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### **Resource Separation in an Napo-Amazonian Gamebird Community**

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### **Repartición de Recursos en una Comunidad de Aves de Caza Napo-Amazonica -**

Nosotros investigamos la posibilidad de separación ecológica en aves de caza Amazónicas (Tinamiformes y Galliformes) de un sitio en el Napo-región de intersección de la Amazonía Peruana Norteña (aprox. 2045'S; 72055'W). Los datos han sido reunidos desde Noviembre de 1993 durante los periodo terminales de las estaciones de lluvias altas y bajas. Los individuos fueron registrados auditiva y/o visualmente usando transectos de contacto de distancia ilimitada, logrado a través de caminatas o yendo en bote. Se depositaron grabaciones seleccionadas en el Laboratorio de Bioacústica de la Universidad de Texas A & M. Las dimensiones del nicho examinadas para la evidencia de separación ecológica incluyeron hábitat (N = 5), estratos (N = 3), tiempo de actividad (N = 5) y tamaño corporal (N = 4). Se usó una matriz de nicho para evaluar solape entre las especies comunes. Adicionalmente, las especies comunes se comparan a "los grupos nulos" de especies raras y ausentes que podrían colonizar la región potencialmente, pero que son raras o ausentes. Todos los casos de solape (N = 3 pares de especies) ocurren entre taxa hermanos, estrechamente relacionados. Sin embargo, los miembros de esta comunidad de aves de caza exhibieron muy bajo solape (6% - 14%) global, indicativo de separación ecológica espacial y temporal. El hábitat y la actividad explican la mayoría de la variación entre las especies, considerando que los estratos y tamaño del cuerpo son filogenéticamente más limitados. El bosque tropical de Terra-firme que es explotado de forma acelerada, alberga más de la mitad de todas las especies y soporta al menos el doble de la diversidad cuando se le compara con la mayoría de los otros hábitats. Adicionalmente, las especies más grandes de crácidos (es decir, paujies) son las especies más raras, atribuible a su pobre candidatura para regimenes de cosecha sustentables. Muchos nichos están vacíos, lo cual es atribuido a la alta diversidad de microhábitats en los trópicos, lo que a su vez soporta alta diversidad faunística. Se proporcionan casos de especies de otras clases (ej. *Dasyprocta fuliginosa*, *Saguius fuscicollis*) que ocupan algunos de estos nichos, pero análisis más completos de estructura de comunidades de múltiples taxa deben esperar una base de datos más extensa.

### **Separação de Recursos em uma Comunidade Caçadora Napoamazônica -**

Investigamos a possibilidade de separação ecológica de aves de caça (Tinamiformes e Galliformes) na Amazônia, em uma localidade da região de Napo no norte da Amazônia Peruviana (aprox. 2°45'S; 72°55'W). Os dados têm sido coletados desde Novembro de 1993 durante os períodos finais das estações chuvosa e seca. Os indivíduos foram registrados auditiva e/ou visualmente usando transectos de distância ilimitada, realizados por caminhadas ou barco. Registro selecionados foram depositados no Laboratório de Bioacústica da Universidade Texas A&M. Dimensões dos nichos examinados para evidenciar a separação ecológica incluem habitat (N = 5), estrato (N = 3), tempo de atividade (N = 5) e tamanho corporal (N = 4). Uma matriz de nichos é usada para avaliar sobreposições entre espécies comuns. No mais, as espécies comuns são comparadas com “grupos nulos” de espécies raras ou ausentes que poderiam potencialmente colonizar a região. Todos os casos de sobreposição (N = 3 pares de espécies) ocorreram entre táxons proximamente relacionados. Contudo, membros destas comunidades de aves de caça exibiram muita baixa sobreposição global (6% - 14%), indicando separação ecológica espacial ou temporal. O habitat e a atividade são os fatores que mais contam para a maioria da variação entre as espécies, enquanto o estrato e o tamanho corporal são filogeneticamente constrictos. A floresta de *terra-firme* que está sendo consumida em taxas elevadas contém mais do que metade de todas as espécies e comporta pelo menos duas vezes mais diversidade quando comparada com a maioria dos outros habitats. Além disso, as maiores espécies de cracídeos (como os mutuns) são as espécies mais raras, possivelmente devido à pobre possibilidade de regimes de exploração sustentável. Muitos nichos estão vagos devido à diversidade de microhabitats nos trópicos que por sua vez suporta uma alta diversidade faunística. Há casos de espécies de outras classes (por exemplo, *Dasyprocta fuliginosa*, *Saguius fuscicollis*) que ocupam alguns dos nichos vagos, mas uma análise mais completa da estrutura de comunidades de múltiplos táxons deve ser realizada.

