Wilson Bull., 96(1), 1984, pp. 108–116

Niche relationships in wintering mixed-species flocks in western Washington.—Mixed-species flocks are common worldwide. Study of these flocks has focused on two major questions: (1) What are the functions of mixed flocks? and (2) What is the importance of interspecific competition within these flocks? It is generally agreed that members of mixed-species flocks may derive benefits of increased foraging efficiency and decreased risk of predation, although the importance of each potential benefit may vary among species or geographical regions (for review see Morse, Bioscience 27:332–339, 1977). The dilemma of interspecific competition within mixed flocks has not been resolved. Many authors have argued that competition is avoided or reduced by species differences in foraging behavior (e.g., Gibb, Ibis 96:513–543, 1954; Austin and Smith, Condor 74:17–24, 1972). Evidence of species differences and/or low niche overlap alone, however, cannot conclusively demonstrate the importance of competition because overlap can assume a variety of levels if resources are not limiting (Sale, Oecologia 17:245–256, 1974).

We studied wintering mixed flocks of insectivorous birds in western Washington to determine: (1) mixed flock characteristics (e.g., species composition, flock size, etc.); (2) the frequency of aggressive encounters (intra- and interspecific) within mixed flocks; and (3) differences in foraging niches of species which regularly participated in mixed flocks (core species). In this report we compare our data with those of Morse (Ecol. Monogr. 40:119–168, 1970; Ibis 120:298–312, 1978) from other north-temperate study sites. Western Washington differs from other study regions in climate, habitat, and the species composition of mixed flocks. Taken as a whole, differences among sites in the parameters examined may provide insight into the competitive relationships within mixed flocks.

Study area and methods.—We conducted this study at the Nisqually National Wildlife Refuge, Thurston Co., Washington. Data were collected along a 3-km wooded dike bordering the Nisqually River. Red alder (*Alnus rubra*) dominated the mature deciduous woodland. Big-leaf maple (*Acer macrophyllum*), black cottonwood (*Populus trichocarpa*), and Oregon ash (*Fraxinus latifolia*) were also common canopy species. Most canopy trees were approximately 25 m tall. Understory species included wild crabapple (*Pyrus fusca*), elderberry (*Sambucus* sp.), blackberry (*Rubus* sp.), Indian peach (*Oemleria cerasiformis*), salmonberry (*Rubus spectabilis*), willow (*Salix* sp.), and snowberry (*Symphoricarpus albus*). Data collection was facilitated because flocks were usually restricted to this narrow band of woodland.

To minimize possible seasonal variation, we collected data from 8 January–13 February 1975. Observations were made between 11:00 and 14:00 approximately 3 days each week. Flock composition and size were determined upon encountering the flock. A flock was operationally defined as two or more individuals travelling and foraging together. Fifteen-second focal-animal samples (Altmann, Behaviour 49:227–267, 1974) were taken of as many flock members as possible. Data were dictated into a cassette recorder and included: (1) number of foraging motions (captures and/or capture attempts); (2) type of foraging behavior used for each foraging motion; and (3) location where foraging motions occurred (microhabitat). Foraging behavior classification, modified from Sturman (Condor 70:307–322, 1968), was based on stance (upright, hang, and fly), and method (glean, peck, tear, and flycatch). Fourteen microhabitats were defined according to structural, vertical, and horizontal components (Fig. 1). These factors seemed appropriate for quantifying foraging niche in view of previous mixed-flock studies (e.g., Ulfstrand, Oecologia 27:23–45, 1977; Austin and Smith 1972; Morse 1970, 1978). Data were analyzed using the Statistical Analysis System (Helwig and Council [eds.], SAS User's Guide, SAS Institute, Inc., Raleigh, North Carolina, 1979).

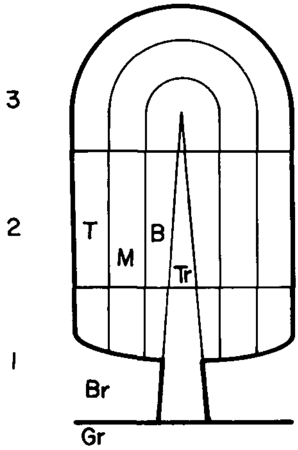

FIG. 1. Microhabitat categories. Gr = ground; Br = brush or understory; Tr = trunk; B, M, T = base, middle, and tips of branches, respectively. Trees were divided into three height classes.

