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COMMUNITY ASSEMBLY PATTERNS OF PARIDS ALONG AN ELEVATIONAL GRADIENT IN WESTERN CHINA

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ABSTRACT.—Eight species of parids commonly occur in the mountains of northern Sichuan Province, People's Republic of China. They represent four monophyletic groups regarded by some authorities as genera, but more traditionally as subgenera of the large genus *Parus*. To test the competition-based hypothesis that less closely related species are more likely to co-occur, we used specimens and observations obtained in October 1989 and May 1991 to delineate the morphology, elevational range, and habitat associations of each species in this rich assemblage. A morphometric cluster analysis did not support the assumption that phylogenetic similarity predicts morphological and hence ecological similarity. Up to five species commonly co-occurred in mixed flocks, as in Europe (where five subgenera are represented), but a randomization test showed that community assembly was random with respect to subgenus. On the other hand, for the entire data set ($P = 0.05$) and during spring ($P = 0.07$), species in the same morphometric cluster were less likely to co-occur than were species with dissimilar morphology. It appears, therefore, that competition between species of similar morphology may play (or have played) some role in structuring assemblages of parids during the breeding season in this area. For this reason, more detailed studies of the parid assemblage in this area are recommended. *Received 2 June 2000, accepted 16 February 2001.*

The coexistence of ecologically similar species is one of the abiding problems of community ecology (Hutchinson 1959; Wiens 1991a, b). Beginning with Grinnell (1904) and Gause (1934), a popular way of addressing this problem was to study geographical and ecological overlap of closely related species. This linkage between ecological overlap and phylogenetic similarity is based on the assumption that closely related species are likely to share ecological characteristics because of recent common ancestry (Brooks and McLennan 1991). In other words, the more closely related are two species, the less likely are they to have evolved niche-partitioning mechanisms that allow coexistence (e.g., Lack 1971). In this classical view, closely related species are thought to be more likely to compete for limiting resources, and owing to competitive exclusion should be less likely to coexist geographically or ecologically than are less closely related species.

Beginning with Wiens (1977), the equilibrial assumptions of this competition-based model were questioned on empirical grounds, and the nonequilibrial "intermediate disturbance" model (Connell 1978) of community organization gained favor (Reice 1994, Meffe and Carroll 1997). In this view occasional disturbances tend to keep an ecosystem at a subclimax level of succession, thereby allowing ecological specialists, generalists, and disturbance-adapted species to coexist, all at densities below carrying capacity (Reice 1994).

Nonetheless, carefully designed studies have shown convincingly that interspecific competition does play a role in community organization, particularly within the avian family Paridae. For example, both observational (Alatalo et al. 1985a, 1986) and experimental (Alatalo et al. 1985b, 1987; Cimprich and Grubb 1994) studies have shown that presence or absence of a species in mixed flocks of parids influences the foraging of the one most closely related species. Also, Dhondt (1977) and Dhondt and Eyckerman (1980) showed experimentally that Blue Tits ("*Cyanistes*" *caeruleus*) and Great Tits ("*Parus*" *major*), which are each other's closest sympatric relatives (Sheldon et al. 1992, Slikas et al. 1996),

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have negative effects on the fitness of each other both during and outside the breeding season. These studies show competitive effects at the local level, where individuals actually meet, that could underlie evolved habitat differences, or allopatry.

Using null models to test competition-based hypotheses.—Rigorously testing the prediction that competition between closely related species influences community assembly requires methods that were not available to Lack (1969, 1971). Diamond (1975) introduced the practice of inferring the past role of interspecific competition from a matrix of presence-absence data of species in a set of sites, but was criticized for inferring a competitive process from statistical patterns without the use of null models of community assembly (Strong 1982; Connor and Simberloff 1983, 1984; but see Gilpin and Diamond 1982). Fox (1987) developed new null models and claimed to find evidence of competition in communities of Australian small mammals (Fox 1989), North American soricids (Fox and Kirkland 1992), and North American desert rodents (Fox and Brown 1993). Stone et al. (1996) refined Fox's models and claimed to find no evidence of competition in the data sets analyzed by Fox and Brown (1993).

Fox (1987, 1989) reasoned that past interspecific competition will have driven present communities to assume "favored states." Favored states are defined as species compositions in which the number of species in coexisting "functional groups" differ by no more than one. Functional groups are defined as "groups of species that are ecologically similar" (Stone et al. 1996:999), such as genera or other taxonomically related groups of species (Fox 1987:201). The rationale for the prediction of favored states is that the community is more likely to accommodate an additional species that is less competitive with those species already present.

Testing the favored state hypothesis with parid assemblages.—The subgenera of the family Paridae clearly qualify, *a priori*, as functional groups. Up to six species of parids co-occur in the same woodlands in Europe (Lack 1969, Herrera 1981), and these are subdivided into five monophyletic taxa (Gill et al. 1989, Sheldon et al. 1992, Slikas et al. 1996). As the competitive process underlying Fox's prediction about community structure has been confirmed for European parids (see above), community assembly in this family should be an ideal subject for investigation with Fox's more rigorous methods.