**Abstract** - We investigate the possibility of ecological separation in Amazonian gamebirds (Tinamiformes and Galliformes) from a site in the Napo-intersect region of the northern Peruvian Amazon (approx. 2°45'S; 72°55'W). Data have been collected since November 1993 during the terminal periods of high and low water seasons. Individuals were recorded auditorily and/or visually using unlimited distance contact transects, accomplished by walking or boating. Selected voucher recordings were deposited in the Bioacoustics Laboratory at Texas A&M University. Niche dimensions examined for evidence of ecological separation include habitat (N = 5), strata (N = 3), time of activity (N = 5) and body size (N = 4). A niche matrix is used to assess overlap among common species. Additionally, the common species are compared to “null groups” of rare and absent species that could potentially colonize the region, but are rare or absent. All cases of overlap (N = 3 species pairs) occur between closely related sister taxa. However, members of this gamebird community exhibited very low overlap (6% - 14%) overall, indicative of spatial and temporal ecological separation. Habitat and activity account for most of the variation among species, whereas strata and body size are more phylogenetically constrained. *Terra-firme* rainforest that is being harvested at rapid rates harbors more than half of all species and supports at least twice the diversity when compared to most of the other habitats. Additionally, the larger species of cracids (i.e.,

curassows) are the rarest species, attributable to poor candidacy for sustainable harvest regimes. Many niche cells are vacant, attributed to the high microhabitat diversity in the tropics which in-turn supports high faunal diversity. Cases are provided of species from other classes (e.g., *Dasyprocta fuliginosa*, *Saguius fuscicollis*) that occupy some of these vacant niche cells, but more complete analyses of multiple-taxa community structure must await a more extensive database.

Neotropical gamebirds are of paramount importance in their ecosystem as a protein source for local people, as seed dispersing/predating agents in shaping the tropical habitats they live in, and as bioindicators of environmental integrity (Strahl and Brooks 1997). Despite their importance, most studies to date have focused upon individual species; those studies that have focused upon entire assemblages include status surveys and sustainable harvest studies, with few (if any) studies focusing upon community organization processes. For example, the latest reference on Neotropical gamebirds (Strahl et al. 1997), although comprehensive (>500 pages comprised of 85 papers and abstracts), does not include a single paper involving community organization. This paper serves as a “first step” in studying community structure of Neotropical gamebirds.

The way in which resources are separated among guild members is an important component of community ecology because it is linked to competition theory and provides insight towards species organization processes in tropical communities. Closely related species often share similar characteristics that reflect divergent mechanisms of resource utilization in response to sympatric situations where interspecific competition is likely (Brown and Bowers 1985).

Several factors may influence resource allocation in Neotropical gamebird communities. Habitat separation helps alleviate the chance for competition in bird communities (e.g., Cody 1974). Size assortment is the probability of persistence of a species being diminished by the presence of a morphologically similar species when competing for the same resources (Case and Sidell 1983). Similarity in bill structure among species correlates with feeding location overlap (Ricklefs and Cox 1977), suggesting that not only are bill morphologies useful for assessing dietary strategy, but they are also instrumental in assessing competition in avian communities. Taking different types and sizes of food by similar guild members alleviates the chance for competition as well, as will temporal partitioning of activity. Most investigations of resource separation in Neotropical avian communities from the Peruvian Amazon have found ecological separation manifested through differences in foraging strategy (Robinson 1994), size assortment (Brooks 1998), and habitat separation (Terborgh 1985) driven by microhabitat preference (Rosenberg 1990) or competitive exclusion (Robinson and Terborgh 1995, Brooks 1997).

When ranking the importance of habitat, food, and temporal dimensions in their relative contribution to resource partitioning, Schoener (1974) found that habitat is the most important and temporal elements are the least important. However, recent studies have shown that when competition occurs asymmetrically, size differences alone could allow

coexistence independently of any sort of resource partitioning (e.g., Basset 1995). Nonetheless, segregation by food type is more important for animals feeding on large food in relation to their own size than it is for animals feeding on relatively small food items (Schoener 1974). Activity patterns of most Neotropical birds are largely constrained by phylogeny (e.g., Strigids, Nyctibiids, Caprimulgids). Nonetheless there are some exceptions such as Neotropical gamebirds that if not strictly nocturnal (e.g., *Nothocrax*), may be active during diurnal, crepuscular, and/or nocturnal periods (e.g., certain species of Tinamids and Cracids). In many cases these activity patterns are a consequence of behavioral shifts to reduce the chance of predation (e.g., Brooks 1996). Differences in activity patterns may influence ecological partitioning as well.

