THE ROLE OF SIZE ASSORTMENT
IN STRUCTURING NEOTROPICAL BIRD COMMUNITIES

Daniel M. Brooks
Houston Museum of Natural Science; Department of Vertebrate Zoology;
One Hermann Circle Dr.; Houston, Texas 77030-1799, USA

ABSTRACT - I tested confamilial size assortment at three different latitudes, representing a gradient of productivity and stability: the northern subtropics (Rio Grande Valley), the equatorial zone (Amazonian Peru) and the austral subtropics (Paraguayan Chaco). Size assortment is the likely diminished persistence of a species by presence of morphologically similar species; temporally synchronous and spatially sympatric species competing for similar resources should exhibit distinct characters in ecomorphological space, molded over time to reduce the chance of competition. Despite least intensive sampling effort at the Amazon site, it is the most speciose (238 species, 78 common) compared to the Chaco (147, 76) and Rio Grande (61, 24) sites. Size assortment was tested by comparing mean mandibular measurements of confamilials in a real pool against those in a null pool. The pattern of size assortment was pervasive in 68% of the 22 families tested, with most being animal consumers or omnivores, represented by a high percentage of insectivores.

EL PAPEL DE LA VARIEDAD DE TAMAÑO EN LA ESTRUCTURACIÓN DE LAS COMUNIDADES DE AVES NEOTROPICALES - La variedad del tamaño confamiliar (miembros de la misma familia) fue probada en tres latitudes diferentes representando un gradiente de productividad y estabilidad: el subtrópico septentrional (Valle del Río Grande), la zona ecuatorial (Amazonas peruano) y el subtrópico austral (Chaco paraguayo). La variedad de tamaño es la persistencia disminuida por la presencia de especies morfológicamente similares; especies sincrónicas temporalmente y simpátricas espacialmente que se encuentran compitiendo por recursos similares deben exhibir caracteres distintos en espacio ecomorfológicos, los cuales son moldeados a través del tiempo con el fin de reducir la competición. A pesar del mínimo esfuerzo de muestreo en el sitio amazónico, este es el más especioso (238 especies, 78 comunes) comparado con los sitios del Chaco (147, 76) y Río Grande (61, 24). La variedad de tamaño fue probada al comparar las medidas de la media mandibular de confamiliares en un "real pool" o grupo verdad (grupo actual de especies) contra un "null pool" o grupo posibilidad (especies que potencialmente podrían estar presentes). El patrón en la variedad de tamaño fue penetrante en 68% de las 22 familias estudiadas, siendo la mayoría animales consumidores u omnívoros, representados por un alto porcentaje de insectívoros.

Elton (1927) first proposed the question of whether communities have 'limited membership'. In his classic work on species assembly, Diamond (1975) suggested that species in a community are selected, and their niches and abundances coadjusted, so that the community possesses "stability". By stability, Diamond implied that species composition would change only if the physical environment did. Such patterns of coexistence in species assemblages with respect to interspecific competition have been the subject of intensive debate by evolutionary ecologists during the latter half of the 1900's. Perhaps one of the reasons for the lengthy and intensive debate is that these hypotheses are so difficult to test in tropical, volant bird communities compared to situations involving terrestrial small mammals (Vassallo 1993) for example, where one can more easily measure direct competition by manipulating study subjects (Brooks 1997a).

The role of competition in determining species composition can be tested against null models of comparative regional assemblages. Additionally, evolutionary ecology has a long history of testing competition for resources by examining morphologies of closely related species (Brown & Bowers 1985). Consider the classic case of Darwin's Galapagos finches, in which a series of empty niches led to rapid evolution of divergent morphologies in colonizing species, permitting coexistence by apportioning empty niche spaces (Darwin 1859, Lack 1947, Grant 1982). Avian competition studies are extrememly important to test hypotheses of species composition processes in volant tropical assemblages (Weiher & Keddy 1999).

The shapes of latitudinal productivity gradients in taxonomic diversity are known for many living organisms, but quantitative data on morphological patterns remain scarce (Roy & Foote 1997). Although some studies have addressed whether communities in similar environments will converge ecomorphologically (Ricklefs & Miles 1994), these studies took place in vegetative communities at opposite ends of the globe, such as California and Chile (Cody 1974, Kelt et al. 1996). Moreover, such studies compare temperate environments or temperate versus tropical environments, but have not addressed how such patterns may vary among avian communities across various sites within the Neotropics. My objective herein is to examine the role of size assortment in structuring Neotropical bird assemblages at three latitudes in the Neotropics, representing a gradient of productivity and seasonality.