Overlap in the use of microhabitats, foraging methods, and stances was calculated for each species pair using Pianka's (Proc. Natl. Acad. Sci. 71:2141–2145, 1974a) formula:

$$O_{jk} = \frac{\sum_{i}^{n} p_{ij}p_{ik}}{\sqrt{\sum_{i}^{n} p_{ij}^2 \sum_{i}^{n} p_{ik}^2}}$$

where p_{ij} and p_{ik} represent the proportional use of category i by species j and k, respectively. The mean proportion of foraging motions in each category was used as a measure of p_i.

TABLE 1

OCCURRENCE AND ABUNDANCE OF CORE SPECIES IN 30 MIXED FLOCKS

Species	N[a]	% in mixed flocks	No. flocks with species	Indiv./flock when in flocks	
				$\bar{x}$ ± SD	Range
Black-capped Chickadee	113	97	29	3.8 ± 2.4	1–10
Chestnut-backed Chickadee	40	100	13	3.1 ± 1.6	1–6
Golden-crowned Kinglet	390	95	27	13.8 ± 8.5	1–35
Ruby-crowned Kinglet	48	85	26	1.6 ± 0.8	1–3
Downy Woodpecker	20	90	14	1.3 ± 0.5	1–2

[a] Total number of individuals observed.

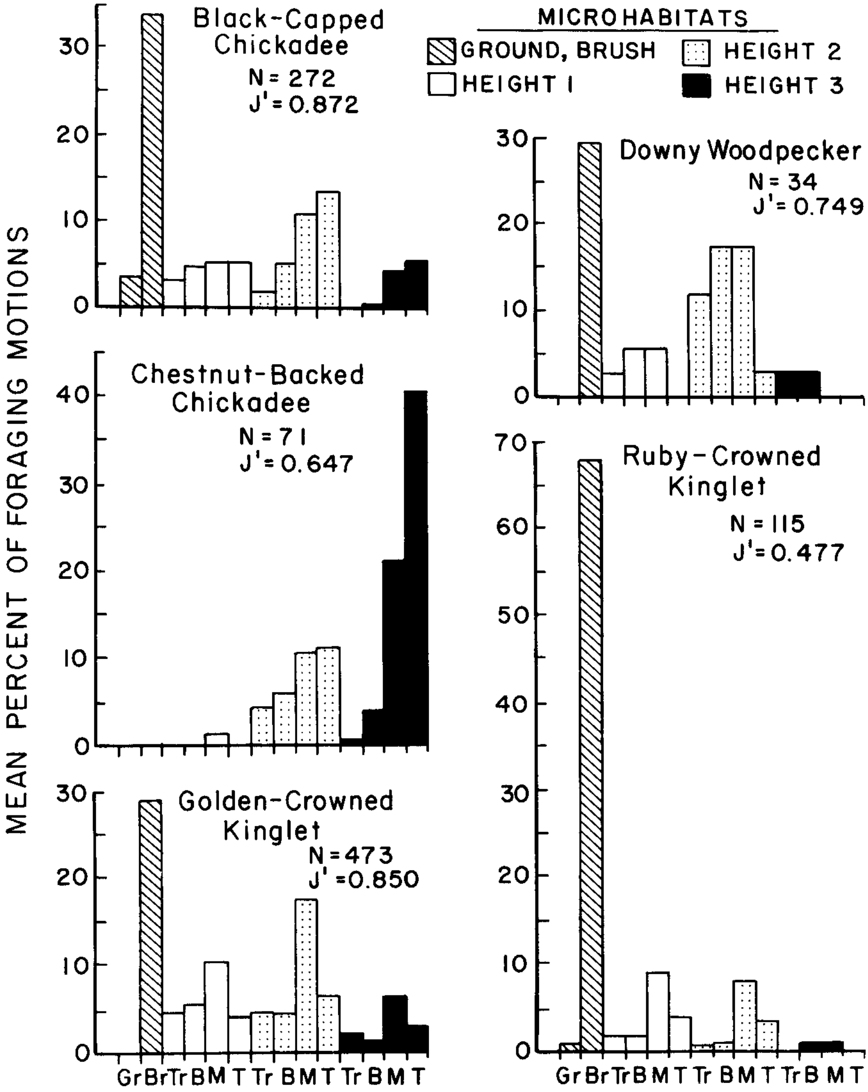

FIG. 2. Use of foraging microhabitats by core species. Abbreviations for microhabitats as in Fig. 1.