Our objective is to test whether ecological partitioning occurs in a Neotropical gamebird community comprised of tinamous and galliformes (mostly cracids) from the Napo-intersect region of the Peruvian Amazon. We will accomplish this by collecting data in the field, examining cell space occupation in niche matrices (Willig 1986) and comparing cell space occupation of common species compared to rare and absent species pools.

## METHODS

### Fieldwork

Sampling took place in the Napo-intersect region, where the Napo River drains into the Amazon River in Peru (approx. 2°45'S; 72°55'W; Fig. 1). The three sites sampled were located next to one-another, bordered to the W by the Sucusari Tributary (1<sup>st</sup> site), to the SE by the Camp (2<sup>nd</sup> site), and to the NE by the ACEER (Figure 1). Habitats sampled are primarily situated along water, within forest, or a transition/edge situation between these habitats. Plant species in the region include primary successional island specialists (e.g., *Cecropia sp.*, *Gynerium sp.*, and *Heliconia sp.*), palms (e.g., *Euterpe sp.*, *Mauritia flexuosa*, *Scheelea sp.*, *Socratea sp.*) and large trees that often form part of the canopy, buttresses, or canopy emergents (e.g., *Cedrela sp.*, *Ceiba pentada*, *Ficus insipida* and *Inga sp.*) (e.g., Remsen and Parker 1983).

**Table 1 - Sampling days at Sucusari Tributary, Camp and ACEER sites**

Site	93	94	5/95	10/95	5-6/96	10/96	3/97	10/97	$\bar{X}$ days/trip
Sucusari Trib.	1	1	1	4	4	4	4	4	2.87
Camp	4	3	4	4	4	1	4	3	3.37
ACEER	9	2	2	2	2	2	4	2	3.12

Data collected in the field include species presence and abundance, habitat and strata association, seasonally temporal asynchrony, dietary observations and activity patterns.

Strip transects were employed at each site, recording birds that can be accurately detected visually or auditorily using unlimited distance contacts (Ralph 1981). Walked transects were complemented with some boat transects because waterways, as opposed to trails, are the primary path for transportation in this region. Unknown species were learned using Hilty and Brown (1986) and Parker et al. (n.d). Species that could not be identified with confidence were excluded from the data. Taxonomy (Tables 2-5) follows Stotz et al. (1996), supplemented with a more recent treatment of cracids by Schmitz and Strahl (1997). Selected voucher recordings were deposited in the Bioacoustics Laboratory at Texas A&M University.

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## Figure 1 – Study sites in Amzonian Peru

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QuickTime™ and a  
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are needed to see this picture.

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**Figure 1:** Study sites in the region. S = Sucusari Tributary, C = Camp, A = ACEER. Field data have been collected primarily during the terminal periods of high water (Nov. - May) and low water (June - Oct.) seasons. Specific sampling periods were November 1993, October 1994, May and October 1995, May and October 1996, and March and October 1997 (Table 1). Sampling took place until we were reasonably confident that all common species were encountered, as incomplete faunal communities may bias the outcome (e.g., Willig and Moulton 1989). The duration of sampling varied at each site but typically ranged 1 - 4 days with a mean of 3.12 days/site (Table 1). The only time that sampling exceeded 4 days at a single site is 9 days at ACEER during the first trip (Brooks 1994).

### Analyses

It is important that species are pervasive or common in the community to be considered serious candidates for current competition. While rare species represent an important part of the community, their low abundance makes them weak influences on community composition processes. Moreover, it is possible that the rarity of certain species can be explained from past competition (Lotka 1925). For example, in cases where two species

shared the same ecological niche, populations of one species could have dwindled to rare abundance or local extinction while populations of the “superior competitor” remained common. All inventoried species are divided into two groups: common and rare. A species is considered common if encountered for at least three of the eight sampling periods, with an average encounter rate (= number of individuals/8 sampling durations) exceeding 0.50. Rare species include those remaining.