We tested the favored state prediction with co-occurrence patterns in an Asian assemblage of tits. Eight species, representing four subgenera, were observed along a montane elevational gradient in western China in 1989 and 1991. Three subgenera contained more than one species (compared with only one in Europe), offering the statistical power of a number of potential states. Our observations in China allow us to address these questions with data based on direct field experience in a restricted locality, which is the scale employed in recent studies of phylogeny and foraging ecology of Indian leaf-warblers (Price 1991, Richman and Price 1992) and Fennoscandian tits (Suhonen et al. 1994).

An assumption of the classical competitive exclusion hypothesis, and of Fox's favored state prediction, is that ecological similarity is correlated with the genetic similarity embodied in subgeneric identity (Brooks and McLennan 1991). Ecological similarity can be inferred from foraging patterns in the absence of potential competitors, or indirectly from morphometric comparisons. We tested the ecological similarity assumption with morphometric data obtained from specimens we collected in the same area from which distribution data were obtained. In Fennoscandian parids closely related to those we studied, "there are clear relationships between morphology and ecology at a functional level" (Wiens 1991a:192).

The objective of this study was to test the classical prediction that less closely related species are more likely to co-occur, in an avian family and local species assemblage especially suited to revisitation of this question. We introduce Fox's method of favored states to the analysis of bird assemblages, using an algorithm that has been used to question some mammalian assemblage patterns (Stone et al. 1996) and therefore should provide a rigorous test of the competition-based hypothesis of community assembly.

STUDY AREA AND METHODS

Study area and field methods.—Our study was conducted in northwestern Sichuan Province, People's Republic of China, on 16–31 October 1989 and 7–19 May 1991. We made casual observations in the urban habitat of Chengdu (elevation 510 m) during both months, and worked at Qingcheng Shan, a forested religious shrine rising from 750–1000 m in the foothills northwest of the city, on one day each in October and May. The steep slopes of Qingcheng Shan were densely forested with broadleaf evergreens.

Systematic observations were made in the Min Shan mountains of Aba Tibetan Autonomous Prefecture, approximately 400 km northwest of Chengdu. Camp 1 (elevation 3950 m), visited in 1989 only, was near the divide between the Huang He and Chang Jiang (Yangtze) drainages, about 55 km northeast of Hongyuan, at the eastern edge of the Tibetan Plateau. Patches of spruce-fir (*Picea-Abies*) forest on north-facing slopes of low peaks were surrounded by vast expanses of wet steppe. Camps 2–5, visited in 1989 and 1991, were along the road that runs north from Songpan to Nanping. They lay along an elevational gradient running from above timberline at Camp 4, near the divide between the Min Jiang and Baishui watersheds (both are tributaries of the Chang Jiang), down a forested valley (hereafter Main Valley). In 1991 we also studied a gradient in the tributary valley occupied by Jiu Zhai Gou National Park (JZG). Elevations were estimated from Defense Mapping Agency aeronautical maps and from multiple readings of an altimeter. In both valleys, subalpine forest of *Picea*, *Abies*, and *Larix* (larch) extended from timberline (roughly 3400 m in the Main Valley) to around 2800 m. From this level, a very diverse mixed forest with many species of conifers and deciduous broadleaf trees extended down to roughly 2100 m. Below 2100 m was pine (*Pinus*) forest.

At Camp 1 and in the Main Valley we concentrated our efforts near camp and did not survey other elevations systematically. In JZG, however, we walked the entire elevational gradient from 1920–2620 m at least once, and parts were covered repeatedly. We noted each species and its associates when seen or heard, as well as a general impression of abundance (usually 2–4 individuals per species). Field identification was based upon Meyer de Schauensee (1984), supplemented with Harrap and Quinn (1995) after the fact, and documented with study skins collected in 1989 and deposited at the Academy of Natural Sciences, Philadelphia; and with >14 h of tape-recorded bird vocalizations, deposited at the Borror Laboratory of Bioacoustics, Ohio State University. Subspecific assignments were based on locality, not upon diagnosis, and follow Cheng (1987).

The species pool.—Recent biochemical studies (Gill et al. 1989, Sheldon et al. 1992, Slikas et al. 1996) have affirmed the monophyly of several of Hellmayr's (1903) subgenera of the genus *Parus* (*sensu lato*), leading to their elevation to generic status by the American Ornithologists' Union (1997, 1998). Because this decision has been controversial, and at any rate does not include the Eurasian taxa that are the subjects of this study, we follow here the more traditional practice of regarding these monophyletic groups as subgenera. Although their monophyly is important to our hypotheses, the taxonomic rank of these taxa does not affect our hypotheses.

We use scientific names throughout, because English names (listed in Table 1) are not standard and subgeneric names help subdivide the taxa meaningfully. Subgeneric names are indicated by quotation marks, and the common generic epithet *Parus* is omitted.

