the food was found. With these in mind, I examined patterns of feeding of species breeding in temperate and tropical alder (*Alnus*) forests.

Measures of niche breadth along these dimensions were calculated using the Information Theory Index of diversity ( $-\sum p_i \ln p_i$ ).

### STUDY AREAS AND METHODS

I studied bird communities in mature forests of Red Alder (*Alnus rubra*) in Washington and *A. jorullensis* in Costa Rica. Forests of *rubra* occur at low to mid elevations from southern Alaska to central California along the Pacific coast of North America. Forests of *jorullensis* occur at mid-montane elevations in Central America and irregularly along the Andes as far south as northern Argentina.

Two plots of approximately 4 ha were each marked in Washington and in Costa Rica. Trails were cut through the plots to facilitate observation. The Washington study sites, (plots 4A and 4B in Stiles, in press; 1-3 are early successional stages of *A. rubra*) were at 122°07'W - 47°51'N, 5 km N Clearview, Snohomish Co., Washington, at an elevation of 155 m. The two Costa Rican plots (plots 5A and 5B) were at 83°40'W - 9°30'N, in the Cordillera Talamanca on the Pan American Highway (Costa Rica Highway 1), 8 and 12 km S Villa Mills, San Jose Province, at elevations of 2650 m and 2500 m, respectively.

Climatic data are available from Monroe, Washington (NOAA, Climatological Data) and Villa Mills, Costa Rica (Servicio Meteorológica 1962, 1963, 1968, Holdridge et al. 1971). Monroe has an elevation of 37 m and is approximately 8 km from the Washington study sites. If we assume a 0.5°C temperature change for each 100 m change in elevation, the temperature curve for the study sites shifts down 0.5°C. Villa Mills, Costa Rica is located at 3096 m; the study sites were lower at 2650 m and 2500 m. The average temperature change on the Pacific side of the Talamancas is about 6.2°C per 1000 m (Dohrenwend, unpubl. data) so that the average temperatures were approximately 2.8°C and 3.7°C higher in the study sites.

The vegetation at all plots was analyzed using the method described by MacArthur and Horn (1969). Foliage density was computed at five-foot (1.52 m) vertical intervals, and from these values foliage profiles of the four plots were drawn.

In censusing, I walked slowly along trails, stopping to observe birds. For each bird encountered I recorded the time, species of bird, age and sex if positively determinable, height above the ground, and foraging movements. Observations in Washington were made during two breeding seasons, May through August 1970 and March through August 1971. Observations in Costa Rica were made during June and July 1972. Over 3,000 foraging observations were made in Washington, and over 2,000 were made in Costa Rica.

### RESULTS

#### VEGETATION

In Costa Rica, as in Washington, the alder forests are second-growth associations that in-

