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AVIAN SEASONALITY AT A LOCALITY IN THE CENTRAL PARAGUAYAN CHACO

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ABSTRACT. Abundances of different species of birds were recorded in the central Paraguayan Chaco from August 1989 to August 1990 to investigate seasonal variation at the guild level. Species were grouped into guilds based upon primary diet or water dependence. The number of species (abundant : rare) in each guild is as follows: insectivores (21:35), granivores and foliovores (20:6), faunivores (14:13), hydrophilic species (4:28), detrivores (3:1), nectarivores (1:1), and frugivores (0:5). Insectivores show the strongest seasonality (SD = 1.63) followed by hydrophilic species (SD = 1.43), nectarivore (SD = 1.41), faunivores (SD = 1.33), granivores and foliovores (SD = 1.20), and detrivores (SD = 0.50). Chi-square tests indicated that differences between numbers of abundant versus rare insectivores ($P < 0.01$), granivores ($P < 0.005$), and hydrophilic species ($P << 0.005$) were highly significant. Results are intrepreted in light of ecological and evolutionary processes.

Key words: seasonality, resources, avian community, Chaco, Paraguay

Estacionalidad en las aves del Chaco Paraguayo central

RESUMEN. Registré la abundancia de especies de aves en el Chaco Paraguayo central, Agosto de 1989 hasta Agosto de 1990, para investigar la variación estacional al nivel de grupo funcional o gremio (guild). Las características usadas para definir grupos funcionales fueron la dependicia del agua o la dieta primaria. El numero de especies (abundancia : raro) por grupo funcional son: insectívoras (21:35), granívoras and folívoras (20:6), faunívoras (14:13), especies asociadas al agua (4:28), detritívoras (3:1), nectarívoras (1:1), y frugívoras (0:5). El grupo con la variación estacional mayor fue las insectívoras (SD = 1.63), siguiéndoles las especies asociado al agua, (SD = 1.43), las nectarívoras (SD = 1.41), faunívoras (SD = 1.33), granívoras and folívoras (SD = 1.20), y detritívoras (SD = 0.50). Pruebas de chi cuadrado indican que la diferencia entre especies abundantes y raras son muy significativas para las insectívoras ($P < 0.01$), granívoras ($P < 0.005$), y especies asociadas al agua ($P << 0.005$). Los resultados se interpretan en términos de procesos de ecología y evolución.

Palabras clave: estacionalidad, recursos, comunidad de aves, Chaco, Paraguay

INTRODUCTION

The Chaco is a mosaic of xeric habitats in the central portion of South America where several different neotropical biomes (including sub-humid forest, pantanal, tropical savannah, and pampas) interdigitate in the areas of southeastern Bolivia, western Paraguay, and northern Argentina. The area is characterized by low avian endemism bio-

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geographically (Short 1975) and is an effective barrier to forest birds, but not woodland or grassland birds (Nores 1992, Hayes 1995).

The Chacoan avifauna was documented by Short (1975), who concentrated on biogeographic aspects. Since then several studies have been undertaken on birds in the Paraguayan Chaco (e.g., Short 1976; Short 1980; Contreras & Mandelburger 1985; Contreras & Gonzalez-Romero 1989; Gonzalez-Romero & Contreras 1989; Hayes *et al.* 1990; Peris 1990; Peris *et al.* 1987; Neris & Colman 1991; Hayes *et al.* 1991; Brooks 1991, 1995, 1997; Hayes 1995). Although some of these studies have investigated seasonal variation for specific assemblages such as shorebirds and waterbirds, none have attempted to investigate seasonal variation for an entire avian community at the guild level (Hayes pers. comm.). The objective of this paper is to determine the role of limiting resources in influencing seasonality of birds from a site in the semi-xeric Paraguayan Chaco.

Seasonal variation can be defined as variation in annual abundance. Many tropical environments are sharply seasonal, and associated with rainfall rather than temperature variations. These changes affect habitat structure and food supplies, and one would expect the bird species to respond (Wiens 1989). Klopfer (1959) suggested that where seasonal environmental fluctuations are minimal, the type of cover, nesting sites, and food which are available remain fairly constant.

