NICHE OVERLAP AMONG FOLIAGE-GLEANING BIRDS:
SUPPORT FOR PIANKA'S NICHE OVERLAP HYPOTHESIS

Pianka (1972) proposed that maximum tolerable niche overlap should be lower in communities where interspecific competition (i.e., diffuse competition) is intense than in environments where competition is weak. This "niche overlap hypothesis" is based on the supposition that, when the demand for resources is low relative to supply, potential competitors can tolerate a relatively high degree of overlap in resource use without experiencing critical levels of competition; when the demand to supply ratio is high, less overlap should be tolerated.

In order to test the niche overlap hypothesis, it is necessary to restate the hypothesis in terms that can be measured in the field. In his test of the hypothesis, Pianka (1974) replaced maximum tolerable niche overlap with a parameter that is more easily estimated, mean nonzero niche overlap within a community. Thus, the hypothesis predicts that mean nonzero niche overlap within communities should be inversely proportional to the intensity of competition.

Tests of this hypothesis also require appropriate measures of the intensity of competition and/or the ratio of resource demand to supply. Since the intensity of competition should be a function of the demand-supply ratio, either measure can be used to test this hypothesis. Pianka (1974) and Brown (1975) used species density (i.e., the number of species that coexist within a community) as an index of competitive intensity. The relative magnitude of the demand-supply ratio is easily determined among communities that show little difference in both species composition and population density, but differ greatly in levels of available resources.

Few empirical tests of the niche overlap hypothesis have been published. Using data from 28 lizard communities on three continents, Pianka (1974) found that the mean nonzero niche overlap in these communities was negatively correlated with species density. M'Closkey (1978) reported a similar pattern among desert heteromyid rodents, where average niche separation increased with increasing species diversity. Brown (1975), however, reported that mean niche overlap was positively correlated with the number of coexisting species in assemblages of granivorous rodents.

Since high levels of density-independent mortality should reduce the intensity of interspecific competition (Pianka 1972), it follows from the "niche-overlap hypothesis" that high levels of density-independent mortality should be associated with higher niche overlaps between potential competitors. A model of exploitative competition constructed by Abrams (1977), however, generates just the opposite prediction; higher density-independent mortality may increase the niche separation necessary for competing species to coexist.

In this paper I present niche overlap data for a guild of insectivorous birds from three areas. In April, May, and June, 1976–1978, I recorded data on microhabitat use by eight species of foliage-gleaning birds in ponderosa pine forests in Arizona

and Colorado. Data were gathered during two breeding seasons at each area. Study areas were located at Manitou Experimental Forest in central Colorado (39°08'N, 105°07'W), near Pagosa Springs in southwestern Colorado (Turkey Springs: 37°17'N, 107°10'W), and in the Santa Catalina Mountains in southeastern Arizona (32°34'N, 110°42'W). (For a more detailed description of the study areas and methods see Rusterholz 1979).

For each foraging observation of a bird, I recorded microhabitat use in five niche dimensions: (1) bird height (BH), (2) height of tree used (TH), (3) perch type (PR), (4) tree compartment (CM), and (5) tree species (TS). A symmetrical measure of niche overlap was calculated between each species pair for each niche dimension:

$$OL_{ab} = 1 - \frac{1}{2} \sum_{c=1}^{n} |P_{ac} - P_{bc}|, \tag{1}$$

where OL_{ab} is niche overlap between species a and species b, n is the number of resource states, and P_{ac} is the proportion of all observations of species a where resource state c was used (Schoener 1970; Colwell and Futuyma 1971). I estimated total microhabitat overlap by combining overlap values from different dimensions in three ways: (1) calculating the arithmetic mean of overlap values between species from the five dimensions (the "summation α''" of Cody [1974], (2) multiplying overlaps from the five dimensions (Cody's [1974] "product α''"), and (3) taking the mean of overlaps in four dimensions which are correlated with one another (BH, TH, PR, CM), and multiplying this by niche overlap along the TS dimension which was potentially independent (combination method).

May (1975) has shown that the summation estimate of overlap is an upper bound of the true multidimensional overlap, while the product overlap may often be an underestimate of the true value. Because of the limitations of using summation and product overlaps, I believe that a combination of these techniques provides a better estimate of true multidimensional overlaps than either method alone (also see Hespenheide 1975).