Grant (1969) recognized that character displacement could arise as a result of: 1) divergent natural selection of coexisting species, or 2) selective survival of immigrating species as a function of distinctness from species already present. It appears that the first pattern evolved into size adjustment, whereas the latter became size assortment (Case & Sidell 1983). One way to investigate fine-scale tuning among interacting species is to look at variation in related taxa because ecological similarity could result in morphological divergence resulting from dietary differences (Karr & James 1975). Size assortment is the likely diminished persistence of a species by presence of morphologically similar species (Case & Sidell 1983). In other words, from a random pool of species that could potentially colonize an area, the species actually present are those that could coexist because they were different sizes and therefore did not compete

for resources. The reason for species not persisting within the community has been debated. The two main theories are that similar-sized species: 1) became locally extinct (Willig & Moulton 1989) or 2) could not colonize a region due to intense competition from a similar-sized species that shared the same resources (Diamond 1975).

I will test size assortment by comparing bill morphologies of confamilials that utilize similar resources (same habitat, similar diet, spatially and temporally sympatric), examining whether ecomorphological distances in a real community are overdispersed compared to a null community. Such phylogenetically related confamilials have similar environmentally constrained phenotypes and therefore are good candidates for testing hypotheses of interspecific competition (Ricklefs & Miles 1994). All taxa that may coexist through other mechanisms (habitat allotopy, temporal asynchrony, dietary differences, asynchronous activity patterns, social mimicry or species packing) will be filtered from analyses, insuring that complete competitiors are used in analyses. I will compare size assortment in the northern subtropics (Rio Grande River Valley), the equatorial tropics (northern Peruvian Amazon), and the austral subtropics (central Paraguayan Chaco). Analysis of pervasiveness of size assortment in the Neotropics will help provide insight of underlying processes that govern these patterns, and therefore mold the communities themselves. My specific hypothesis is: size assortment is equally prevalent among different latitudinal gradients.

METHODS

Methods are provided in detail in Brooks (1998), but are summarized below. I collected data along transects in the field to determine community composition at each of the three sites (Rio Grande - $26^0 15$'N; $98^0 30$'W, Amazonia ~ $2^0 45$'S; $72^0 55$'W, and Chaco - $22^0 33$'S; $60^0 30$'W), and also to study the ecology of species within those communities; this was important to designate which species could be used in analyses. From the comprehensive species lists, I designated confamilials for size assortment analyses. Although competition could occur among more distantly related taxa, my objective is to examine competition in species with similar morphologies; hence comparisons at the confamilial level were used.

Accounting for other factors that may enhance coexistence *a-priori* will increase the chance that species selected to test hypotheses are (or were) competitors. Therefore, upon determination of confamilial groups, I excluded species from analyses that might coexist through mechanisms other than size differences. Ecological factors controlled for include species used in analyses being common (at least 2 individuals/sampling duration, for at least one-third of all durations), temporally synchronous seasonally, spatially sympatric (in terms of habitat use), utilizing similar dietary resources, and temporally synchronous daily (sharing activity periods). Additionally, evolutionary factors to be controlled for include: species used in analyses must not be constrained by social mimicry (two more distantly related species appearing more chromatically similar than other, more closely related species), phylogeny (restricted to familial level, see above), or be candidates for species packing (reverse pattern of size assortment - real pool

pool underdispersed when compared to null pool). While species filtered from analyses may have been morphologically structured within their communities, I could not test my hypotheses without analyzing patterns in fully competing species.

I considered competing species remaining after filtering as the real pool, and I constructed regional null pools of potentially colonizing species to compare against real pools for analyses. A null pool is a pooled assemblage occurring within a designated geographic region that shares characteristics (residents or semi-residents, sharing similar habitat/diet/activity patterns, and lacking potential for social mimicry) with actual species from the study site (real pool) (slightly modified from Ricklefs 1987). Null pools are used to test for structured patterns in bird communities, by comparing the real pool against the null pool. I selected the geographic region for each null pool by drawing a concentric circle from the study site using a radius of approximately 333 km. I selected this radius based upon its relative capacity to encircle biomes at country-wide scales for the South American sites (the Peruvian Napo-intersect region, the Paraguayan Chaco), whereas the Rio Grande site encompassed the Texas Rio Grande Valley (south of Corpus Christi) and portions of two northeastern states in Mexico (central and eastern Nuevo Leon, and north and central Tamaulipas). I obtained the source pools and data on habitat association, migrant status, and other ecological attributes by sampling bird communities at nearby localities, supplemented with available regional avifauna references. These data from other sites, complemented with references, provide complete and accurate species lists for comparison, insuring availability of an adequate pool for comparison (Willig & Moulton 1989). I did not analyze communities where null and real pools contained the same species, because lack of species selection in the real pool is a rare occurrence, resulting in uncomparable species pools (Willig & Moulton 1989).