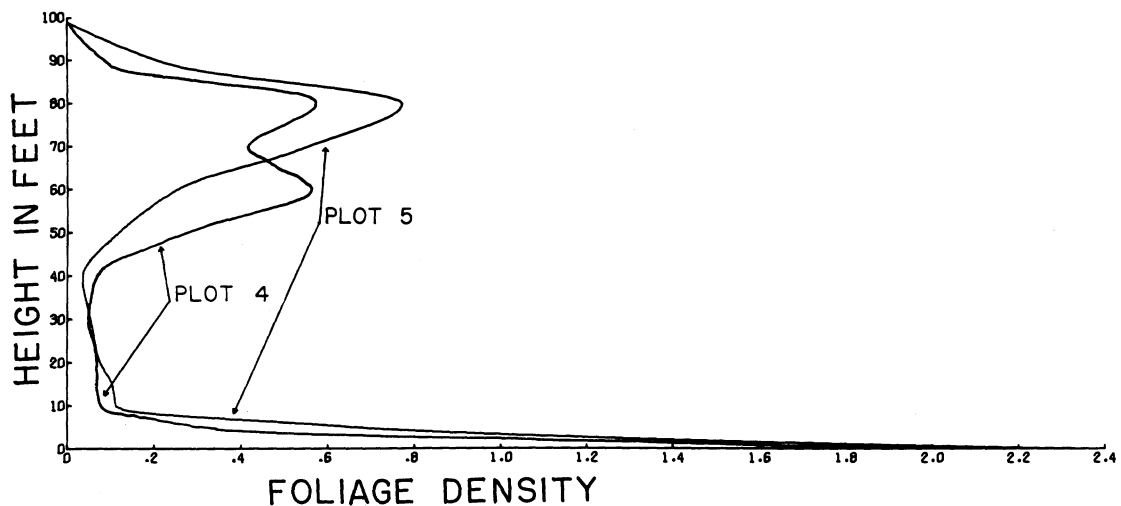


FIGURE 1. Foliage density profiles for mature alder forests in Washington (Plot 4) and Costa Rica (Plot 5).

vade after disturbances. Slash-burn logging or forest fires are the primary disturbances in Washington; landslides usually open areas for invasion of *A. jorullensis* in Costa Rica, at least in the areas where I worked. *A. jorullensis*, like *rubra*, grows to heights of over 30 m. It is eventually replaced by a climax association of oaks (*Quercus* spp.). Red Alder is eventually replaced by Western Hemlock (*Tsuga heterophylla*) and Western Red Cedar (*Thuja plicata*).

Primary productivities of the Washington and Costa Rican forests were probably similar. Both fall within the same hexagon in the Holdridge Life Zone Classification System (Holdridge 1947, pers. comm.). They have similar leaf surface area, adequate water, and similar mean temperatures during the avian breeding season, and should, therefore, have roughly similar measures of primary productivity. This assumption may be incorrect if more plant material is available to insects in Washington because of the spring flush of new leaves, but I have no data to support this. I chose sites in Costa Rica to resemble the vegetation structure of those in Washington as closely as possible. Except for the presence of more mosses, epiphytic lichens, and scattered bromeliads on the trunks and branches of the alder trees, and some larger and more conspicuous flowers in the understory of the Costa Rican forests, the sites were physiognomically almost identical. In Costa Rica, moisture-laden fog invades the alder forest most days shortly after noon and often is followed by heavy rain (Holdridge et al. 1971). This provides an excellent atmosphere for epiphytes.

The foliage profiles for the temperate and tropical alder forests were more alike than those of many other kinds of forest profiles. They differed, however, in the lack of a bimodal distribution of leaves in the canopy in Costa Rica. The slightly larger number of leaves over a random point in the forest (4.57 in Washington and 5.28 in Costa Rica) in Costa Rica is due to the denser understory there. In Costa Rica 36.8% of the total leaf biomass was alder while in Washington 51% was alder. Above 10 ft, the number of leaves over a random point was 2.25 in Washington and 2.28 in Costa Rica. Of these, 88.9% in Costa Rica and 94.8% in Washington were alder. The profiles of the replicates were similar enough to combine in the analysis of the bird community structure (Fig. 1).

Fewer vascular plant species were found in Washington (46) than on the Costa Rican sites (63) even though I spent less time in Costa Rica. Much (45%) of the difference, however, was due to ferns which probably offer little insect food for birds. In addition to *Alnus*, several other genera (*Rubus*, *Gaultheria*, *Cornus*, *Polypodium* and *Smilacina*) were common to both sites. Similar morphotypes were represented in both temperate and tropical sites by different genera: *Loasa* and *Cedrela* in Costa Rica and *Oplopanax* and *Rhamnus* in Washington occupied the same physiognomic place in the two sites.