Eight species (Table 1), representing four of these subgenera, were the subjects of our study. Three species are found west to western Europe, but are taxonomically and morphologically distinct (see illustrations in Harrap and Quinn 1995). The Great Tits ("*Parus*" *major tibetanus*) in our study area (Cheng 1987) represent the "*minor*" semispecies (Snow 1954, Harrap and Quinn 1995), and local Coal Tits ("*Periparus*" *ater aemodius*) are crested, like the other representatives of "*Periparus*" in this part of Asia. The Willow Tits occurring in this part of China ("*Poecile*" *montanus weigoldicus*) are considered part of a separate species, the Songar Tit ("*Poecile*" *songarus*) by some authorities (e.g., Cramp and Perrins 1993, Harrap and Quinn 1995), but recent studies of vocalizations (Martens and Nazarenko 1993, Thönen 1996) do not support this position. The other five species in Table 1 are restricted to temperate elevations in China and contiguous countries. The Yellow-bellied Tit (*Parus venustulus*) was observed a few times in 1991. Because of its scarcity, it was not included in the analyses that follow.

Analytical methods.—To confirm that subgenera are appropriate functional groups for the hypothesis of competition-based community assembly, we tested the assumption that subgeneric identity accurately reflects ecological similarity. We did this with a multivariate morphometric analysis. Masses were measured during field preparation of specimens in 1989. Wing, tail, tarsus, and bill lengths, and bill depth were measured from skins housed at the Academy of Natural Sciences, Philadelphia, in 1993. Wing chord was unflattened, culmen length was measured from the nasofrontal hinge, bill depth was measured at the nostril, and tarsus was measured from the proximal end of the tarsometatarsus to the last undivided scute above the foot.

To estimate morphometric distances among species, we submitted standardized species means for the six variables to hierarchical cluster analysis, using all five joining algorithms implemented in JMP (SAS Institute Inc. 1995). To allow comparison of these morphometric relationships with published results from Europe (Suhonen et al. 1994), we submitted the same data to principal components analysis (Proc Princomp, SAS version 6.04) of the correlation matrix, and plotted species scores on the first two principal component axes.

To test the prediction that functional groups are in favored states, we used a Monte Carlo simulation, written for SAS version 6.04 by DAM, to produce 5000 "notional" presence-absence matrices, in which the species remained the same, but subgeneric affiliation was randomly assigned, according to the ratio 2:2:1:3 ("*Parus*":"*Periparus*":"*Lophophanes*":"*Poe-*

TABLE 1. Tit species occurring in the Min Shan Mountains of northern Sichuan Province, People's Republic of China, October 1989 and May 1991, selected measurements of specimens, and first two principal components. Values are means ± SD (*n*).

Species	Bill length (mm)	Bill depth (mm)	Wing length (mm)	Tail length (mm)	Tarsus length (mm)	Mass (g)
"*Parus*" *major tibetanus*[a]	10.87 ± 0.58	4.46 ± 0.41	69.14 ± 1.86	59.33 ± 1.63	19.15 ± 0.35	14.05 ± 0.42
Great Tit[b]	(3)	(7)	(7)	(6)	(2)	(4)
"*Parus*" *monticolus yunnanensis*	9.90 ± 0.17	4.00 ± 0.13	64.71 ± 2.56	49.14 ± 2.19	17.85 ± 0.92	12.78 ± 1.15
Green-backed Tit	(3)	(7)	(7)	(7)	(2)	(7)
"*Periparus*" *ater aemodius*	8.03 ± 0.12	3.23 ± 0.15	58.33 ± 2.52	38.67 ± 0.58	15.77 ± 0.70	7.33 ± 0.58
Coal Tit	(3)	(3)	(3)	(3)	(3)	(3)
"*Periparus*" *rubidiventris beavani*	8.23 ± 0.06	4.03 ± 0.35	65.50 ± 0.87	45.33 ± 0.58	18.53 ± 0.58	9.63 ± 0.23
Rufous-vented Tit; Black-created Tit	(3)	(3)	(3)	(3)	(3)	(3)
"*Lophophanes*" *dichrous dichroides*	9.70 ± 0.29	3.98 ± 0.29	74.25 ± 4.99	51.33 ± 3.51	20.52 ± 0.33	13.75 ± 0.50
Grey-crested Tit; Brown-cresed Tit	(4)	(4)	(4)	(3)	(4)	(4)
"*Poecile*" *montanus weigoldicus*	8.67 ± 0.29	4.35 ± 0.10	65.00 ± 2.31	54.75 ± 2.75	17.70 ± 0.37	10.88 ± 0.85
Willow Tit	(4)	(4)	(4)	(4)	(4)	(4)
"*Poecile*" *superciliosus*	8.14 ± 0.65	4.80 ± 0.27	62.50 ± 1.47	60.83 ± 2.48	18.15 ± 0.07	10.71 ± 0.57
White-browed Tit	(5)	(6)	(7)	(6)	(2)	(7)
"*Poecile*" *davidi*	8.83 ± 0.55	4.47 ± 0.15	66.0 ± 0.00	48.33 ± 1.53	17.40 ± 0.53	10.33 ± 0.58
Rusty-breasted Tit; Red-bellied Tit; Père David's Tit	(3)	(3)	(3)	(3)	(3)	(3)
EIGENVECTORS						
PCl, Eigenvalue = 3.996, % variance = 66.6	0.391	0.301	0.432	0.377	0.444	0.480
PC2, Eigenvalue = 1.285, % variance = 21.4	−0.318	0.675	−0.318	0.540	−0.172	−0.143

[a] Subspecies based on Cheng (1987) and geography, not diagnosis.