METHODS

STUDY AREA

Species included in this study (Table 1) were found within a 35 km radius of Estancia Fortín Toledo proper (hereafter, referred as Toledo) (22°33'S,60°30'W), Department Boquerón, 35 km W of the Mennonite Colony, Filadelfia. This area, like much of the central Paraguayan Chaco, has been extensively cleared for cattle production (Benirschke *et al.* 1989). The second-growth habitat in the vicinity of Toledo is a mosaic of "quebracho" woodland and grassland (Short 1975), characterized by thorny bushes, shrubs, and cacti, with scattered trees up to 13 m high. *Prosopis ruscifolia*, a thorny legume, and *Opuntia* sp. cactus are the dominant species (López *et al.* 1987). Isolated tracts of thick, impenetrable, thorny forest are sometimes left when land is being cleared for agrarian purposes. The understory in such forest consists of thorny *Bromelia serra* and *Cleistocactus baumanii* (Stabler 1985). *Tajamares* (man-made, seasonal ponds) and filled gulleys from massive rains are present throughout the study area.

SAMPLING METHODS

This study took place from August 1989 to August 1990. Narosky & Yzurieta (1987), Meyer de Schauensee (1982), and Dunning (1987) were used to identify unknown species. Abundance data were obtained from observations of live birds and were ranked numerically using a standardized scale for all taxa. During some months certain species were absent from Toledo proper but present within the 35 km radius of the centerpoint, so a special rank (1) was used to indicate such situations of local movements. Additionally, ranks of 2 and 3 were indicative of singletons being present rather than multiple individuals, reflecting transitory movements or a low point during migration. The following monthly scale was used: 0 = absent: not observed during a given month; 1 = local movements: observed within 35 km of the study area's centerpoint but not at Toledo proper; 2 = monthly transient individual: observation of one individual per month persisting in study area no more than 24 hrs.; 3 = monthly resident individual: observation of one individual per month persisting in study area more than 24 hrs; 4 = uncommon: two to five individuals observed per survey day; 5 = common: six to nine individuals observed per survey day; 6 = abundant: ten or more individuals observed per survey day.

Data were collected by walking an average of 1.75 km of transect daily through a

Table 1. Abundant Species at Toledo+

GUILD Species	Months SONDJFMAMJJA	SD score
INSECTIVORES		
Dark-billed Cuckoo *Coccyzus melacoryphus*	000445444242	1.86
Smooth-billed Ani *Crotophaga ani*	045544440241	1.83
Guira Cuckoo *Guira guira*	644555656544	0.79
White Woodpecker *Leuconerpes candidus*	020004454440	2.09
Narrow-billed Woodcreeper *Lepidocolaptes angustirostris*	444344444244	0.62
Rufous Hornero *Furnarius rufus*	044544440000	2.15
Crested Hornero *Furnarius cristatus*	064245444454	1.52
Chotoy Spinetail *Schoeniophylax phryganophila*	000222444444	1.73
Little Thornbird *Phacellodomus sibilatrix*	000004445544	2.23
Lark-like Brushrunner *Coryphistera alaudina*	654454444554	0.67
Small-billed Elaenia *Elaenia parvirostris*	000444445544	1.94
White Monjita *Xolmis irupero*	144445444454	0.99
Black-backed Water-tyrant *Fluvicola albiventer*	045444444200	1.88
Cattle Tyrant *Machetornis rixosus*	444424445544	0.73
Tropical Kingbird *Tyrannus melancholicus*	066445444044	1.91
Fork-tailed Flycatcher *Tyrannus savana*	465545400000	2.49
Crowned-slaty Flycatcher *Griseotyrannus aurantioatrocristatus*	066554400000	2.67
Great Kiskadee *Pitangus sulphuratus*	065654444444	1.52
White-banded Mockingbird *Mimus triurus*	444000055544	2.19
Masked Gnatcatcher *Polioptila dumicola*	444445455444	0.45
Epaulet Oriole *Icterus cayanensis*	054024044204	1.97
(n=21)	Mean SD =	1.63
GRANIVORES AND FOLIOVORES		
Brushland Tinamou *Nothoprocta cinerascens*	545420142444	1.60
Spotted Tinamou *Nothura maculosa*	222444424454	1.08
Greater Rhea *Rhea americana*	445654544454	0.67
Chaco Chachalaca *Ortalis canicollis*	414444444144	1.16
Picazuro Pigeon *Columba picazuro*	566545665444	0.85
Eared Dove *Zenaida auriculata*	000554544444	2.00
Picui Ground-dove *Columbina picui*	666655566655	0.51
White-tipped Dove *Leptotila verreauxi*	655442344455	1.05
Blue-crowned Parakeet *Aratinga acuticaudata*	045444446544	1.41
Nanday Parakeet *Nandayus nenday*	044440440040	2.05
Monk Parakeet *Myiopsitta monachus*	666646655444	0.93
Blue-fronted Parrot *Amazona aestiva*	455645444444	0.66
House Sparrow *Passer domesticus*	044444421042	1.65
Red-crested Cardinal *Paroaria coronata*	666445556655	0.75
Many-colored Chaco-finch *Saltatricula multicolor*	000004445454	2.23
Red-crested Finch *Coryphospingus cucullatus*	544444204566	1.65
Saffron Yellow-Finch *Sicalis flaveola*	044545444444	1.26
Golden-billed Saltator *Saltator aurantiirostris*	654444444455	0.66
Bay-winged Cowbird *Molothurus badius*	666444544444	0.90
Shiny Cowbird *Molothurus bonariensis*	666654444444	0.96
(n=20)	Mean SD =	1.20
FAUNIVORES		
Plumbeous Ibis *Theristicus caerulescens*	454444424454	0.73
Buff-necked Ibis *Theristicus caudatus*	444544545444	0.45
White-tailed Kite *Elanus leucurus*	000225244444	1.83
Snail Kite *Rostrhamus sociabilis*	002244544240	1.83
Great Black-Hawk *Buteogallus urubitinga*	444421204245	1.53
Savannah Hawk *Buteogallus meridionalis*	234455444444	0.79
Roadside Hawk *Buteo magnirostris*	104425456654	1.89
White-tailed Hawk *Buteo albicaudatus*	004455444044	1.94
American Kestrel *Falco sparverius*	014454444444	1.44
Aplomado Falcon *Falco femoralis*	024440144242	1.62
Red-legged Seriema *Cariama cristata*	141444454444	1.24
Black-legged Seriema *Chunga burmeisteri*	454444444444	0.28
Southern Lapwing *Vanellus chilensis*	454500444444	1.67