#### VARIABILITY AND PREDICTABILITY

Temperature and rainfall patterns strongly influence resource variability and predictability for many feeding guilds of birds. Both Wash-

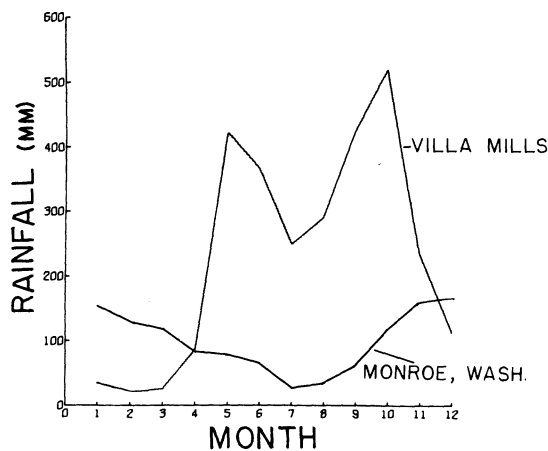


FIGURE 2. Mean monthly rainfall at Monroe, Washington (29 years) and Villa Mills, Costa Rica (16 years).

ington and Costa Rican sites have wet and dry periods during the year (Fig. 2), but the amount of rainfall during the breeding seasons in the two areas differs markedly. Long periods of rain may hinder birds by making less food available or interfering with foraging. Although rainfall is greater in Costa Rica, its occurrence may be less of a hindrance for foraging birds. During the breeding season in the Costa Rican study sites, morning hours are typically rainless, and rain often stops before sunset providing a long period in the morning and a short period before nightfall for foraging.

In Washington, rainfall generally is moderate, of long duration, and not associated with

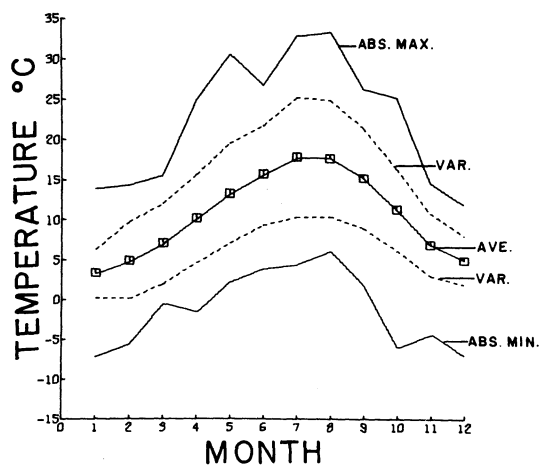


FIGURE 3. Monthly temperatures for Monroe, Washington. AVE. = 11 year average. VAR = AVE.  $\pm$  (Mean monthly high minus Mean monthly low). ABS.MAX. and ABS.MIN. = the absolute monthly maxima and minima for 1971.

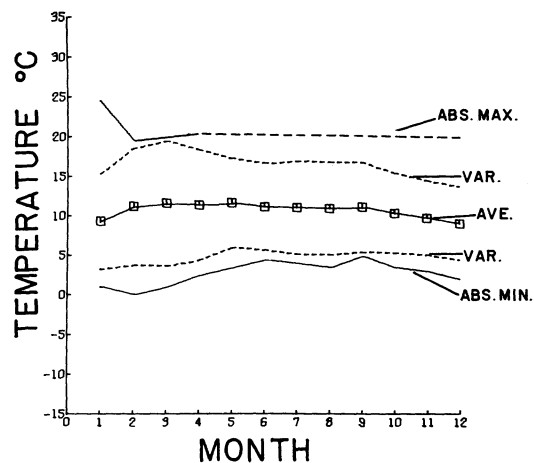


FIGURE 4. Monthly temperatures for Villa Mills, Costa Rica. AVE. = 16 year average. VAR = AVE.  $\pm$  (Mean monthly high minus Mean monthly low). ABS.MAX. and ABS.MIN. = the absolute monthly maxima and minima for 1963 (ABS.MAX. not available for May–December 1963).

a diurnal cycle. Early in the breeding season (May or early June), storms may last for several days and may handicap incubation and fledging. Later, however, rain is very light and infrequent.

Temperature may be important in determining availability of food. Periods of rain during the breeding seasons are usually accompanied by cooler temperature, and temperatures differ strikingly between the two areas. I have used temperature, therefore, to compare variability and predictability between them (Cody 1974).