Overall overlap for species pairs was measured in two ways. Product overlap ($\Pi\ O_{jk}$), the product of overlap values for each dimension, is appropriate when complete independence of niche dimensions exists. Summation overlap ($\Sigma\ O_{jk}$), the arithmetic mean of overlap values, is appropriate when complete dependence of dimensions occurs. In reality, these

TABLE 2

RESULTS OF ANALYSES OF VARIANCE AND DUNCAN'S NEW MULTIPLE RANGE TESTS FOR BETWEEN-SPECIES (WITHIN-ROW) COMPARISONS OF MICROHABITAT USE

Microhabitat[a]	ANOVA *P*	Species differences[d]				
		BCC[c]	CBC	GCK	RCK	DW
Gr	0.0001	a	b	b	b	b
Br	0.0001	b	c	b	a	b
Tr 1	0.23	—	—	—	—	—
B 1	0.12	—	—	—	—	—
M 1	0.02	b	b	a	ab	ab
T 1	0.20	—	—	—	—	—
Tr 1	0.005	bc	bc	b	c	a
B 2	0.001	b	b	b	a	b
M 2[b]	0.03	—	—	—	—	—
T 2	0.002	a	ab	b	b	b
Tr 3[b]	0.03	—	—	—	—	—
B 3	0.32	—	—	—	—	—
M 3	0.0001	bc	a	b	c	c
T 3	0.0001	b	a	bc	c	bc

[a] Gr = ground, Br = branch, Tr = trunk, B = base of branch, M = middle of branch, T = tip of branch; numbers refer to height classes.

[b] No species differences were detected by Duncan's new multiple range test.

[c] Species common names abbreviated, see Table 1.

[d] Species with the same letter are not significantly different in their proportional use of a microhabitat.

two measures tend to underestimate and overestimate actual overlap, respectively, because neither complete independence nor dependence is likely (Cody, Competition and the Structure of Bird Communities, Princeton University Press, Princeton, Massachusetts, 1974; Pianka 1974a).

Niche breadth (foraging diversity) was estimated for each dimension using the formula $J' = H'/H'_{max}$ (Pielou, J. Theoret. Biol. 13:131–144, 1966) where $H' = \sum_{i}^{n} p_i \log p_i$, p_i is the proportion of observations in resource state i, and H'_{max} is the maximum possible diversity, i.e., when p_i's are equal. Small values of J' (approaching 0) indicate specialization; large values (approaching 1) indicate generalization.

Flock composition and size.—Mixed-flock size ranged from 3–108 individuals ($\bar{x} = 30.4$, SD ± 24.8, N = 30). Number of individuals of core species in flocks ranged from 2–45 ($\bar{x} = 19.4$, SD ± 11.2). Core species and their order of abundance in flocks were: Golden-crowned Kinglets (*Regulus satrapa*) > Black-capped Chickadees (*Parus atricapillus*) > Chestnut-backed Chickadees (*P. rufescens*) > Ruby-crowned Kinglets (*R. calendula*) > Downy Woodpeckers (*Picoides pubescens*). Dark-eyed Juncos (*Junco hyemalis*), Yellow-rumped Warblers (*Dendroica coronata*), Pine Siskins (*Carduelis pinus*), and Bushtits (*Psaltriparus minimus*) occasionally flocked with core species. Statistics describing the occurrence and abundance of core species in mixed flocks are presented in Table 1.