Table 1 (continuation)

Rufous-legged Owl *Strix rufipes*	404440454442	1.65
(n=14)	Mean SD =	1.33
HYDROPHILIC SPECIES		
Ringed Teal *Calonetta leucophrys*	654446666544	0.95
Whistling Heron *Syrigma sibilatrix*	444444444454	0.28
Great Egret *Casmerodius albus*	400050445544	2.19
Black-crowned Night-heron *Nycticorax nycticorax*	004455544000	2.31
(n=4)	Mean SD =	1.43
DETRIVORES		
Black Vulture *Coragyps atratus*	444444445544	0.38
Turkey Vulture *Cathartes aura*	444445544444	0.38
Crested Caracara *Polyborus plancus*	654555654444	0.75
(n=3)	Mean SD =	0.50
NECTARIVORES		
Glittering-bellied Emerald *Chlorostilbon aureoventris*	455640444444	1.41
(n=1)	Mean SD =	1.41

+Taxonomy follows Hayes 1995.

mosaic of habitat types, including two tajamars. This was complemented by an average of 225 min of observation from one of three blinds daily. Two of the blinds were located in quebracho woodland at feeding sites baited primarily with succulent cactus, squash and corn. The third blind was elevated approximately 9 m off the ground and located next to a mulberry tree where many passerine species foraged.

Although these methods accounted for most of the species present in the study, longer road transects through all habitats were employed to increase the sampling area. Road transects were easily performed in the relatively open central Chaco, in contrast to more closed forest where many species would go undetected. The predominant habitats along road transect 1 (RT1) included quebracho woodland, agrarian pasture, and grassland, although forest edge and some tajamares were also present. In addition to the habitats represented along RT1, road transect 2 (RT2) contained one of the largest, most contiguous tracts of forest in the study area. This forest was sampled by direct scanning to insure that forest species were adequately accounted for. RT1 was sampled weekly and involved 70 km surveys conducted through eastern Toledo to Filadelfia and back. RT2 was sampled monthly and involved surveys extending 9.3 km through western Toledo. Approximately one stop per survey was averaged to identify species that were not immediately recognizable. Birds would occasionally retreat to cover (e.g., deeper into the brush) before it was possible to identify the species. These individuals were excluded from the data.