COMPETITIVE INTENSITIES

Two lines of evidence suggest that the intensity of competition is greatest in southeastern Arizona and lowest in central Colorado. Within the guild considered here, species density decreases to the north (table 1). Density-independent mortality, likely to be negatively correlated with competitive intensities (Pianka 1972), would also be expected to decrease to the north as environmental conditions become harsher (e.g., as the length of the potential breeding season decreases, or resource availability decreases or becomes less predictable). As a result competitive intensities should decrease to the north in a manner independent of species densities. The effect of density-independent mortality is also likely to be less pronounced in small, steep mountain ranges such as the Santa Catalinas where birds can escape inclement weather by traveling several kilometers downslope to lower elevations. This option is not as readily available to birds inhabiting more extensive highlands in the other areas.

TABLE 1

NICHE OVERLAP, RESOURCE AVAILABILITY, AND SPECIES
DENSITY IN THREE PONDEROSA PINE FORESTS

	Location					
	Santa Catalina Mts., Arizona		Turkey Springs, Colorado		Manitou Experimental Forest, Colorado	
	1976	1977	1976	1978	1977	1978
Mean overlap						
summation	.732	.728	.745	.706	.771	.770
product	.219	.218	.239	.173	.258	.270
combination	.534	.564	.660	.598	.686	.703
Mean total overlap						
summation	2.197	2.183	1.863	1.766	1.156	1.156
product	.658	.656	.598	.432	.388	.405
combination	1.602	1.693	1.650	1.494	1.029	1.055
Foliage arthropod						
biomass index*	3.45	6.57	7.39	5.71	2.11	2.84
Species density	7		6		4	

* Biomass index expressed as the number of insect biomass units collected per sweep of pine foliage; 1 biomass unit = 1 insect 1 mm in length.

Competitive intensities should also be dependent on resource availability. Therefore, provided that population densities of competing species remain relatively constant, average niche overlap within a guild or community should be higher in years when resource abundance is greatest.

RESULTS

The results discussed here support two predictions of the niche overlap hypothesis: (1) average (nonzero) niche overlap decreases with the number of species in the guild and (2) average niche overlap is greater in years when resources are more abundant. Table 1 reveals that mean pairwise niche overlap determined by the combination method is inversely related to species density ($r = -.92$, $P < .01$). These results are plotted in figure 1. Except for mean overlap values from Turkey Springs, Colorado in 1978, results obtained using the summation and product methods of combining niche axes yield the same result (table 1).

Average niche overlap values as determined by the combination technique vary considerably between years at Pagosa Springs and at the Arizona site. At both sites higher average niche overlaps occurred when resource availability, as determined from sweep samples of pine foliage, was high.

Pianka (1974) further noted that, rather than remaining constant, (average) total niche overlap within his lizard communities increased with increasing species density. My data show a similar pattern. Total niche overlap is positively correlated with the number of species in the guild regardless of the method used to combine niche dimensions (table 1).
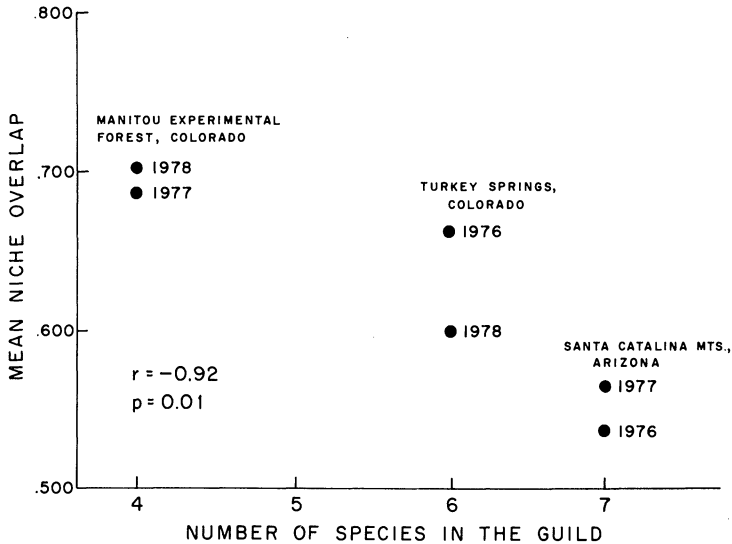
FIG. 1.—Species density and mean microhabitat niche overlap within a guild of foliage-gleaning birds in three ponderosa pine forests. Microhabitat niche overlap was calculated by combining overlaps using a combination of summation and product methods.

In conclusion, the data presented here support the hypothesis that mean pair-wise niche overlap within a guild or community is inversely proportional to the intensity of interspecific competition. These results further emphasize the importance of considering the total competitive effects of all interspecific competitors when analyzing guild or community structure.

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