[b] English names from Sibley and Monroe (1990); other commonly used English names appended for cross reference.

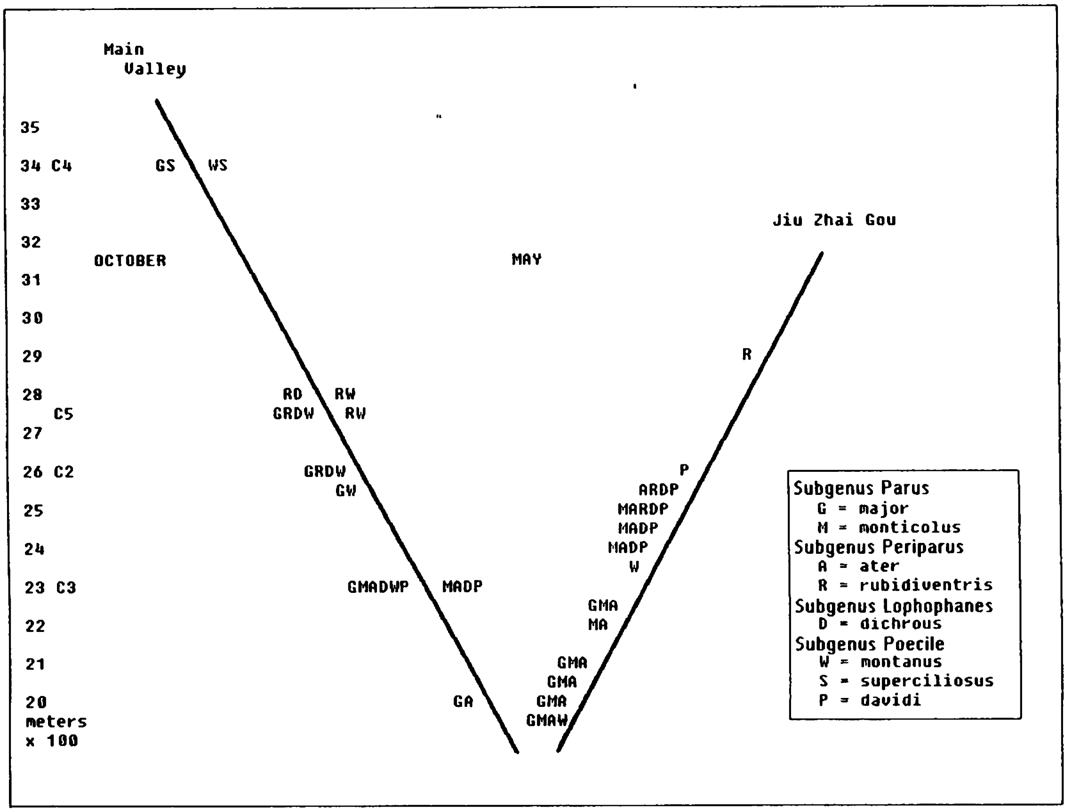

FIG. 1. Schematic of elevations at which eight species of tits were observed in October 1989 and May 1991 in two montane valleys in northcentral Sichuan, China. The slope on the left refers to a tributary valley of the Baishui River occupied by the road from Songpan to Nanping; that on the right to a secondary tributary valley occupied by Jiu Zhai Gou National Park. Each species is symbolized by a unique letter (see box). Observations made in October (Main Valley only) are on the outside of the sloping line; those made in May are on the inside of the sloping lines. Elevations of Camps 2–5 are indicated along the left margin. Each string of letters represents the species found at a single spatio-temporal site in the analysis of favored states. Co-occurrence of members of the same subgenus was not less frequent than expected by chance (P = 0.203 for October, P = 0.556 for May).

cile''). This elegant method, developed by Stone et al. (1996), preserves the uniqueness of the range, physiological tolerances, and dispersal capabilities of each species, unlike previous methods (Fox 1987, 1989; Fox and Brown 1993) that randomize the presence-absence matrix itself. The randomization test estimates the discrete probability distribution (Manly 1991), for a specific data set, of the percentage of sites in favored states when generic identities are randomly assigned.