Weather elements often trigger increased or decreased reproductive or foraging activity that could alter detectability of samples resulting in overcounted or missed individuals (Robbins 1981). To test whether such biases in detectability occurred, abiotic variable data were collected to correlate with abundance of species that were present at Toledo year-round, without ranks of 0 or 1 for any given month. Temperature was recorded using a standard high-low celcius thermometer, rainfall was recorded in millimeters using a standard rain gauge, cloud cover (clear = 1, partly cloudy = 3, cloudy = 5, overcast = 7, or rainy = 9) and relative wind velocity (stagnant = 1, occasional light breeze = 3, consistent light wind = 5, or windy = 7) were recorded an average of five times per day. Monthly means were obtained for temperature, cloud cover, and relative wind velocity; a monthly total

was obtained for rainfall. An intercorrelated suite of these four abiotic factors was computed with principal component analysis (PCA) using Pearson product-moment correlations with the computer program SYSTAT (Wilkinson 1986). PCA scores for each month were calculated using the first principle component which accounted for 55% of the total variation among the four variables. Spearman rank correlations were used to measure the effects of these abiotic factors upon detectability. Each abiotic variable was paired with abundance of each species that was present year-round (Table 2)

Table 2. Rarer Species at Toledo with Insufficient Data for Analyses+

GUILD	Months
Species	**SONDJFMAMJJA**
INSECTIVORES	
Little Nightjar *Caprimulgus parvulus*	000000040001
Scissor-tailed Nightjar *Hydropsalis brasiliana*	102000000000
Ashy-tailed Swift *Chaetura andrei*	000000640000
White-fronted Woodpecker *Melanerpes cactorum*	000020200100
Checkered Woodpecker *Picoides mixtus*	022240202442
Lineated Woodpecker *Dryocopus lineatus*	020000022000
Black-bodied Woodpecker *Dryocopus schulzi*	040020022420
Cream-backed Woodpecker *Campephilus leucopogon*	020100444052
Scimitar-billed Woodcreeper *Drymornis bridgesii*	044200002522
Yellow-throated Spinetail *Certhiaxis cinnamomea*	000000002000
Firewood-Gatherer *Anumbius annumbi*	000000004000
Rufous Cacholote *Pseudoseisura cristata*	000000000100
Great Antshrike *Taraba major*	000000004241
Barred Antshrike *Thamnophilus doliatus*	002000000442
Variable Antshrike *Thamnophilus caerulescens*	000000004402
Stripe-backed Antbird *Myrmorchilus strigilatus*	000040000020
Olive-crowned Crescent-chest *Melanopareia maximilliani*	000000004000
Pearly-vented Tody-tyrant *Hemitriccus margaritaceiventer*	000200002454
Greater Wagtail-tyrant *Stigmatura budytoides*	000400000400
Vermillion Flycatcher *Pyrocephalus rubinus*	440000044224
Black-crowned Monjita *Xolmis coronata*	000000000002
Brown-crested Flycatcher *Myiarchus tyrannulus*	444000000000
Variegated Flycatcher *Empidonomus varius*	040400000000
Streaked Flycatcher *Myiodynastes maculatus*	004444400000
Piratic Flycatcher *Legatus leucophaius*	000000002000
Crested Becard *Pachyramphus validus*	000200200000
Rufous-browed Peppershrike *Cyclarhis gujanensis*	020000020242
Creamy-bellied Thrush *Turdus amaurochalinus*	020000004444
House Wren *Troglodytes aeodon*	046444000220
Creamy-bellied Gnatcatcher *Polioptila lactea*	044400000000
Southern Martin *Progne modesta*	400000000000
Gray-breasted Martin *Progne chalybea*	000100000000
Barn Swallow *Hirundo rustica*	000020000000
Tropical Parula *Parula pitiayumi*	000000200202
Troupial *Icterus icterus*	400000002000
(n=35)	
HYDROPHILIC SPECIES	
White-tufted Grebe *Rollandia rolland*	000000032000
Least Grebe *Tachybaptus dominicus*	200000000540
Pied-billed Grebe *Podilymbus podiceps*	000004444024
Neotropic Cormorant *Phalacrocorax brasilianus*	330440100000
Southern Screamer *Chauna torquata*	000240000200
White-faced Whistling-duck *Dendrocygna viduata*	000004000000
Masked Duck *Oxyura dominica*	300000030000
Muscovy Duck *Cairina moschata*	330442422000
Comb Duck *Sarkidiornis melanotos*	000044000000
Brazilian Teal *Amazonetta brasiliensis*	000000440000
Snowy Egret *Egretta thula*	025000100000