Variability, or seasonality, differs at the two sites (Figs. 3, 4). This difference can be quantified by computing the mean deviation of

TABLE 1. Mean temperatures for months of highest breeding activity for the study sites, and the absolute maximum minus the absolute minimum temperatures for those months.

Study site	Mean temperature °C		
	May	June	July
Washington, 155 m <sup>a</sup>	12.5	15.2	17.3
Costa Rica, 2650 m <sup>b</sup>	14.6	14.2	14.1
Costa Rica, 2500 m <sup>c</sup>	15.5	15.1	15.0

Weather station	Maximum minus minimum temp. °C		
	May	June	July
Monroe, WA <sup>d</sup>	26.9	24.5	24.7
Villa Mills, C.R. <sup>e</sup>	10.4	11.1	11.9

<sup>a</sup> Monroe, WA temperature minus 0.5°C.

<sup>b</sup> Villa Mills temperature plus 2.8°C.

<sup>c</sup> Villa Mills temperature plus 3.7°C.

<sup>d</sup> Average for 11 years.

<sup>e</sup> Average for 2 years.

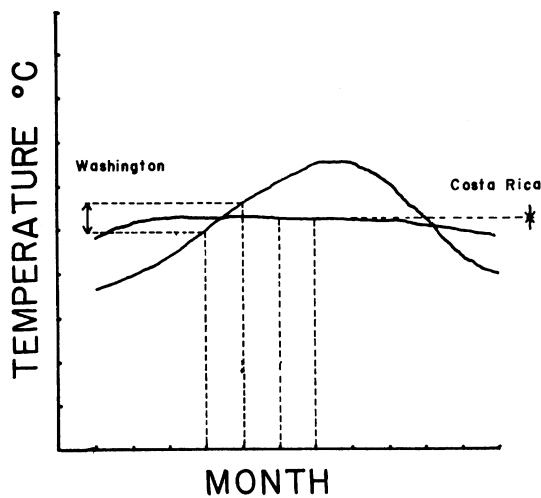


FIGURE 5. The change in average temperature caused by a one month shift in the annual temperature cycle for April–May in Washington and June–July in Costa Rica.

monthly mean temperature from the annual mean temperature (Cody 1974). The mean deviation of monthly means at Monroe, Washington was 4.46, while the mean deviations at the Costa Rican weather stations were 0.17 and 0.52, respectively. During the three months of highest breeding activity in both areas, May, June and July, mean temperatures

in Costa Rica and Washington were similar (Table 1).

In this study, levels of predictability refer to the probability that a bird will experience any set of environmental conditions at any specific time of the year. The mean monthly high temperature minus the mean monthly low indicates the variation around the mean monthly temperature (Figs. 3, 4). For May, June, and July the differences between maximum and minimum temperatures in Washington are more than twice as great as those in Costa Rica (Table 1). Where annual variation in temperature is small, a shift in the annual cycle will cause little change in the expected temperature at any given time (Fig. 5). On the other hand, where fluctuation in the annual temperature is highly variable, small shifts in the annual cycle can profoundly affect the expected temperature. In monthly and annual variation, temperature is more predictable at the Costa Rican sites.

#### BIRD COMMUNITY COMPOSITION

More species of breeding birds were present in the Costa Rican plots ( $N = 26$ , Table 2) than in Washington ( $N = 17$ , Table 3). Functional replacements of species between Washington and Costa Rica can be compared by examining foraging modes. A scratching bird

TABLE 2. Foraging characteristics<sup>a</sup> of birds observed in Costa Rica.