For our analyses, a site was defined as a single habitat type in Qingcheng Shan or Camp 1, or a 50-m elevational range in one of the two valleys (Fig. 1), in either October or May. Each row of the data matrix (Appendix 1) was based on multiple sightings of tits. The sites in Fig. 1 with one or no species were not sampled adequately for inclusion in the data set. The overall N of 25 sites was distributed as follows: 21 sites from the two valleys, 2 from Qingcheng Shan (one habitat type, two seasons), and 2 from Camp 1 (two habitat types, one season each). For example, the assemblage at 2800 m in the Main Valley in May had two species, ''*Periparus*'' *rubidiventris* and ''*Poecile*'' *montanus*, and was in a favored state because all subgenera were represented by either 0 or 1 species.

RESULTS

We observed all local species except ''*Poecile*'' *davidi* repeatedly in both years. Each occurred in a characteristic range of elevations (Fig. 1, Appendix 1). Transects taken on the same date allowed us to quantify each gradient on an ordinal scale, but absolute elevations on different gradients (e.g., Main Valley vs. JZG) may not be exactly comparable, because

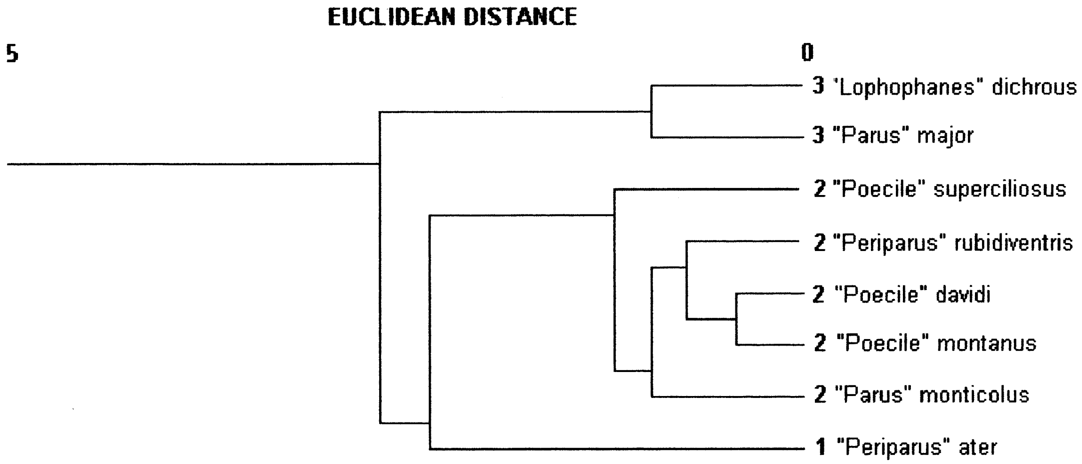

FIG. 2. Dendrogram of morphometric similarity among eight species of tits, observed in October 1989 and May 1991 in northcentral Sichuan, China. See Table 1 for univariate descriptive statistics. Clusters 1–3, based on Ward's minimum variance method, were also recovered by four other algorithms. Co-occurrence of members of these clusters was less frequent than expected by chance in spring ($P = 0.07$) and in the seasonally pooled data set ($P = 0.05$).

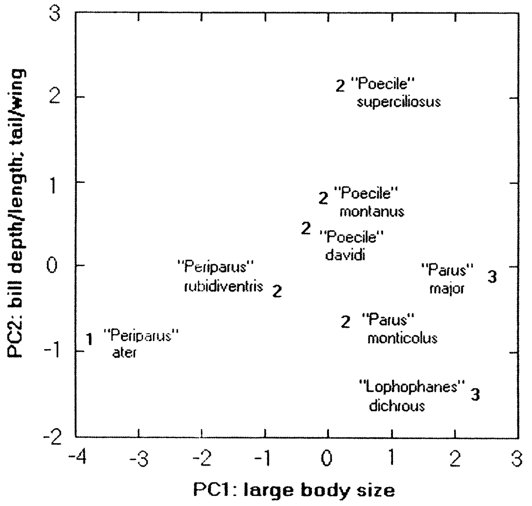

FIG. 3. Morphometric relations of species and subgenera of tits, observed in October 1989 and May 1991 in northcentral Sichuan, China, on Principal Components 1 and 2 (unrotated). See Table 1 for eigenvalues and eigenvectors of this PCA. Plotting symbols are cluster numbers from Fig. 2. Though "*Parus*" *monticolus* and "*Periparus*" *rubidiventris* are the nearest neighbors of their closest relatives, they appear to have converged on the size range of *Poecile,* yielding the morphometric clusters of Fig. 2.

altimeter readings for single sites varied by up to 100 m from day to day.

Morphometrics.—The dendrogram resulting from the cluster analysis (Fig. 2) showed that the subgenera in our study did not cluster morphometrically. Although branch lengths differed somewhat, the five cluster methods available in JMP (Ward's, average linkage, single linkage, centroid, and complete linkage) all identified the three clusters defined in Fig. 2.