We will examine cell space occupation in niche matrices (Willig 1986) to determine whether ecological separation is occurring within the gamebird community. Specifically, we will compare cell occupation by common species in relation to rare species, and species that are absent. Distributions among species within niche cells may be relatively even with no overlap, or conversely may be relatively clumped with multiple cells occupied. If distribution of common species among niche cells is relatively even compared to rare and absent species, this would suggest that ecological separation is occurring through more relaxed packing of species within the community.

The rare and absent species will comprise separate null pools. A null pool is considered a pooled assemblage that is associated with the same habitat as the study site, but occurring within a designated geographic region (slightly modified from Ricklefs 1987). The geographic region for the null pool is selected by drawing a concentric circle from the study site using a radius of approximately 333 km. This radius is selected based upon its relative capacity to encircle biomes at country-wide scales (e.g., the Peruvian Napo-intersect region). The source pool for absent species is drawn from the Iquitos region of the Northern Peruvian Amazon using Parker et al. (n.d.) complemented with data from surveys we conducted at other sites. Combining species checklists with additional follow-up surveys provides an accurate species list, insuring that an adequate pool is available for comparison (Willig and Moulton 1989). We will use Hilty and Brown (1986), English and Parker (1992), Strahl et al. (1997) and Montes (1977) to obtain information on habitat and activity for absent species, and to bolster our ecological data of rare species. Additionally, we will use Blake (1977) to obtain data on size; flattened wing chord (mm) is used since it serves as a good indicator of overall size, eliminating biased weights from longer tails or ornamentation. The median value for ranges of wing chord measurements is obtained by pooling minimum and maximum values from both sex classes; this median value is used to group species into one of four different size classes: small (<195 mm), medium (195-280 mm), large (280-365 mm) and jumbo (>365 mm).

## **RESULTS AND DISCUSSION**

### **Abundance**

A total of five species were common (three tinamous, two cracids), eight rare (five tinamous, two cracids, one quail), and three not present at the site (all cracids) (Table 2).

It is not too surprising that cracids are among the rarest species and the only family of gamebirds that are absent, considering that they are the largest of the gamebirds and



**Table 3 - Habitat and strata association of individual species**

	<u>Habitat Association</u>					<u>Strata Association</u>		
	RF	TF	FE	SF	V	A	S	T
<b>Tinamidae</b>								
<i>Tinamus guttatus</i>	-	x	-	-	-	-	-	x
<i>Tinamus tao</i>	-	x	-	-	-	-	-	x
<i>Tinamus major</i>	-	x	x	-	-	-	-	x
<i>Crypturellus bartletti</i>	x	-	-	-	-	-	-	x
<i>Crypturellus cinereus</i>	x	-	-	-	-	-	-	x
<i>Crypturellus soui</i>	-	-	x	x	-	-	-	x
<i>Crypturel. undulatus</i>	-	-	-	-	x	-	-	x
<i>Crypturel. variegatus</i>	-	x	-	-	-	-	-	x
<b>Cracidae</b>								
<i>Ortalis guttata</i>	-	-	x	x	x	-	x	-
<i>Penelope jacquacu</i>	-	x	x	-	-	x	-	-
<i>Pipile cumanensis</i>	x	-	-	-	x	x	-	-
<i>Nothocrax urumutum</i>	x	x	-	-	-	-	x	-
<i>Crax globulosa</i>	-	-	-	-	x	x	-	-
<i>Mitu salvini</i>	-	x	-	-	-	-	x	-
<i>Mitu tuberosa</i>	x	x	-	-	-	-	x	-
<b>Odontophoridae</b>								
<i>Odontophorus gujan.</i>	-	x	-	-	-	-	-	x
# spp./niche dimens.	5	9	4	2	4	3	4	9

**Habitat Codes:** RF = riverine forest, TF = *terra-firme*, FE = forest edge, SF = secondary forest, V = varzea  
**Strata Codes:** A = primarily arboreal, S = primarily scansorial, T = primarily terrestrial

### Community Structure

The niche matrix produced a total of 300 cells, attributed by three strata parameters, four size parameters, and five parameters each for habitat and activity (Tables 3-5). Of these, six species occupied a single cell (one common, four rare, one absent), four species occupied two cells (one common and three rare), four species occupied three cells (three common and one absent), and two species occupied four cells (one rare and one absent).