Niche relationships.—All core species foraged throughout the habitat (Fig. 2), but each differed to some degree in the proportional use of each microhabitat (Table 2). Feeding was concentrated in brush for all species except the Chestnut-backed Chickadee. As a result, microhabitat overlap was high (Table 3). Microhabitat niche breadth (J') was relatively large

TABLE 3

SPECIES-PAIR OVERLAP FOR MEASURED NICHE DIMENSIONS

Species[a] pair	Microhabitat	Method	Stance	Overall	
				$\Pi\ O_{jk}$	$\Sigma\ O_{jk}$
BCC × GCK	0.951	0.996	0.958	0.907	0.968
BCC × RCK	0.908	0.993	0.812	0.732	0.904
BCC × DW	0.855	0.725	0.732	0.689	0.771
GCK × RCK	0.857	0.999	0.907	0.777	0.921
GCK × DW	0.899	0.713	0.657	0.421	0.756
RCK × DW	0.777	0.711	0.279	0.154	0.589
CBC × BCC	0.325	0.998	0.985	0.319	0.769
CBC × GCK	0.331	0.989	0.932	0.305	0.751
CBC × RCK	0.051	0.986	0.722	0.036	0.586
CBC × DW	0.197	0.706	0.841	0.117	0.581
$\bar{x}$	0.615	0.882	0.783	0.446	0.760
SD	±0.346	±0.145	±0.208	±0.309	±0.142

[a] Species common names abbreviated, see Table 1.

for all species except the Ruby-crowned Kinglet which foraged almost exclusively in brush (Fig. 2).

Gleaning was the most common foraging method used by all core species except the Downy Woodpecker. Accordingly, foraging method overlap was high (Table 3) and niche breadth (J') small (Fig. 3). Species usually foraged in an upright or hanging stance (Fig. 4). To a lesser extent, Golden-crowned and Ruby-crowned kinglets flew in pursuit of food; hovering (gleaning while flying) was more common than flycatching. Stance overlap was high for all species pairs, except Ruby-crowned Kinglets and Downy Woodpeckers; Downy Woodpeckers usually hung whereas Ruby-crowned Kinglets were usually upright when foraging (Table 3). J' for stance was high for all species except the Downy Woodpecker (Fig. 4).

Overall niche overlap was highest among Black-capped Chickadees, Golden-crowned Kinglets, and Ruby-crowned Kinglets (Table 3; mean species-pair $\Pi\ O_{jk} = 0.805$, mean species-pair $\Sigma\ O_{jk} = 0.931$); other species pairs exhibited little overall niche overlap.

Aggression.—All observed aggressive interactions (N = 79) were intraspecific and involved the following species (number of interactions in parentheses): Golden-crowned Kinglet (57), Black-capped Chickadee (10), Ruby-crowned Kinglet (7), and Chestnut-backed Chickadee (5).

Discussion.—The relationship between niche overlap and competition between species has been the subject of considerable controversy in the field of community ecology. Problems have arisen when measures of overlap have been erroneously equated with the competition coefficient of the Lotka-Volterra competition equation (Pianka 1974a). Substituting in this way, one would conclude that competition is greatest in communities where overlap is high. Alternatively, if resources are abundant relative to use, overlap between potential competitors could be great without the negative consequences of competition. Indeed, current theory predicts that maximum tolerable overlap should be greater where competition is reduced (niche overlap hypothesis [Pianka, Am. Nat. 106:581–588, 1972; Sale 1974; Schoener,