Principal components analysis of the same morphometric data set shows that overall size (Rising and Somers 1989) probably is the main contributor to this subdivision. The first two principal components, which together captured 88% of the variance in the data set (Table 1), appear to represent size and shape, as expected of morphometric data (Rising and Somers 1989). PC1, with coefficients ranging from 0.30 to 0.48, is a gradient of increasing size. PC2 is a gradient of increasing tail length and bill depth, and decreasing wing length and bill length. This is equivalent to the ratios tail: wing and bill depth:bill length. These shape characteristics are associated with foraging styles in European parids (Norberg 1979). A scatterplot of the first two PCs (Fig. 3) shows that the subgenera occupy discrete zones of morphometric space, but that "*Periparus*" *rubidiventris* and "*Parus*" *monticolus* appear more similar in size to "*Poecile*" spp. than to the members of their own subgenera. Their convergence on the central part of PC1 leads to the clusters seen in Fig. 2.

If morphological similarity reflects ecological similarity, then the assumption that subgenera are ecological functional groups appears incorrect. We therefore tested Fox's favored state prediction on morphometrically-defined functional groups as well as subgenera. We identified three morphometric functional groups (Fig. 2, Appendix 1), representing the robust results of the five clustering methods, as described above. These assignments reflect overall size differences (Fig. 3), perhaps the most commonly cited means by which closely related species avoid competition in sympatry (see Wiens 1991a, chapter 7, for review), and so offer a plausible alternative to the phylogenetic hypothesis that motivated this study.

Co-occupancy of habitat.—Fig. 1 shows the patterns of co-occurrence among all species in the Main Valley and JZG, and Appendix 1 translates these data into a presence-absence matrix, which also includes the data from Qingcheng Shan and Camp 1. As many as six species occurred in close proximity, up to five were seen together in mixed flocks in two localities, and four co-occurred commonly. Thus, maximal assemblage size was similar to that in Europe (Lack 1971, Herrera 1981), and much greater than in North America and Africa (Lack 1969, 1971).

For the analysis of favored states (Fox 1987, 1989), each site (Appendix 1) was regarded as an independent sample. Sixteen of the 25 sites (64%) had assemblages in favored states. When the subgeneric identity of each species was randomly assigned in 5000 notional presence-absence matrices that were otherwise identical to the observed matrix (Stone et al. 1996), 36% of the resulting notional matrices had as many or more favored states than the observed matrix. In other words, a percentage of favored states as high as 64% would occur randomly with a probability of $P = 0.362$. Separate tests for the October assemblages (80% of 10 sites in favored states, $P = 0.203$) and the May assemblages (53% of 15 sites in favored states, $P = 0.556$) were also not significant. We therefore failed to reject the null hypothesis that the observed presence-absence matrix is random with respect to subgenus.

On the other hand, randomization tests for morphometric functional groups suggested that the number of favored states for the entire data set (16, or 64%) was nonrandom ($P = 0.053$). This effect apparently was due mainly to the spring data, which approached significance (73.3%, $P = 0.068$). The five favored states in the fall data (50%) were not significantly different from random ($P = 0.419$).

DISCUSSION

Our results are clearly provisional, as the morphometric study is based on a small sample of specimens, and the ecological data were gathered during 2–3 wk periods in spring and fall. However, studies in this part of the world are rare, and the results reported here suggest that more detailed work in this area would be well worth the effort required to reach the area, from academic centers in China as well as from other parts of the world.

Analytical methods: morphometrics.—Morphometrics performs two important functions in this study: (1) showing that subgenera in this assemblage are not good functional groups, and (2) suggesting functional group assignments that better fulfill the ecological assumptions of Fox's (1987, 1989) method. Because of this, we elaborate on our methods here. It was suggested that we drop mass from the morphometric analysis so we could use the covariance matrix for PCA, which is preferred by statisticians (James and McCulloch 1990), despite the widespread use of the correlation matrix in studies such as ours and the finding that "analyses using the variance-covariance matrix are influenced by the variation of each character relative to the variation of all other characters" (Rising and Somers 1989:672). We retained mass in the multivariate data set for both biological and heuristic reasons.

In Eurasian Paridae, all the other morphological features we measured vary with foraging style (Norberg 1979, Wiens 1991a, Suhonen et al. 1994), so mass is needed to anchor a general size component, which PC1 is normally expected to be. If we omit mass and use the covariance matrix, PC1 is driven by tail length (Table 1). Moreover, the species with the greatest score on this axis is "*Poe-*

cile" *superciliosus,* which is only the fourth heaviest species in the data set (Table 1). Taking the approach recommended for purely statistical reasons, therefore, omits the primary component of morphological variation, size.

On the heuristic side, when mass is included and the correlation matrix of species means is used (as by Suhonen et al. 1994), the unusual shape of "*Poecile*" *superciliosus* is displayed on PC2, and the similarities between Chinese and European tits (Suhonen et al. 1994) are much more apparent (see below). The same arguments apply for cluster analysis, which also can use either a covariance or correlation matrix.