Some of the species occupying multiple niche cells were not necessarily distributed in a straight row. For example, *Tinamus major* is active in *terra-firme* forest during afternoon and night, but in edge situations only active at nighttime. This may reflect increased vulnerability to predation/hunters during the daytime along the open edge habitat; consequently shifting diurnal activity to inside the relatively closed forest.

**Table 4 - Sizes and activity patterns of individual species**

	<u>Size</u>				<u>Activity Patterns</u>				
	S	M	L	J	M	A	S	N	D
<b>Tinamidae</b>									
<i>Tin. guttatus</i>	-	x	-	-	-	x	-	-	-
<i>Tinamus tao</i>	-	x	-	-	-	-	x	-	-
<i>Tin. major</i>	-	x	-	-	-	-	x	x	-
<i>Cryp. bartletti</i>	x	-	-	-	-	-	-	x	-
<i>Cryp. cinereus</i>	x	-	-	-	x	x	-	-	-
<i>Cryptur. soui</i>	x	-	-	-	-	x	-	-	-
<i>Cr. undulatus</i>	x	-	-	-	x	x	-	-	-
<i>Cr. variegatus</i>	x	-	-	-	-	-	x	-	-
<b>Cracidae</b>									
<i>Ortalis guttata</i>	-	x	-	-	x	-	-	-	-
<i>Pen. jacquacu</i>	-	-	x	-	-	x	-	-	x
<i>Pipile cuman.</i>	-	-	x	-	x	-	-	-	x
<i>Nothocrax ur.</i>	-	-	x	-	-	-	-	x	-
<i>Crax globul.</i>	-	-	-	x	-	-	-	x	-
<i>Mitu salvini</i>	-	-	-	x	x	x	-	x	-
<i>Mitu tuberosa</i>	-	-	-	x	-	x	-	x	-
<b>Odontophoridae</b>									
<i>Odon. gujan.</i>	x	-	-	-	-	-	x	-	-
# spp./n dim.	6	4	3	3	5	7	4	6	2

**Size Codes:** S = small, M = medium, L = Large, J = jumbo

**Temporal Activity Codes:** M = diurnal during morning, A = diurnal during afternoon, S = crepuscular at sundown, N = nocturnal, D = crepuscular at dawn

A total of 30 cells (only 10%) were occupied total. None of the species from the common (real) pool jointly shared any cells, indicative of complete lack of ecological overlap for the four parameters examined. When the rare pool is added, two pairs of species overlap. *Crypturellus undulatus* (common) and *C. soui* (rare) overlap in one-third and one-half of their niche cell breadths, respectively. *Tinamus major* (common) overlaps one-third of its niche cell breadth with *T. tao* (rare). Only a portion of the realized niche overlaps for three of these four species when the rare pool is considered (*T. tao* being the exception). Moreover, with the addition of the absent pool only one additional species pair overlap occurs, albeit twice: *Mitu tuberosa* (rare) and *M. salvini* (absent). However, due to the rarity of *Mitu* (see discussion below) and the fact that in most situations these sibling taxa are separated by fluvial systems (e.g., Scheuerman 1977), the likelihood of their occurring at the site simultaneously is low. In sum, the

amount of ecological overlap (i.e., 6% - 13%) in this Amazonian gamebird community is very low. The high amount of empty niche cells can be explained to high diversity of microhabitats and complex habitat heterogeneity in the tropics, producing an abundance of ecological niche spaces for species to occupy. Additionally, it is interesting to note that the most likely species to overlap are congeners or sister taxa, reflecting the intricate evolutionary and biogeographic processes attributing to high speciation rates in this region.

**Table 5 - Niche cell matrix**

	RA	TA	EA	SA	VA	RS	TS	ES	SS	VS	RT	TT	ET	ST	VT
SM	-	-	-	-	-	-	-	-	-	-	cc	-	-	-	<b>cu</b>
SA	-	-	-	-	-	-	-	-	-	-	cc	od	cs	cs/cu	<b>cu</b>
SS	-	-	-	-	-	-	-	-	-	-	-	<b>cv</b>	-	-	-
SN	-	-	-	-	-	-	-	-	-	-	cb	-	-	-	-
SD	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
MM	-	-	-	-	-	-	-	<b>og</b>	<b>og</b>	<b>og</b>	-	-	-	-	-
MA	-	-	-	-	-	-	-	-	-	-	-	tg	-	-	-
MS	-	-	-	-	-	-	-	-	-	-	-	<b>tm/tt</b>	-	-	-
MN	-	-	-	-	-	-	-	-	-	-	-	<b>tm</b>	<b>tm</b>	-	-
MD	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
LM	<i>pc</i>	-	-	-	<i>pc</i>	-	-	-	-	-	-	-	-	-	-
LA	-	pj	-	-	-	-	-	-	-	-	-	-	-	-	-
LS	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
LN	-	-	-	-	-	<b>nu</b>	<b>nu</b>	-	-	-	-	-	-	-	-
LD	<i>pc</i>	-	pj	-	<i>pc</i>	-	-	-	-	-	-	-	-	-	-
JM	-	-	-	-	-	-	<i>ms</i>	-	-	-	-	-	-	-	-
JA	-	-	-	-	-	mt	mt/ <i>ms</i>	-	-	-	-	-	-	-	-
JS	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
JN	-	-	-	-	<i>cg</i>	mt	mt/ <i>ms</i>	-	-	-	-	-	-	-	-
JD	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