I obtained measurements from museum specimens for species comprising the null and real pools. I analyzed the data using graphic analyses, by plotting mean bill height against mean bill width of species in two-dimensional space, and comparing the segment lengths between species comprising real and null pools.

I used shortest spanning trees (hereafter referred to as SSTs), as used by Ricklefs & Travis (1980) following the idea of a Prim Network (Prim 1957). An SST represents the shortest composite line that connects all congeners in a guild and contains one fewer line segments than the number of species in the community (if N-species in a guild, the SST has N - 1 line segments). Each individual line segment between species measures nearest neighbor distance (hereafter referred to as NND) between species. Measurement of segment lengths (NNDs) between related taxa provides an index of ecomorphological distance between species (Brooks 1997a).

I plotted the ecomorpholocial means between species in each community on two-dimensional graphs using the computer program SPSS (SPSS 1996). Using a statitical package to create graphs permits standardization of axes for each SST across sites, insuring that measurements among separate taxa and sites would not be biased. Using the two-dimensional graph plots, I measured NNDs from real pool and null pool SSTs.

I tested size assortment by comparing mean NNDs of the real and null pool assemblages in cases where the real pool was hyperdispersed to the null (Strong et al.

1979, Willig & Moulton 1989). If mean NNDs of the real species are hyperdispersed in ecomorphological space compared to the null pool this indicates that size assortment governs these assemblages (Willig & Moulton 1989). A graphic depiction is provided in Figure 1, where mean NND length of the null pool (n = 8 NNDs) = 18.7 (21 + 29.5 + 25.5 + 19 + 20 + 12 + 5.5 + 17 / 8) and mean NND length of the actual species assemblage (n = 2 NNDs) = 36.8 (56.5 + 17 / 2). In this example the assemblage is significantly overdispersed from the null pool (36.8 versus 18.7, respectively); therefore size assortment structures this icterid assemblage at the Amazon site.

I applied the goodness-of-fit chi-square test (Sokal & Rohlf 1969, Ricklefs & Travis 1980, Case & Sidell 1983) to test for significance ($P \leq 0.05$) between NND means of real and null confamial groups.

RESULTS

Sampling Effort and Species Richness. I covered a total of 7.3 km of transects during each of 9 sampling periods at the Rio Grande site, 8.4 km during each of 7 sampling periods at the Amazon site, and 7.1 km during each of 12 sampling periods at the Chaco site, yielding total km covered per site at 65.7, 58.8, and 85.2, respectively (209.7 km total). The Amazon site had the lowest number of total transect km covered, fewest sampling periods, and similar sampling durations. Nonetheless, the Amazon site is still by far the most speciose site compared with with the other two, harboring 238 species of which 78 are common, followed by the Chaco site with 147 species of which 76 are common, and the Rio Grande site with 61 species of which 24 are common (Table 1). However, familial diversity at the Amazon and Chaco sites are similar with 42 (26 common) and 45 (30 common) families, respectively (Table 1). Familial diversity at the Rio Grande site is considerably lower with 26 families, of which 13 are common (Table 1).

I did not encounter any new common species at the Rio Grande site after the 3rd sampling session (plateauing with the 4th session), at the Amazon site after the 5th sampling session (plateauing with the 6th session) and at the Chaco site after the 6th sampling session (plateauing with the 7th session). This suggests that all common species are accounted for at each site, insuring that only the most abundant species were accounted for prior to analyses.

Size Assortment. Families eliminated from analyses due to coexistence mediated through other mechanisms are summarized in Table 1 (full species appendix available in Brooks 1998). The strongest pattern, concordant with the results of Terborgh (1985) and others (Schoener 1974, Cody 1974), is species in 12 families showing strong evidence for habitat separation at the Amazon site, and 10 at the Chaco site (species used in analyses are tabularized and available from the author upon request).