Analytical methods: randomization test.—A randomization test (Manly 1991) is the correct way to estimate the likelihood that community patterns arose by chance. The data are clearly spatially autocorrelated (Fig. 1) and should not be analyzed with conventional parametric tests, which assume spatial independence. Spatial independence of samples is not an assumption of our randomization test (Stone et al. 1996). Indeed, one of the problems with previous randomization procedures (Fox 1987, 1989; Fox and Kirkland 1992; Fox and Brown 1993) was that randomizing the presence-absence matrix, rather than functional group assignments, destroyed the spatial autocorrelation structure inherent in the geographic distributions of the species pool (Stone et al. 1996). Moreover, the area we sampled was smaller than those sampled by Fox and Brown (1993), which lessens the potentially confounding effect of nonoverlapping geographic ranges (Stone et al. 1996).

The result of each randomization test is specific to its own data set (Manly 1991). Thus it is possible for 64% favored states to be significant in one case (morphometric functional groups) and not in another (phylogenetic functional groups). This outcome underscores the importance of estimating the probability distribution of possible outcomes with resampling techniques (Manly 1991).

Sample size (number of sites) also appears to influence the power of this test. For example, the highest value (80%, fall phylogenetic functional groups, $n = 10$ sites, $P = 0.204$) was clearly not significant, while values of 73% (spring morphometric functional groups, $n = 15$, $P = 0.068$) and 64% (all morphometric functional groups, $n = 25$, $P = 0.053$) had much lower P-values. It may be, therefore, that a larger sample of sites in fall would have produced a significant test for phylogenetic functional groups. These results should therefore be interpreted cautiously, and call for further study of this assemblage.

Morphometrics and ecology.—Suhonen et al. (1994) ordinated seven species (three of which also occurred in our study), one each from the subgenera "*Periparus,*" "*Parus,*" "*Cyanistes,*" and "*Lophophanes,*" and three from "*Poecile.*" The loadings on PC1 were much higher in that study than in ours, but morphological relationships among subgenera were nonetheless very similar. In both cases the three "*Poecile*" species were intermediate in size, and had shorter and deeper bills than members of the other three subgenera represented in both data sets. "*Parus*" *major* and "*Periparus*" *ater* formed the extremes of the size continuum in both assemblages, with their closest relatives in Sichuan ("*Parus*" *monticolus* and "*Periparus*" *rubidiventris,* respectively) converging on the size range of "*Poecile.*" Finally, in both assemblages, the local representative of "*Lophophanes*" had the longest and thinnest bill for its size. These commonalities suggest that subgeneric morphologies are highly conserved in Eurasian parids. On the other hand, in North America, which lacks "*Lophophanes*" and "*Periparus,*" thin-billed conifer specialists have evolved within the subgenus "*Poecile,*" e.g., "*Poecile*" *gambeli* and "*Poecile*" *rufescens.*

Perhaps we should not have relied on morphometric analysis to test the ecological similarity assumption, but instead should have gathered field data on foraging. Aside from the common use of morphometrics for this purpose (many examples in Wiens 1991a, b; see also Price 1991, Suhonen et al. 1994), and the established relationship between morphology and foraging differences in Fennoscandian parids (Norberg 1979, Wiens 1991a), we would argue that morphology (which changes on an evolutionary time scale) is preferable to foraging behavior (which can change instantaneously; Alatalo et al. 1985b) for testing this assumption, at least with reference to Fox's model, which clearly invokes past competition as the cause of current community patterns. Moreover, as competition is implicated only for the breeding season data, and overall size rather than foraging morphology (e.g., bill shape, tarsus length, tail length) is the main attribute defining our morphometric functional groups, it may be that the observed co-occurrence patterns owe more to interspecific territoriality than to foraging behavior. These conjectures are testable with more detailed field studies.

Community assembly patterns.—Up to five species traveled together in mixed flocks, as in Europe (Lack 1971). This extends the pattern identified by Lack (1969) for Europe, America, and Africa, i.e., the more subgenera the more co-occurring species. Our randomization tests of community assembly, however, suggest that assemblages of tits in northern Sichuan are not structured according to subgeneric identity. The high percentage of sites in favored states in October (80%, $P = 0.20$), though, suggests that a larger number of sites should be studied at this time of year.

The hypothesis that competition played a role in community structure was not, however, refuted by these results, because the key assumption that phylogenetic similarity maps onto ecological similarity was not supported by our morphometric analysis. For this parid assemblage, morphological groups are more pertinent to the competition hypothesis than are phylogenetic ones. Because our randomization tests were significant for pooled data and nearly so for spring data, it appears that, in spring at least, morphologically dissimilar species were more likely to co-occur than were morphologically similar species. This is consistent with Fox's (1987, 1989) competition-based hypothesis. Further, although Stone et al. (1996) challenged the adequacy of Fox's algorithm for generation of null models, they did not challenge his definition of favored states. It would therefore seem that the hypothesis that competition played a role in causing the patterns we observed has withstood a rigorous test.

Zoogeography.—Cheng et al. (1965) used Chinese and western literature records and their own specimen data for a zoogeographic analysis of the avifauna of northwestern Sichuan. They described the following three zones: (1) cold plateau meadow and scrub zone, (2) cold plateau subalpine coniferous forest zone, and (3) mixed forest bordering the Sichuan Red Basin. Judging from their map and descriptions of vegetation, our camps 1 and 4 were clearly in zone 1, while subtropical Qingcheng Shan was in zone 3. The Main Valley and JZG appeared transitional between zones 2 and 3.