Bird species	No. observations	Height	Technique
Green Violetear ( <i>Colibri thalassinus</i> )	13	0.000	0.000
White-throated Mountaingem ( <i>Lampornis castaneiventris</i> )	58	2.091	0.864
Collared Trogon ( <i>Trogon collaris</i> )	24	1.592	0.287
Hairy Woodpecker ( <i>Picoides villosus</i> )	42	2.465	0.559
Spot-crowned Woodcreeper ( <i>Lepidocolaptes affinis</i> )	88	2.675	0.438
Ruddy Treerunner ( <i>Margarornis rubiginosus</i> )	62	2.480	0.809
Buffy Tuftedcheek ( <i>Pseudocolaptes lawrencii</i> )	26	1.927	0.649
Silvery-fronted Tapaculo ( <i>Scytalopus argentifrons</i> )	7	0.956	1.004
Black-capped Flycatcher ( <i>Empidonax atriceps</i> )	77	2.176	0.651
Yellowish Flycatcher ( <i>Empidonax flavescens</i> )	9	0.636	0.636
Paltry Tyrannulet ( <i>Tyranniscus villosus</i> )	14	1.730	0.683
House Wren ( <i>Troglodytes aedon</i> )	10	2.025	0.325
Mountain Wren ( <i>Troglodytes solstitialis</i> )	55	2.067	0.734
Gray-breasted Woodwren ( <i>Henicorhina leucophrys</i> )	63	0.619	0.565
Ruddy-capped Nightingale-thrush ( <i>Catharus occidentalis</i> )	12	0.287	0.287
Black-billed Nightingale-thrush ( <i>Catharus gracilirostris</i> )	68	0.693	1.045
Long-tailed Silky-flycatcher ( <i>Ptilogonys caudatus</i> )	33	1.993	0.995
Yellow-winged Vireo ( <i>Vireo carmioli</i> )	99	2.195	1.570
Slaty Flower-piercer ( <i>Diglossa baritula</i> )	16	1.160	0.673
Flame-throated Warbler ( <i>Vermivora gutturalis</i> )	358	2.606	0.758
Collared Redstart ( <i>Myioborus torquatus</i> )	203	2.573	1.325
Black-cheeked Warbler ( <i>Basileuterus melanogenys</i> )	306	1.318	1.099
Sooty-capped Bush-tanager ( <i>Chlorospingus pileatus</i> )	107	2.507	0.433
Large-footed Finch ( <i>Pezopetes capitalis</i> )	127	0.186	0.115
Yellow-thighed Finch ( <i>Pselliophorus tibialis</i> )	135	2.025	1.476
Chestnut-capped Brushfinch ( <i>Atlapetes brunneinucha</i> )	15	0.000	0.000

<sup>a</sup> Calculated using the Information Theory Index of diversity ( $-\sum p_i \ln p_i$ ).

TABLE 3. Foraging characteristics<sup>a</sup> of birds observed in Washington.

Bird species	No. observations	Height	Technique
Downy Woodpecker ( <i>Picoides pubescens</i> )	75	2.354	1.234
Willow Flycatcher ( <i>Empidonax traillii</i> )	166	2.070	0.668
Western Flycatcher ( <i>Empidonax difficilis</i> )	354	2.470	0.618
Western Wood Pewee ( <i>Contopus sordidulus</i> )	41	1.322	0.000
Chestnut-backed Chickadee ( <i>Parus rufescens</i> )	192	2.704	1.833
Brown Creeper ( <i>Certhia familiaris</i> )	115	1.945	0.838
Winter Wren ( <i>Troglodytes troglodytes</i> )	45	1.664	0.753
American Robin ( <i>Turdus migratorius</i> )	55	2.089	1.386
Swainson's Thrush ( <i>Catharus ustulatus</i> )	344	2.219	1.110
Red-eyed Vireo ( <i>Vireo olivaceus</i> )	254	2.189	0.879
Warbling Vireo ( <i>Vireo gilvus</i> )	241	2.320	1.157
Black-throated Gray Warbler ( <i>Dendroica nigrescens</i> )	32	1.703	0.689
Wilson's Warbler ( <i>Wilsonia pusilla</i> )	246	2.238	0.748
Western Tanager ( <i>Piranga ludoviciana</i> )	120	2.165	0.951
Black-headed Grosbeak ( <i>Pheucticus melanocephalus</i> )	101	2.502	0.879
Dark-eyed Junco ( <i>Junco hyemalis</i> )	182	2.285	1.526
Song Sparrow ( <i>Melospiza melodia</i> )	672	1.447	1.117

<sup>a</sup> Calculated using the Information Theory Index of diversity ( $-\sum p_i \ln p_i$ ).