Size assortment is pervasive among the three sites, with significant findings for all families (*n* = 2) at the Rio Grande site, 57% (*n* = 7) of the familes at the Amazon site, and 69% (*n* = 13) of the families at the Chaco site (Table 2). At the Rio Grande site the

woodpecker and icterid groups both showed significant size assortment (Appendix 1). At the Amazon site the woodpecker, cotinga, swallow, and icterid groups showed significant size assortment, whereas the raptor, toucan, and manakin groups did not (Appendix 1). At the Chaco site the tinamou, falcon, pigeon, woodpecker, hornero, edge flycatcher, savannah flycatcher, pond flycatcher, and finch groups showed signficant size assortment, whereas the heron, raptor, parrot, and hummingbird groups did not (Appendix 1).

When all sites are pooled, most species are animal consumers (66%, $n = 10$) or omnivores (13%, $n = 2$) rather than plant consumers (20%, $n = 3$) (Table 2). Additionally, 90% ($n = 15$) of all animal consumers are insectivores (Table 2), reflecting the strong relationship between prey size and mandible size in insectivores (Hespenheide 1971). This pattern is strongest at the Rio Grande site (all are insectivores), and at the Chaco site, where 83% (all but one) of the animal predator families are insectivores (Table 2).

When considering all sites, size assortment is strongest in open or transitional habitat (66%, $n = 10$) and weakest in closed forest (33%, $n = 5$) (Table 2). The edge habitats that comprise transitional forest (forest edge) and riverine edge are popular to many species as foraging sites, in addition to those that are primarily associated with edge habitat (Remsen & Parker 1983). Consequently competition should be higher in edge situations, whereby ecological separation in a widely used habitat is manifested through size assortment. Aquatic habitat is most strongly associated with the Amazon site (75%, $n = 4$) for this pattern, whereas the other macrohabitat types are most strongly associated at the Chaco site (73%, $n = 11$).

DISCUSSION

The Role of Size Assortment in Structuring Neotropical Bird Communities. I found evidence of size assortment among different species of birds representing Neotropical communities, although many species were filtered from analyses *a-priori*. I began with 446 species total (61 at the Rio Grande site, 238 at Amazon site, and 147 at Chaco site) and filtered most of these species from the analyses because they are rare, attained ecological separation through other modes (habitat and dietary differences, temporal and spatial asynchrony, social mimicry) were too distantly related, or candidates for size assortment. This left the numbers of species that I could test at 59, or 13% of the original pool. Thus, I filtered out most species because they are not good candidates for strong competition and, therefore, poor subjects for analyses. Although these species may have been morphologically structured within their communities, I could not measure this without compromising the strength and rigor of testing these patterns in fully competing species. However, where the patterns occurred for the remaining groups that could be tested, morphological structure among different species of birds within communities is apparent. For example, I obtained signficant results for 68% of the 22 groups tested for size assortment.

Recent studies, such as those of Basset (1995), have found that size differences alone could allow coexistence among species without any other factors accounting for resource

partitioning. However, after doing my research, based upon what I learned while collecting data in the field, I am most inclined to believe that Neotropical avian communities are structured by a suite of factors rather than any single given factor.

General Trends. Size assortment is a strong pattern for all three sites, with significant findings for more than one-half the families analyzed for this pattern at each site. Both the Amazon (57%, $n = 7$) and Chaco sites (69%, $n = 13$) showed strong size assortment, although the pattern is stronger at the latter site. Although the Amazon site has higher diversity (238 species versus 147 in the Chaco), the number of common species is virtually indistinguishable (78 species) when compared to the Chaco (76 species). Moreover, familial diversity is slightly lower at the Amazon site (42 families, 26 common) than the Chaco (45 families, 30 common). In comparison to subtropical regions, perhaps equatorial regions are characterized by constant invasion of less abundant taxa despite higher diversity. Diminished abundance per species may be the compensatory mechanism or ecological trade-off for high diversity.

Most groups showing strong size assortment at the Amazon site are associated with riverine tributary. Remsen & Parker (1983) indicated that riverine habitats harbor a high number of species associated only with that habitat. Additionally, edge habitats, comprising a transition between open and closed forest or between a river and closed forest, represent important foraging sites to many species (Diamond & Terborgh 1967). Consequently, more species using the same habitat for foraging enhances the chances for competition, explaining why size assortment is more pervasive along edge habitats at the Amazon site. A case example has been documented in ramphastids, in which a "superior" competing aracari (*Pteroglossus* sp.) will exclude a congener from a certain habitat, as evidenced by the "inferior" competitor occupying the better habitat in the absence of the other (Brooks 1997a). Concordant with this, the preferred habitat in the aracari example is edge habitat (Brooks 1997a), the same habitat that groups structured by size assortment at the Amazon site are predominately associated with.