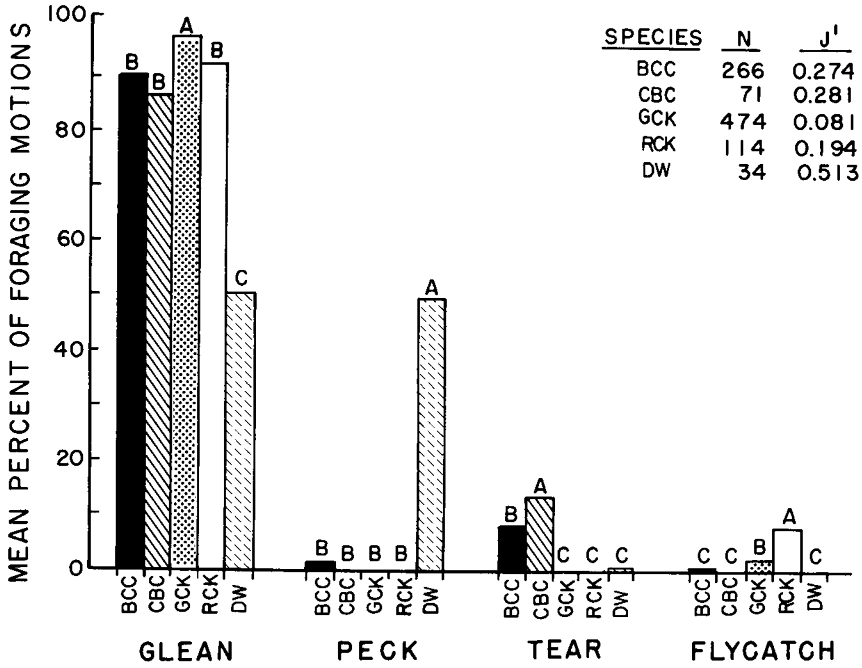

FIG. 3. Foraging methods used by core species. Abbreviations of species' common names given below bars. Means with the same letter (top of bars) are not significantly different (Duncan's new multiple range test, within-method comparisons only).

Science 185:27–39, 1974; Wiens and Rotenberry, Oecologia 42:253–292, 1979]). Data from a variety of locations and organisms seem to support the niche overlap hypothesis (Alerstam et al., Oikos 25:321–330, 1974; Pianka 1974a; Yeaton, Ecology 55:959–973, 1974; Diamond and Marshall, Emu 77:61–72, 1977; Rotenberry and Wiens, Ecology 61:1228–1250, 1980; Rosenberg et al., Auk 99:260–274, 1982; Schluter, Ecology 63:1504–1517, 1982).

For comparative purposes, we used data from Morse (1970, 1978) to calculate O_{jk} for wintering mixed flocks in deciduous woodland sites in England, Maryland, Louisiana, and Maine. Foraging microhabitat was the only niche dimension comparable among studies, but, this may be the most relevant dimension for niche differentiation in insectivorous, arboreal birds (MacArthur and MacArthur, Ecology 42:594–598, 1961; Pianka, Evolutionary Ecology, Harper and Row, New York, New York, 1974b). Additionally, morphological changes are not essential for many shifts in microhabitat usage, but are usually necessary for changes in foraging stance, foraging method, and diet (Yeaton 1974, Diamond and Marshall 1977). Thus, one might expect species to be able to adjust microhabitat use to the prevailing competitive milieu as documented in the bark-foraging guild of central Illinois (Williams and Batzli, Condor 81:122–132, 1979a; Wilson Bull. 91:400–411, 1979b). Indeed, Black-capped Chickadees, Golden-crowned and Ruby-crowned kinglets, and Downy Woodpeckers foraged in different microhabitats in different geographical regions. Brush was used

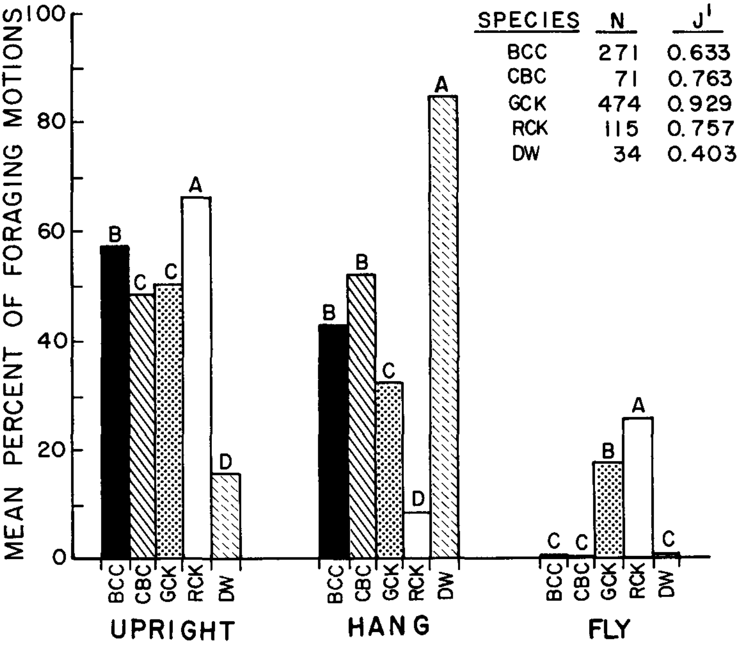

FIG. 4. Foraging stances used by core species. Abbreviations of species' common names given below bars. Means with the same letter (top of bars) are not significantly different (Duncan's new multiple range test, within-stance comparisons only).