(*Pezopetes capitalis*, Table 4) was present in Costa Rica, whereas no such forager was present in Washington. The Rufous-sided Towhee (*Pipilo erythrophthalmus*), which also scratches, breeds in earlier stages of alder forests in Washington but was not present in the later successional stages analyzed here (Stiles, in press). I found three nectarivorous species in the Costa Rican alder forests but none in Washington, related to the greater number of flowers attractive to birds in Costa Rica (Lovejoy 1975). The Costa Rican bird community also included five more insectivorous species than the Washington forests.

## DISCUSSION

My observations indicate that more species forage in the Costa Rican than in the Washington alder forest. During the study period in Costa Rica, over 75% of the species were breeding, as judged by presence of an active brood patch on adults captured in mist nets,

by observations of adults carrying food or nest material, or by sightings of newly fledged young. In Washington, breeding started in early April and continued through August. Breeding in Costa Rica apparently was fairly synchronous as it was in Washington. Synchronous breeding in tropical birds has been documented in several instances (Ricklefs 1966, Fogden 1972, Cody 1974, D. L. Pearson, pers. comm., R. S. Fleming, pers. comm.), and the presence of additional species in Costa Rica cannot be explained by spreading activities over more time.

Greater climatic predictability, which provides a more predictable food supply for birds, should favor specialization on a smaller range of food items, foraging heights, and methods of feeding. If so, this might allow more species to coexist in the alder forests of Costa Rica.

Competition between birds and mammals may be involved in the presence or absence of the scratching mode. I could not discover any other factor that would adversely affect the towhee and cause it to be absent from the older Washington alder stands. I did not see any small insectivorous mammal in the Costa Rican sites, but I commonly saw vagrant shrews (*Sorex vagrans*; one per 10 h observation) in Washington. Three species of shrews have been collected in Costa Rica (Choate 1970), at least one of which may occur on or near my study site. However, Goodwin (1946) reported that shrews "do not seem to be very abundant anywhere in Costa Rica."

The greater structural complexity of Costa Rican forests, due mainly to the epiphyte load on the trees, appears to affect the foraging of

TABLE 4. Numbers of species of birds using the different foraging modes in Washington and Costa Rica.

	Washington	Costa Rica
Gleaning	9 (12) <sup>a</sup>	14 (16)
Snatching	6 (6)	4 (6)
Pecking	1 (2)	1 (1)
Sallying	1 (1)	2 (3)
Scratching	0 (0)	1 (1)
Nectar	1 (1)	3 (5)
Probing	0 (0)	1 (1)
Total species	17 (22)	26 (33)
Foliage Height Diversity	1.069	1.094

<sup>a</sup> Number without rare species (total number of species).

several species. Five species of birds in the Costa Rican plots spent over 90% of their time foraging from the epiphytes on the alders. In Washington, only the Brown Creeper feeds predominantly in that manner although several others spend part of their foraging time exploiting areas covered by epiphytes. The greater number of epiphytes per se probably is not, however, responsible for the greater number of these species. If insects are limited by the availability of hiding places rather than by the level of available plant productivity, more epiphytes may permit an increase in the number of insects even though the epiphytes are not a food for herbivorous insects (Ehrlich and Raven 1965). The richness of insect morphotypes (aspect diversity) may be limited by the richness of available substrates (Rand 1967, Ricklefs and O'Rourke 1975, J. C. Schultz, pers. comm.). If a greater amount of epiphytes supports more insects, then more bird species may be present in very wet Red Alder forests on the Olympic Peninsula, Washington, where epiphytes are abundant, as in Costa Rica (Pechanec and Franklin 1968, pers. observ.). However, no additional species that use epiphytes on alders are present on the Olympic Peninsula. This suggests that the greater abundance of epiphytes alone does not account for the greater number of bird species in Costa Rica. If the latter were primarily due to an increase in the structural complexity of the forests in the form of epiphytes, I would expect no decrease in the average breadths along foraging dimensions of the gleaning and snatching guilds. In this case the species who glean and snatch insects from epiphytes should not affect the feeding niche breadths of other gleaners and snatchers because the epiphytes would provide a different resource in the way nectar does.