Table 2 (continuation)

White-necked Heron *Ardea cocoi*	000024100010
Striated Heron *Butorides striatus*	003440400000
Bare-faced Ibis *Phimosus infuscatus*	000000000010
Roseate Spoonbill *Ajaja ajaja*	002000000000
Wood Stork *Mycteria americana*	003214420000
Maguari Stork *Ciconia maguari*	000012000000
Jabiru Stork *Jabiru mycteria*	000000000004
Giant Wood-Rail *Aramides ypecaha*	000020000000
Purple Gallinule *Porphyrio martinica*	000043400000
Spot-flanked Gallinule *Gallinula melanops*	000032000300
White-winged Coot *Fulica leucoptera*	010000000000
Limpkin *Aramus guarauna*	000022320000
Wattled Jacana *Jacana jacana*	000014444300
Upland Sandpiper *Bartramia longicauda*	001000000000
Solitary Sandpiper *Tringa solitaria*	000002000000
Pectoral Sandpiper *Calidris melanotos*	554440100002
Ringed Kingfisher *Ceryle torquata*	000020300000
(n=28)	
FAUNIVORES	
Cattle Egret *Bubulcus ibis*	000000000014
Pearl Kite *Gampsonyx swainsonii*	000020020010
Mississippi Kite *Ictinia mississippiensis*	000000002000
Rufous-thighed Hawk *Accipiter erythronemius*	000000000033
Crane Hawk *Geranospiza caerulescens*	434404202142
Harris' Hawk *Parabuteo uncinctus*	000002000004
Black-collared Hawk *Busarellus nigricollis*	000000002200
Black-chested Buzzard-eagle *Geranoaetus melanoleucus*	000000000100
Laughing Falcon *Herpetotheres cachinnans*	002000242454
Greater Ani *Crotophaga major*	000000020000
Barn Owl *Tyto alba*	114000000000
Great-horned Owl *Bubo virginianus*	000000040202
Burrowing Owl *Athene cunicularia*	200000040202
Plush-crowned Jay *Cyanocorax chrysops*	000000110050
(n=13)	
GRANIVORES	
Ruddy Ground-dove *Columbina talpacoti*	205541440000
Hooded Siskin *Carduelis magellanica*	420000000001
Black-capped Warbling-finch *Poospiza melanoleuca*	000040004454
Blue-black Grasquit *Volatina jacarina*	002004400000
Lined Seedeater *Sporophila lineola*	000244500000
Grayish Saltator *Saltator coerulescens*	000000400000
(n=6)	
FRUGIVORES	
Red-eyed Vireo *Vireo olivaceus*	001002000000
White-lined Tanager *Tachyphonus rufus*	000000002000
Sayaca Tanager *Thraupis sayaca*	054422202202
Blue-and-yellow Tanager *Thraupis bonariensis*	044220000342
Purple-throated Euphonia *Euphonia chlorotica*	000020000000
(n=5)	
DETRIVORES	
King Vulture *Sarcoramphus papa*	000000002141
(n=1)	
NECTARIVORES	
Blue-tufted Starthroat *Heliomaster furcifer*	000444420000
(n=1)	

+Taxonomy follows Hayes 1995. *Progne modesta* is not included in his list. *Asturina nitida* and *Saltator maximus* were tentatively not included in the above list until species designation is further verified.

over time (n=12 months) using STATGRAPHICS (STSC 1986). The alpha level was set at 0.02 to control for bias due to Type II error.

SEASONALITY

Monthly abundance ranks were obtained for all species. Species were divided into two groups: abundant species (defined as those species having an abundance rank of 4-6 for at least 6 months - Table 1), and rarer species (all other species - Table 2). Ranks for abundant species in Table 1 (i.e., species with sufficient data for analysis) were subjected to standard deviation (SD) computation using a TI-35X statistical calculator (Texas Instruments 1992) to measure seasonality.

All species were grouped into guilds based upon primary diet (insectivores, faunivores, detrivores, granivores/foliovores, frugivores, and nectarivores) or water dependence (hydrophilic species) from direct field observations supplemented with information from Hilty & Brown 1986, Ffrench 1980, and Terborgh *et al.* 1990. Means of SDs were obtained for each guild in Table 1 to assess how seasonality is constrained by limiting resources. The higher the mean SD value, the more seasonal variation exhibited by a guild for a particular resource.