heavily by all species in Washington, but this zone was little used in Morse's (1970, 1978) study areas except by Ruby-crowned Kinglets (an apparent brush specialist). In the east, Black-capped and Carolina chickadees foraged most on the middle section of branches; Golden-crowned Kinglets foraged most in low tips and brush; and Downy Woodpeckers foraged mainly on tree trunks (Morse 1970). Comparison of microhabitat overlap values among geographic regions, then, may be most illustrative of the relative importance of competition in light of the niche overlap hypothesis.

Mean species-pair overlap in microhabitat use (all core species considered) decreased geographically as follows: Washington (five species, $\bar{x} = 0.615$, SD ± 0.236), England (six species, $\bar{x} = 0.576$, SD ± 0.236), Maryland (seven species, $\bar{x} = 0.484$, SD ± 0.304), Louisiana (seven species, $\bar{x} = 0.466$, SD ± 0.287), and Maine (three species, $\bar{x} = 0.395$, SD ± 0.236), although this trend was not statistically significant (one-factor ANOVA, $F_{(4,65)} = 0.801$, $P > 0.50$). Overlap in microhabitat use for species pairs common to Washington and Morse's (1970) North American study areas did exhibit a significant geographical trend, in which species-pair overlap declined from Washington to Maine (Table 4).

Niche breadth should be greater under less intense competition and, therefore, should be positively correlated with niche overlap (Ulfstrand 1977, Wiens and Rotenberry 1979). Data from North American flocks suggest such a trend but are incomplete. Microhabitat J' for Black-capped Chickadees (and Carolina Chickadees) decreased from Washington (0.87),

TABLE 4

MICROHABITAT OVERLAP FOR SPECIES PAIRS COMMON TO SEVERAL STUDY AREAS[a]

Species pair[b]	Washington	Maryland[c]	Louisiana	Maine
BCC × GCK	0.951	0.830	0.618	0.544
BCC × RCK	0.908	—	0.602	—
BCC × DW	0.855	0.586	0.632	0.519
GCK × DW	0.899	0.391	0.299	0.123
RCK × DW	0.777	—	0.260	—

[a] Data for Maine, Maryland, and Louisiana were reanalyzed from Morse (1970).

[b] Significant location ($F_{(3,6)} = 10.132$, $P < 0.01$) and species-pair effects ($F_{(2,6)} = 7.285$, $P < 0.03$) were detected with two-factor ANOVA.

[c] Carolina Chickadees (*P. carolinensis*) were used in place of Black-capped Chickadees in overlap calculations for Maryland and Louisiana. Carolina Chickadees replace Black-capped Chickadees in east-central and southern states and the species are considered ecological equivalents (Brewer, Auk 80:9–47, 1963).

Maryland (0.74), Maine (0.70), and Louisiana (0.60); *J′* for Golden-crowned Kinglets decreased from Washington (0.85), Maryland (0.61), and Maine (0.59) (this study; Morse 1970).

The above evidence suggests that interspecific competition within western Washington mixed flocks in winter is low relative to other North American flocks. Two other pieces of information support this interpretation: large flock size (Washington mean >2 times mean flock sizes reported by Morse [1970, 1978]) and the absence of observed interspecific aggression in Washington (interspecific aggression was observed commonly in all flocks studied by Morse [1970, 1978]). A decline in the frequency of aggression might also occur in an intensely competitive environment where costs outweighed benefits. If this were the case, however, it would be surprising to observe intraspecific aggression as frequently as we did.