In my study, there are 9 temperate and 14 tropical gleaners and 6 temperate and 4 tropical snatchers. If we plot average niche breadth of the Costa Rican birds against that of the Washington birds for foraging height and technique, the points for gleaners and snatchers should lie on a 45° line if the niches are equal, and below the 45° line if the tropical niches are broader than the temperate ones. In all four comparisons—gleaners/height ( $t = 1.78$ ,  $df = 21$ ,  $P < 0.05$ ), gleaners/technique ( $t = 2.338$ ,  $df = 21$ ,  $P < 0.025$ ), snatchers/height ( $t = 1.926$ ,  $df = 8$ ,  $P < 0.05$ ), and snatchers/technique ( $t = 0.346$ ,  $df = 8$ ,  $P < 0.25$ ), tropical feeding niches are narrower than temperate ones (Fig. 6). These relationships remain the same if one considers

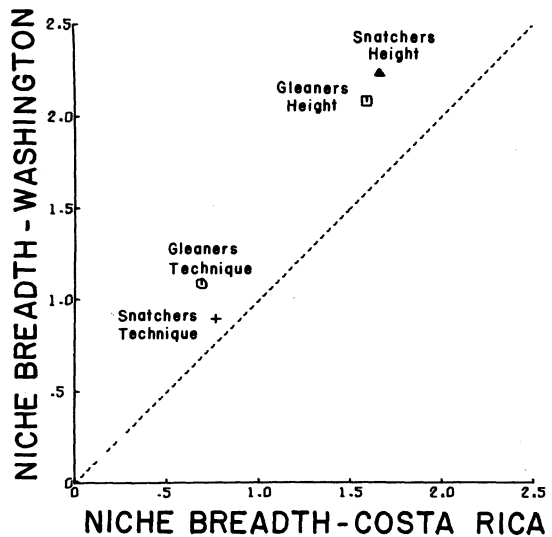


FIGURE 6. Comparison of niche breadths for Washington and Costa Rican gleaners and snatchers in terms of foraging height and technique.

subsamples, or eliminates from the calculations the five tropical species which specialize on trunks and branches, or eliminates the Chestnut-capped Brushfinch (*Atlapetes brunneinucha*), which feeds only on the ground. The relationship is not an artifact of sample size because the diversity index for many species reaches a plateau relatively early at about 20 to 30 observations (Pearson 1971, this study). Comparisons of only those species with more than 25 observations yielded the same relationship as when all species were considered.

This finding supports my hypothesis that predictability of the weather in the Costa Rican alder forests and, hence, predictability of food resources, have enabled birds to evolve more specialized foraging methods. The greater number of species coexisting in Costa Rica than in Washington may be a result of this specialization.

The distribution of food resources in the forests should affect foraging techniques within bird communities. Since the Washington and Costa Rica forests had similar structure, one might expect that the overall distribution of foraging techniques of all species would be similar (Table 5). Techniques of gleaning leaves, sallying, and fruit-eating are used in similar proportions in both regions. Scratching, gleaning twigs, branches and trunks, snatching from leaves, twigs, branches and trunks, pecking, and nectar-feeding are used in different proportions.

The difference in the proportional use of

TABLE 5. Proportional use of different foraging techniques by birds in Washington and Costa Rica (some lesser-used techniques have been combined in the table). Percent use = % of all foraging observations for all species.