The fact that most groups showing significant size assortment are animal consumers rather than primary plant consumers is not surprising, considering stronger competitive forces in animal consumers, driven by territorial defense of a potentially more limited food resource base (Schoener 1965, Grant 1968, Snow 1985). But perhaps even more significant is the pervasiveness of insectivores. Indeed, both cases showing significance in the Rio Grande site are insectivores, and 90% of all animal consumers are insectivores (especially at the Chaco site, where all but one is insectivorous). This reflects the strong relationship between prey size and mandible size in insectivores (Hespenheide 1971). Moreover, this suggests that it is not neccessarily easier to detect ecomorphological patterns from measuring larger mandibles, which would imply sampling bias (Schoener 1974). In my data set, animal consumers are primarily larger species (herons and raptors), whereas the largest-bodied groups accounting for insectivores are much smaller (woodpeckers and flycatchers). However, insectivores show far greater signficance (all significant, $n = 9$) than vertebrate consumers (25% significant, $n = 4$) despite their larger

body size, and consequently pervasiveness of ecomorphological pattern does not appear to be a consequence of larger mandible size.

Conclusion. More than 85% of the original species pool was filtered before analyses to insure that I compared the strongest candidates of competition, inherent for the hypotheses I was testing. Of the groups that could be tested, morphological structure among species of birds within communities is indeed apparent (significant results for 68% of size assortment tests). Additionally, the taxa showing evidence of size assortment are vertebrate consumers (especially insectivores) and occupy open habitat rather than closed forest.

Size assortment is strong at all three sites, but most pervasive at the Rio Grande site (though the sample size is limited). Size assortment is a stronger pattern at the Chaco versus Amazon site, and this is likely attributable to more common, resident species despite less seasonality and higher rainfall (>2500 versus 865 mm) at the Amazon site. In comparison to subtropical regions, equatorial regions may be characterized by constant invasion of less abundant taxa from source pools, despite higher overall diversity; diminished abundance per species may be the compensatory mechanism for high diversity.

Despite these patterns and the processes explaining them, the importance of a suite of factors, including other morphometric measurements (Leisler 1977), cannot be underestimated in determining community structure. Nonetheless, these findings help bring community and evolutionary ecologists one step closer to understanding the mechanisms that account for increased diversity as one approaches the equator, as Wallace (1878) so eloquently described more than a century ago.

LITERATURE CITED

American Ornithologists' Union. 1998. Check-list of North American Birds, 7th Ed. American Ornithologists' Union, Washington, DC.

Basset, A. 1995. Body size-related coexistence: an approach through allometric constraints on home-range use. Ecology 76:1027-1035.

Brooks, D.M. 1997a. ¿Son la competencia, el tamaño y la superposición de dietas pronosticadores de la composición de Ramphastidae? Pages 283-288 *in* Manejo de Fauna Silvestre en la Amazonia (T.G. Fang, R.E Bodmer, R. Aquino, y M. Valqui, Eds.). La Paz, Bolivia.

Brooks, D.M. 1998. Competition and coexistence in Neotropical birds: a latitudinal comparison. Ph.D. diss., Texas A&M University, College Station, Texas.

Brown, J.H. & M.A. Bowers. 1985. Community organization in hummingbirds: relationships between morphology and ecology. Auk 102:251-269.

Case, T.J. & R. Sidell. 1983. Pattern and chance in the structure of model and natural communities. Evolution 37:832-849.

Cody, M.L. 1974. Competition and the Structure of Bird Communities. Princeton University Press, New Jersey.

Darwin, C. 1859. On the Origin of Species. John Murray, London, United Kingdom.

Diamond, J.M. 1975. Ch. 14: Assembly of species communities. Pages 342-444 *in* Ecology and Evolution of Communities (M.L. Cody & J.M. Diamond, Eds.). Belknap Press, Cambridge, Massachusetts

Diamond, J.M. & J. Terborgh. 1967. Observations on bird distribution and feeding assemblages along the Rio Callaria, Departamento of Loreto, Peru. Wilson Bulletin 79:273-282.

Elton, C. 1927. The Ecology of Animals. Sedgwick and Jackson, London, England, United Kingdom.

Grant, P.R. 1968. Bill size, body size, and the ecological adaptations of bird species to competitive situations on islands. Systematic Zoology 17:319-333.

Grant, P.R. 1969. Colonization of islands by ecologically dissimilar species of birds. Canadian Journal of Zoology 47:41-43.