Chi-square tests (Sokal & Rohlf 1969) were used to test for significant differences between numbers of guild members in abundant (Table 1) versus rare (Table 2) species. Significant differences would reflect ecological and evolutionary processes (e.g., resource distribution, competition, etc.) that influence species packing mechanisms within guilds, to be entertained in the discussion to follow.

RESULTS

Of the 24 species (16% of the community) represented at Toledo year-round, the only species significantly correlating with abiotic factors were the Guira Cuckoo with cloud cover (r=.737, P=.015), and Golden-billed Saltator with rainfall (r=-.825, P=.006) and the abiotic suite of variables (r=.798, P=.008) (Table 3). Because only two species were significantly correlated with three factors, detectability was not strongly biased due to behavioral cues triggered by weather elements.

The avian community at Toledo is comprised of 152 species in 47 families. Number of species belonging to each guild is as follows: 21 insectivores, 20 granivores and foliovores, 14 faunivores, 4 hydrophilic species, 3 detrivores and 1 nectarivore in the abundant species group (Table 1); 35 insectivores, 28 hydrophilic species, 13 faunivores, 6 granivores, 5 frugivores, and 1 each for detrivores and nectarivores in the rare species group (Table 2).

Insectivores show the strongest seasonality (SD = 1.63) followed by hydrophilic species (SD = 1.43), nectarivore (SD = 1.41), faunivores (SD = 1.33), granivores and foliovores (SD = 1.20), and detrivores (SD = 0.50) (Table 1).

Results of Chi-square tests indicated that differences between numbers of abundant versus rare insectivores ($X^2 = 3.25$, $P < 0.01$), granivores ($X^2 = 8.25$, $P < 0.005$), and hydrophilic species ($X^2 = 20.15$, $P << 0.005$) were highly significant. In contrast, analyses were not performed for faunivores, detrivores, and nectarivores due to similar numbers or low sample size.

DISCUSSION

The most diverse families in this study were also the most diverse families at an Argentine Chaco locality. The number of species follow each family name parenthetically for Paraguay (this study) and Argentina (Capurro & Bucher 1988), respectively, as follows: Tyrannidae (17, 24), Emberizidae (13, 18), Accipitridae (13, 12), and Furnariidae (8, 11).

SPECIES CONSUMING INSECTS

Insectivores are the most speciose guild in both abundant (21) and rare (33) species groups, although number of abundant insectivores versus number of abundant grani-

Table 3. Avian Species Present Year-Round at Toledo.

Spotted Tinamou	Savannah Hawk	Narrow-billed Woodcreeper
Greater Rhea	Crested Caracara	Lark-like Brushrunner
Ring Teal	Black-legged Seriema	Cattle Tyrant
Whistling Heron	Picazuro Pigeon	Masked Gnatcatcher
Plumbeous Ibis	Picui Ground-dove	Red-crested Cardinal
Buff-necked Ibis	Monk Parakeet	Golden-billed Saltator*
Black Vulture	Blue-fronted Parrot	Bay-winged Cowbird
Turkey Vulture	Guira Cuckoo*	Shiny Cowbird

* Significant correlations with P≤.02 (to control for type II error) were found only with Guira Cuckoo and cloud cover (r=.737, P=.015), and Golden-billed Saltator with rainfall (r= –.825, P=.006) and the abiotic suite of variables (r=.798, p=.008).

vores (20) is virtually indistinguishable.

Insectivore abundance may result from insects being an evenly distributed resource at Toledo (pers. obs.). Despite even distribution, insects are often a thinly distributed resource in Neotropical environments, resulting in increased territoriality and competition among insectivores (e.g. Snow 1976). Such competitive forces can yield more "supertramp" species (superior dispersers, inferior competitors; Diamond 1975) within the community reflected by the significantly higher number of rare species. However, it is possible that "rescue effect" (Brown & Kodric-Brown 1977) occurs temporally with incoming migrants replacing conspecific migrants that are leaving (see discussion below).

These findings are concordant with Karr's (1976) hypothesis that insectivores show the most seasonality of all guilds. Additionally, Avery & Van Riper (1989) attributed an insectivore-dominated community to a spatially broad array of insect distribution within California woodlands, where insects occupy a variety of niches.