Technique	Percent use	
	Costa Rica	Washington
<b>INSECTS</b>		
Scratching in litter	6.0	—
Gleaning leaves	38.4	34.7
Gleaning twigs	7.9	6.6
Gleaning branches	10.9	1.6
Gleaning trunks	6.6	5.9
Snatching leaves	10.8	34.4
Snatching twigs, branches, trunks	2.8	—
Sallying	8.1	9.2
probing	0.9	—
Pecking	2.2	6.2
<b>FRUIT</b>		
All techniques	1.9	1.3
<b>NECTAR</b>		
all techniques	3.4	—
<b>TOTAL</b>	<b>99.9</b>	<b>99.9</b>

snatching between Washington (34.4%) and Costa Rica (13.6%) is the most striking. If the greater amount of epiphytes provided diurnal hiding places for insects feeding on the alder foliage, one would expect a proportional shift in foraging technique from the leaves to the epiphytes on the twigs, branches and trunks. These surfaces were explored (including probing) more than twice as much in Costa Rica (29.1%) as in Washington (14.1%). The difference in proportional use of pecking in Washington and Costa Rica also may be affected by dense epiphyte cover, reducing availability of substrate for pecking. I cannot account for the difference in proportional use of snatching from leaves while there is no difference in gleaning from leaves.

The interpretation of niche overlap values has been a continuing problem in studies of community structure. May and MacArthur (1972), May (1974), and others have demonstrated theoretically that species reach a maximal overlap that is relatively insensitive to environmental fluctuation unless the latter is very severe. If so, overlap should be less important in comparing structurally similar temperate and tropical communities. However, certain models (Pianka 1974, 1976) suggest that niche overlap should decrease as the number of competing species increases. Diffuse competition (MacArthur 1972) may be more important in species-rich environments, such

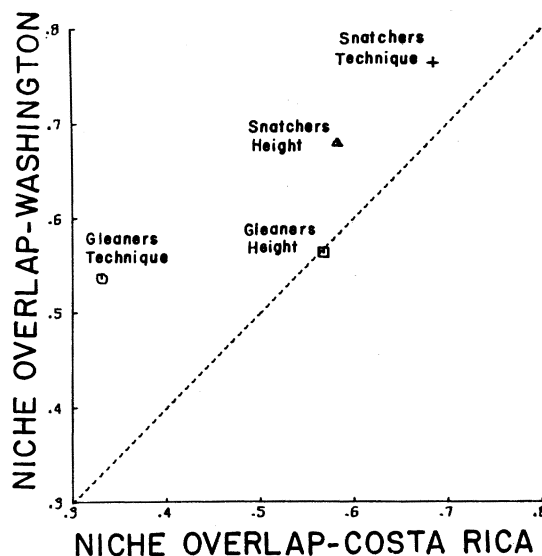


FIGURE 7. Comparison of overlap for Washington and Costa Rican gleaners and snatchers in terms of foraging height and technique.

as the Costa Rican alder forests, and may lead to narrower niche overlap between pairs of species.

A tentative prediction from this hypothesis is that the average overlap for the two dimensions I measured should be greater in the Washington alder forest birds. This is supported by the data for these two dimensions for the Washington and Costa Rican snatchers and gleaners (Fig. 7). All values would fall on the 45° line if the average overlap values were equal. In three of four instances the points fall above the line indicating that the Costa Rican guilds have narrower average overlap.

Bird communities in most seasonal environments experience a less predictable climate than those in environments with less seasonality. My study suggests that in more predictable environments birds feed in more specialized ways, allowing more species to coexist.

## SUMMARY AND CONCLUSIONS

Bird communities in mature alder forests in Washington and Costa Rica were studied to assess the influence of predictability and seasonality of climate. Foraging height and technique (two measures of feeding niche) were recorded for individual species. Differences in foraging behavior between the areas seem to be related to differences in vegetation, which indicate differences in the availability of food. Birds that glean or snatch insects have narrower average foraging niches in Costa Rica

than in Washington, and all species overlap less in their foraging behavior.

More bird species were present in the Costa Rica than in the Washington study plots. This can be partly attributed to the greater availability of nectar and to the greater specialization in feeding habits.

Climatic predictability may be important in affecting availability of food (resulting in more specialized foraging by tropical forest species) and the predictable presence of food resources that support more bird species.

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