Grant, P.R. 1982. The role of interspecific competition in the adaptive radiation of Darwin's finches. *in* Patterns of Evolution in Galapagos Organisms (A. Levinton & R.I. Bowman, Eds.). Special Publication of the American Association for the Advancement of Science 1.

Hayes, F.E. 1995. Status, Distribution, and Biogeography of the Birds of Paraguay. American Birding Association Monographs in Field Ornithology 1.

Hespenheide, H.A. 1971. Food preference and the extent of overlap in some insectivorous birds, with special reference to the Tyrannidae. Ibis 113:59-72.

Hilty, S.L. & W. Brown. 1986. A Guide to the Birds of Colombia. Princeton University Press, New Jersey.

Howell, S.N.G. & S. Webb. 1995. The Birds of Mexico and Northern Central America. Oxford University Press.

Karr, J.R. & F.C. James. 1975. Chapter 11: Eco-morphological configurations and convergent evolution in species and communities. Pages 258-291 *in* Ecology and Evolution of Communities (M.L. Cody & J.M. Diamond, Eds.). Belknap Press, Cambridge, Massachusetts

Kelt, D.A., J.H. Brown, E.J. Heske, P.A. Marquet, S.R. Morton, J.R.W. Reid, K.A. Rogovin & G. Shenbrot. 1996. Community structure of desert mammals: comparisons across four continents. Ecology 77:746-761.

Lack, D. 1947. Darwin's Finches. Cambridge University Press, London.

Leisler, B. 1977. Ökomorphologische Aspekte von Speziation un adaptiver Radiation bei Vögeln. Vogelwarte 29:139-153.

Prim, R.C. 1957. Shortest connection networks and some generalizations. Bell Systems Technology Journal 36:1389-1401.

Remsen, J.V. & T.A. Parker. 1983. Contribution of river-created habitats to bird species richness in Amazonia. Biotropica 15:223-231

Ricklefs, R.E. 1987. Community diversity: relative roles of local and regional processes. Science 235:167-171.

Ricklefs, R.E. & D.B. Miles. 1994. Ch. 2: Ecological and evolutionary inferences from morphology: an ecological perspective. Pages 13-41 *in* Ecological Morphology: Integrative Organismal Biology (P.C. Wainwright & S.M. Reilly, Eds.). University of Chicago Press.

Ricklefs, R.E. & J. Travis. 1980. A morphological approach to the study of avian community organization. Auk 97:321-338.

Roy, K. & M. Foote. 1997. Morphological approaches to measuring biodiversity. Trends in Ecology and Evolution 12:277-281.

Schoener, T.W. 1965. The evolution of bill size differrences among sympatric congeneric species of birds. Evolotion 19:189-213.

Schoener, T.W. 1974. Resource partitioning in ecological communities. Science 185:27-39.

Snow, D.W. 1985. The Web of Adaptation: Bird Studies in the American Tropics. Quadrangle, Times Book Co., New York.

Sokal, R.R. & F.J. Rohlf. 1969. Biometry. W.H. Freeman & Company, San Francisco, California.

SPSS. 1996. SPSS 7.5 for Windows.

Strong, D.R., L.A. Szyska & D.S. Simberloff. 1979. Tests of community-wide character displacement against null hypotheses. Evolution 33:897-913.

Stotz, D.F., J.W. Fitzpatrick, T.A. Parker III & D.K. Moskovits. 1996. Neotropical Birds: Ecology and Conservation. University of Chicago Press.

Terborgh, J. 1985. Habitat selection in Amazonian birds. Pages 311-338 *in* Habitat Selection in Birds (M.L. Cody, Ed.). Acad. Press, New York.

Vassallo, A.I. 1993. Habitat shift after experimental removal of the bigger species in sympatric *Ctenomys talarum* (Rodentia: Octodontidae). Behaviour 127:247-263.

Wallace, A.R. 1878. Tropical Nature and other Essays. MacMillan, London, United Kingdom.

Weiher, E. & P. Keddy. 1999. Ecological Assembly Rules: Perspectives, Advances, Retreats. Cambridge University Press, United Kingdom.

Willig, M.R. & M.E. Moulton. 1989. The role of stochastic and deterministic processes in structuring Neotropical bat communities. Journal of Mammalogy 70:323-329.

TABLE 1. Differences among sites in filtering communities for analyses.