SPECIES CONSUMING PLANT PARTS

The number of granivores decreases dramatically from the abundant (20) to rare (6) species groups. Species such as *Ortalis* consume more foliage than seed parts (e.g., Caziani & Protomastro 1994), but such foliovores comprise a small subset of the abundant species group.

The high number of abundant granivorous species that co-occur compared to the low number of rare species may be a consequence of plant parts not being a spatially predictable resource, permitting higher levels of coexistent with minimal competition. It is not beneficial for birds to defend territories if the food plants may not bloom within that territory. Rather, it is beneficial for species to share resource clumps, synchronously or asynchronously.

The results herein are concordant with the findings of other studies in the Argentine Chaco (Capurro & Bucher 1982), Monte (Marone 1992) and Venezuelan xeriscape (Poulin *et al.* 1993) where a positive relationship exists between density of granivores and seeds. Moreover, Capurro & Bucher (1982) found no correlation between diversity of granivores and seeds in the Argentine Chaco, in contrast to the correlation between diversity of insectivores and insects, suggesting considerable dietary overlap among sympatric granivores.

FRUGIVORES

The unpredictable blooming strategy of fruit attributes to the low number of frugivorous species (5) included in the rare species group (none present in the abundant species group). Similarly, Poulin *et al.* (1993) speculated that a temporally patchy presence of fruit attributes to most frugivores being transients.

NECTARIVORES

A similar situation is revealed by the low numbers of nectarivores (1 species abundant, 1 rare). Hummingbirds specialize on repro-

ductive plant parts that are not temporally predictable, attributing to the low diversity at Toledo (N=2 species). Hummingbirds increase during the rainy season when nectary sources increase at different sites in the Neotropics (e.g., Toledo & Venezuelan Mangroves, Lefebvre *et al.* 1994),.

WATER-DEPENDENT SPECIES

Hydrophilic species are significantly more speciose in the rare species group (28 species) than the abundant group (4 species), attributable to the stochastic and xeric nature of the Chaco. Permanent water is a spatio-temporally unpredictable resource at Toledo, with only one tajamar containing water throughout the year. Nonetheless this tajamar would reach a depth of < 1 m during the drier periods versus > 4 m during extensive showers in the rainy season. Toledo is located virtually in the center of the Chaco, which is centered in the continent, and is surrounded by several major aquatic systems: the Pilcomayo River to the southwest, the Paraguay River to the east, and the vast Pantanal wetland to the north. Numerous aquatic species may stop-over briefly at a tajamar or other "staging area" (Myers 1983) in transit from one region to the next, reflecting the high number of rare species versus abundant species.

Hayes & Fox (1991) suggest that the evolution of migration for certain hydrophilic species (e.g., shorebirds) is influenced by seasonal precipitation cycles and the effects on habitat availability.

SPECIES CONSUMING MEAT

Faunivores represent a guild with relatively little variation between abundant (14) and rare (13) species. Hayes (1991) found that raptor abundance is most likely influenced by availability of preferred prey and foraging strategy. Raptors are important keystone species as they have a strong influence on prey populations (Robinson 1994). Detrivores showed less than 1/3 the SD as that of the most seasonal group (insectivores), attributable to a constant supply of road-killed carcasses.

FINAL COMMENTS

Resource tracking plays a vital role in shaping the community, through resource "explosions" (e.g., fruit) and seasonal changes that affect resource abundance (e.g., water) in one area, forcing the consumer to move to another. Year-to-year variation in food availability may have a significant impact on species abundance (Karr 1976). Although data were collected for a continuous year, it is possible that at least some of the species in this study are typically more, or less, abundant than during this particular year of data collection.

Birds exhibiting seasonality in one region may occur year-round or during different parts of the year in other regions. Moreover, northern austral migrants can be replaced by incoming conspecific southern austral migrants and vice-versa in certain cases where South American species have extensive latitudinal ranges. In such instances it is more difficult to detect idiosyncrasies of seasonality at the local level. Nonetheless the importance of documenting seasonality at specific sites can not be overemphasized because birds may occur year-round when including samples from several different sites as a data set.

Habitat may play an important role in determining which guild is the most diverse in a community. For example, in a Costa Rican tropical, mesic forest insectivores were the most speciose guild in the understory, whereas frugivores dominated the canopy (Loiselle 1988).

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