Why would the level of competition vary among these locations? Decreasing niche overlap values among regions are paralleled to some extent by decreasing mean winter temperature and presumably a concomitant decrease in arthropod availability. Louisiana is the exception to this climate/overlap trend because it has higher average winter temperatures than the other study locations but moderate overlap values.

Western Washington winters are typically wet and mild (mean temperature approximately 4.4°C). Flying insects were often observed during our study. Similar winter weather conditions occur in England (also with high niche overlap values [Morse 1978]), and continued growth and reproduction of arthropods were reported by Gibb (Ibis 102:163–208, 1960).

Alternative hypotheses can be proposed which could conceivably account for the observed trends in niche overlap. For example, the availability of microhabitats in different locations may affect competition and/or niche relationships. Thus, most species in Washington may concentrate feeding in brush and exhibit higher overlap because brush microhabitats were more plentiful than in other locations. However, we would not expect such species convergence in microhabitat use if food resources were limiting. The distribution of food among microhabitats could also affect foraging patterns. It is difficult to assess the importance of these environmental variables at present because data are not available for each site. At any rate, it is quite possible that more than one factor contributes to the observed niche relationships in mixed flocks.

Whereas our data are suggestive, longer term studies, preferably encompassing a variety of environmental conditions (climate, food abundance, etc.) should be conducted to increase our understanding of the mechanics involved in niche relationships within mixed flocks. Changes in niche overlap, niche breadth, interspecific aggression, and flock size would be particularly illustrative, although niche relationships can be completely understood only when knowledge of resource abundance and dynamics is secure (Wiens and Rotenberry 1979).

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Sexual dimorphism and parental role switching in Gila Woodpeckers.—Since the seminal work of Selander (Condor 68:113–151, 1966) sexual dimorphism in woodpeckers has generally been considered to be a mechanism for the reduction of competition for food between mates. For a pair of monogamous birds to raise young successfully, they must not only provide food, but must also excavate new nest cavities, clean the nest of fecal material, guard the young, defend the food supply from other birds, and so on. These activities can represent conflicting demands. Using an optimality approach, for instance, Martindale (Behav. Ecol. Sociobiol. 10:85–89, 1982) showed that an individual cannot simultaneously maximize both nest defense and food delivery rate. Size dimorphism may be used to advantage in performing various tasks simultaneously if the pair coordinates their activities, dividing the labor so that each bird specializes in those behaviors for which its size makes it more efficient. In this note, we document the size dimorphism of Gila Woodpeckers (*Melanerpes uropygialis*) and demonstrate that mates coordinate their activities. We consider sexual differences not only in morphology, but also in foraging behaviors, the propensities to attack other birds, and to guard the young as opposed to feeding them. We also present evidence of facultative role switching between mates.

Methods.—Four hundred Gila Woodpeckers were mist-netted in Tucson, Pima Co., Arizona, during the winter months, November–April, from 1971–1979. Lamm banded each bird; its exposed culmen, wing and tail lengths, and weight were measured before it was released. All lengths were measured to the nearest 1.0 mm, and weights to the nearest 0.1 g.

Behaviors were observed by Martindale in Saguaro National Monument (Tucson Mountain Unit), 25 km W of Tucson, during the breeding seasons of 1978–1980. Twelve pairs of birds were observed for at least 20 h. When the woodpeckers foraged on a desert shrub (foothill paloverde [*Cercidium microphyllum*] or desert ironwood [*Olneya tesota*]), the size of the branch the bird was on was noted as small (tertiary branches with leaves, < 2 cm in diameter), medium (secondary branches between the main trunk and the leaf branches, roughly 2–10 cm in diameter), or large (main trunks, >10 cm in diameter). Records were kept of all aggressive interactions with other birds, distances from the nest of individual birds, and delivery rates of food items to the nestlings (trip/h).

For the morphological measurements, summary statistics ($\bar{x}$, SD), parametric (t) tests for the differences between the sexes, and product-moment correlation coefficients (r) among variables were calculated with the BMDP software package on a UNIVAC 1100/82 computer. Two-way contingency tables were used to test for differences between sexes in the categorical data, i.e., parts of shrubs used and species of birds attacked. For ease of interpretation, these tables are summarized here as proportions of observations in each category