COMPARISON	R^	A^	C^
Species richness	61	238	147
Common species	24	78	76
Familial richness	26	42	45
Common families	13	26	30
Common families filtered due to phylogenetic constraints	7	8	12
Common families filtered as species packing candidates	2	6	4
Common families filtered due to social mimicry	0	1	0
Common species filtered due to temporal asynchrony	0	6	5
Common species filtered due to habitat differences	4	14	13
Common species filtered due to dietary differences	0	1	1
Common species filtered due to activity differences	0	1	0

^R = Rio Grande Site, A = Amazonian Site, C = Chacoan Site

TABLE 2. Summary of results for size assortment.

	RIO GRANDE		AMAZONIAN		CHACOAN	
	* (%)	ns (%)	* (%)	ns (%)	* (%)	ns (%)
TOTAL	2 (100)	-	4 (57)	3 (43)	9 (69)	4 (31)
PRIMARY DIET						
Vertebrates	-	-	-	1 (14)	1 (8)	2 (15)
Insectivore	2 (100)	-	2 (28)	-	5 (38)	-
Omnivore	-	-	1 (14)	-	1 (8)	-
Granivore	-	-	-	-	2 (15)	1 (8)
Frugivore	-	-	1 (14)	2 (28)	-	-
Nectarivore	-	-	-	-	-	1 (8)
PRIMARY MACROHABITAT						
Aquatic	-	-	3 (43)	1 (14)	1 (8)	1 (8)
Open	-	-	-	-	3 (23)	1 (8)
Transitional Forest	1 (50)	-	-	-	2 (16)	2 (16)
Closed Forest	1 (50)	-	1 (14)	2 (28)	3 (23)	-

Only species groups that could be analyzed (signficant or non-significant) are included in this table.

KEY: - = not analyzed, * = statistically significant (X^2), ns = not significant

MACROHABITATS: Aquatic (tajamar, riverine and lake edge, sawgrass marsh and streams); Open (savannah, chapparal, floodplain, agrarian pasture/grassland); Transitional Forest (second growth and edge); Closed Forest (primary forest, woodland and thorn Forest)

APPENDIX 1. Species used in size assortment analyses.

RIO GRANDE SITE

PICIDAE - Real: *Melanerpes aurifrons*, *Picoides scalaris*; Null: *Sphyrapicus varius*, *Piculus rubiginosus*, *Dryocopus lineatus*. ICTERIDAE - Real: *Quiscalus mexicanus*, *Molothrus ater*; Null: *Icterus cucullatus*, *I. gularis*, *Sturnella magna*, *S. neglecta*, *Euphagus cyanocephalus*, *Molothrus aeneus*.

AMAZON SITE

ACCIPITRIDAE - Real: *Ictinia plumbea*, *Buteo magnirostris*; Null: *Leptodon cayanensis*, *Rostrhamus sociabilis*, *R. hamatus*, *Geranospiza caerulescens*, *Accipiter superciliosus*, *A. bicolor*, *Leucopternis schistacea*, *L. melanops*, *L. nitidus*, *Buteogallus urubitinga*, *Busarellus nigricollis*, *Buteo albonotatus*, *Morphnus guianensis*, *Spizaetus tyrannus*. RAMPHASTIDAE - Real: *Pteroglossus castanotis*, *P. pluricinctus*, *Ramphastos tucanus*; Null: *Pteroglossus inscriptus*, *Selenidera reinwardtii*. PICIDAE - Real: *Celeus grammicus*, *Dryocopus lineatus*; Null: *Piculus chrysochloros*, *Celeus elegans*, *Campephilus rubricollis*. PIPRIDAE - Real: *Pipra erythrocephala*, *P. coronata*;
Null: *Schiffornis turdinus*, *Tyranneutes stolzmanni*, *Machaeropterus regulus*, *Chiroxiphia pareola*, *Pipra pipra*. COTINGIDAE - Real: *Lipaugus vociferans*, *Cotinga cayana*, *Querula purpurata*; Null: *Phoenicircus nigricollis*, *Iodopleura isabellae*, *Cotinga maynana*. HIRUNDINIDAE - Real: *Tachycineta albiventer*, *Atticora fasciata*; Null: *Progne tapera*, *P, chalybea*, *Notiochelidon cyanoleuca*, *Neochelidon tibialis*, *Stelgidopteryx ruficollis*. ICTERIDAE - Real: *Psarocolius decumanus*, *P. angustifrons*, *Cacicus cela*; Null: *Icterus jamacaii*, *Psarocolius oseryi*, *P. viridis*, *Cacicus solitarius*, *Molothrus bonariensis*, *Scaphidura oryzivora*.