Our geographic data are completely consistent with the range maps Cheng (1987) derived from the work of Cheng et al. (1965) and Li et al. (1976). "*Periparus*" *ater* and "*Poecile*" *davidi* were found only in the Main Valley/JZG area. "*Parus*" *monticolus* was restricted to the same area plus lower elevations near Chengdu (i.e., zone 3). Our study area therefore may have straddled the western edge of the ranges of all three taxa. Moreover, "*Poecile*" *montanus* localities in this area of Sichuan are all slightly west of "*Poecile*" *davidi* localities (Cheng 1987, maps 704 and 706; Harrap and Quinn 1995, Fig. 57.1). This zoogeographic information does not invalidate the community level patterns we documented for the Main Valley and JZG, but it does suggest that the large species assemblages we observed are not to be expected either west or east of the boundary between zones 2 and 3. Our study area, then, would be an excellent place in which to conduct long term studies of competition and coexistence among parids.

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Appendix 1. Presence/absence data used in randomization tests. Except for Camp 1 and Qingcheng Shan, all sites are shown on Figure 1. Data for sites in favored states are printed in boldface. A favored state occurs when the numbers of species in the functional groups differ by no more than one. Functional groups are defined by subgenus and, alternatively, by morphometric cluster.

			Presence/Absence										
			By Subgenus and Species								By Morphological Group		
Sites			"*Parus*"		"*Periparus*"		"*Lophophanes*"	"*Poecile*"					
Month	Locality	Elevation (m)	*major*	*monticolus*	*ater*	*rubidiventris*	*dichrous*	*montanus*	*superciliosus*	*davidi*	I *P. ater*	II *P. major* & *P. dichrous*	III others
May	Qingcheng Shan	—	**0**	**1**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**1**
May	JZG Valley	1950	1	1	1	0	0	1	0	0	**1**	**1**	**2**
May	JZG Valley	2000	1	1	1	0	0	0	0	0	**1**	**1**	**1**
May	JZG Valley	2050	1	1	1	0	0	0	0	0	**1**	**1**	**1**
May	JZG Valley	2100	1	1	1	0	0	0	0	0	**1**	**1**	**1**
May	JZG Valley	2200	**0**	**1**	**1**	**0**	**0**	**0**	**0**	**0**	**0**	**1**	**1**
May	JZG Valley	2250	1	1	1	0	0	0	0	0	**1**	**1**	**1**
May	JZG Valley	2400	**0**	**1**	**1**	**0**	**1**	**0**	**0**	**1**	**1**	**1**	**2**
May	JZG Valley	2450	**0**	**1**	**1**	**0**	**1**	**0**	**0**	**1**	**1**	**1**	**2**
May	JZG Valley	2500	**0**	**1**	**1**	**1**	**1**	**0**	**0**	**1**	1	1	3
May	JZG Valley	2550	0	0	1	1	1	0	0	1	**1**	**1**	**2**
May	Main Valley (Camp 3)	2300	**0**	**1**	**1**	**0**	**1**	**0**	**0**	**1**	**1**	**1**	**2**
May	Main Valley (Camp 5)	2750	**0**	**0**	**0**	**1**	**0**	**1**	**0**	**0**	0	0	2
May	Main Valley	2800	**0**	**0**	**0**	**1**	**0**	**1**	**0**	**0**	0	0	2
May	Main Valley (Camp 4)	3400	0	0	0	0	0	1	1	0	0	0	2
October	Qingcheng Shan	—	1	1	0	0	0	0	0	0	**0**	**1**	**1**
October	Camp 1 (woodland)	—	**0**	**0**	**0**	**1**	**1**	**1**	**0**	**0**	0	1	2
October	Camp 1 (tundra)	—	0	0	0	0	0	1	1	0	0	0	2
October	Main Valley	2000	**1**	**0**	**1**	**0**	**0**	**0**	**0**	**0**	**1**	**1**	**0**
October	Main Valley (Camp 3)	2300	**1**	**1**	**1**	**0**	**1**	**1**	**0**	**1**	2	1	3
October	Main Valley	2550	**1**	**0**	**0**	**0**	**0**	**1**	**0**	**0**	**0**	**1**	**1**
October	Main Valley (Camp 2)	2600	**1**	**0**	**0**	**1**	**1**	**1**	**0**	**0**	0	2	2
October	Main Valley (Camp 5)	2750	**1**	**0**	**0**	**1**	**1**	**1**	**0**	**0**	0	2	2
October	Main Valley	2800	**0**	**0**	**0**	**1**	**1**	**0**	**0**	**0**	**0**	**1**	**1**
October	Main Valley (Camp 4)	3400	**1**	**0**	**0**	**0**	**0**	**0**	**1**	**0**	**0**	**1**	**1**