CHACO SITE

TINAMIDAE - Real: *Nothoprocta cinerascens*, *Nothura maculosa*; Null: *Crypturellus undulatus*, *C. tataupa*, *Rhynchotus rufescens*, *Nothura boraquira*, *Eudromia formosa*.
ARDEIDAE - Real: *Nycticorax nycticorax*, *Syrigma sibilatrix*, *Casmerodius alba*; Null: *Ardeola ibis*, *Butorides striatus*, *Egretta thula*, *Ardea cocoi*. ACCIPITRIDAE - Real: *Elanus leucurus*, *Buteogallus urubitinga*, *B. meridionalis*, *Buteo magnirostris*, *B. albicaudatus*; Null: *Gampsonyx swainsonii*, *Circus buffoni*, *Geranoaetus melanoleucus*, *Buteo albonotatus*. FALCONIDAE - Real: *Falco sparverius*, *F. femoralis*, Null: *Milvago chimachima*, *M. chimango*. COLUMBIDAE - Real: *Columba picazuro*, *Columbina talpacoti*, *C. picui*; Null: *Columbina squammata*, *Claravis pretiosa*.
PSITTACIDAE - Real: *Aratinga acuticaudata*, *Nandayus nenday*, *Myiopsitta monachus*,

Amazona aestiva; Null: *Aratinga leucophthalmus, Brotogeris versicolurus.*
TROCHILIDAE - Real: *Chlorostilbon aureoventris, Heliomaster furcifer*; Null:
Hylocharis chrysura. PICIDAE - Real: *Melanerpes candidus, Campephilus leucopogon*;
Null: *Picumnus cirratus, Melanerpes cactorum, Piculus chrysochloros, Celeus
flavescens, Dryocopus lineatus, D. schulzi.* FURNARIIDAE - Real: *Furnarius rufus, F.
cristatus, Coryphistera alaudina*; Null: *Ochetorhynchus certhioides, Asthenes baeri.*
TYRANNIDAE - Real: *Elaenia parvirostris, Tyrannus savana*; Null: *Sublegatus
modestus, Suiriri suiriri, Elaenia spectabilis, Euscarthmus melorhyphus, Hemitriccus
margaritaceiventer, Cnemotriccus fuscatus, Myiarchus tyrannulus, Myiodynastes
maculatus, Empidonomus varius, E. aurantioatrocristatus, Xenopsaris albinucha,
Pachyramphus validus.* TYRANNIDAE - Real: *Pyrocephalus rubinus, Xolmis irupero,
Machetornis rixosus, Tyrannus melancholicus*; Null: *Sublegatus modestus, Suiriri
suiriri, Elaenia spectabilis, Inezia inornata, Stigmatura budytoides, Euscarthmus
melorhyphus, Knipolegus striaticeps, Myiarchus swainsoni, M. ferox.* TYRANNIDAE -
Real: *Pyrocephalus rubinus, Fluvicola albiventer, Pitangus sulphuratus*; Null:
*Polystictus pectoralis, Xolmis cinerea, Hymenops perspicillatus, Alectrurus risorus,
Satrapa icterophrys.* EMBERIZIDAE - Real: *Poospiza melanoleuca, Saltatricula
multicolor, Coryphospingus cucullatus*, Null: *Zonatrichia capensis, Lophospingus
pusillus.*

Family and generic taxonomy follows American Ornithologists' Union (1998) and Stotz
et al. (1996); specific taxonomy follows Howell & Webb (1995), Hilty & Brown (1986)
and Hayes (1995).

FIG. 1. Visual depiction of size assortment in Amazon Icterids, where the real pool mean NND (large squares connected by dashed line) is greater than the null pool mean NND (small and large squares connected by solid line). All NND measurements in mm. Since the mean NND of the real pool (36.75) is greater than the mean NND of the null pool (18.68), this suggests character release is significant in Amazon Icterids. This is verified using a goodness-of-fit X^2 test (36.75 vs. 18.68, $X^2 = 5.89$, ts = 3.84, $P < 0.05$, df = 1). Since 5.89 > 3.84, the null hypothesis is rejected in favor of the alternate hypothesis ($P < 0.05$): Species in this Icterid assemblage are structured by size assortment at the Amazon site. Species in this plot listed from largest to smallest by mandible width: *Psarocolius oseryi*, *P. decumanus*, *P. angustifrons*, *P. viridis*, *Scaphidura oryzivora*, *Cacicus cela*, *C. solitarius*, *Icterus jamacaii*, *Molothrus bonariensis*.