**Species Key:** bold font = common species, normal font = rare species, *italicized font* = absent species, tg = *Tinamus guttatus*, **tm** = *T. major*, tt = *T. tao*, cb = *Crypturellus bartletti*, cc = *C. cinereus*, cs = *C. soui*, **cu** = *C. undulatus*, **cv** = *C. variegatus*, **og** = *Ortalis guttata*, pj = *Penelope jacquacu*, *pc* = *Pipile cumanensis*, **nu** = *Nothocrax urumutum*, *ms* = *Mitu salvini*, mt = *M. tuberosa*, *cg* = *Crax globulosa*, od = *Odontophorus gujanensis*

**Habitat Key:** R = riverine forest, T = *terra-firme*, E = forest edge, S = secondary forest, V = varzea

**Strata Key:** A = primarily arboreal, S = primarily scansorial, T = primarily terrestrial

**Size:** S = small, M = medium, L = Large, J = jumbo

**Temporal Activity Key:** M = diurnal during morning, A = diurnal during afternoon, S = crepuscular at sundown, N = nocturnal, D = crepuscular at dawn

## General Patterns

A number of interesting trends are immediately apparent by looking at the tabularized data. For example, smaller species are increasingly terrestrial (Table 5). This is largely constrained by phylogeny because most tinamous (terrestrial) fall into the small or medium sized categories, whereas most cracids (scansorial and arboreal) fall into the large and jumbo categories.

Perhaps more compelling are the exclusive subsets of the niche matrix that are occupied (e.g., smaller and medium sized terrestrial species, large arboreal species, and jumbo scansorial species). This leaves several ecological niches mostly vacant, potentially occupied by other taxa, including small/medium sized arboreal/scansorial species (e.g., smaller birds and tamarins), large terrestrial species (e.g., large caviid rodents), and jumbo arboreal and terrestrial species (e.g., larger primates and artiodactyls). The capacity for these species to coexist without overlap is possible. For example, black agoutis (*Dasyprocta fuliginosa*) are terrestrial edge specialists during afternoon and sundown crepuscular periods (DMB, unpubl. data), an ecological niche that is unoccupied by other gamebirds from this region (Table 5). Similarly, saddleback tamarin monkeys (*Saguinus fuscicollis*) occupy arboreal strata of *terra-firme* forest during daylight hours (DMB, unpubl. data), again vacant of similar-sized species (Table 5). More complete community structure analyses of multiple families and classes must await more extensive data that is currently lacking for certain taxa.

Strata association is largely constrained by phylogeny, with all species of tinamou and quail being terrestrial, arboreality restricted to guans and *Crax globulosa*, and the remaining cracids being scansorial (Table 3). Similarly, size is somewhat phylogenetically constrained, with all *Crypturellus* tinamous and quail falling into the small category, *Tinamus* tinamous and chachalaca in the medium category, guans and *Nothocrax* in the large category, and most curassows in the jumbo category (Table 4).

In contrast, there is extensive variation within the parameter of activity pattern (Table 4), and even more variation with habitat association (Table 3). It would appear that these two parameters are the more important in Amazonian gamebird ecological separation, with habitat perhaps being the most important, concordant with the findings of Schoener (1974).

Indeed, it is important to note that more than one-half (56%) of all species from the three pools were associated with primary, *terra-firme* rainforest. The second most important habitat, riverine forest, harbored less than one-third of all species (31%). Primary, *terra-firme* rainforest harbors a diverse array of organisms and is currently being harvested at unprecedented levels throughout the tropics (e.g., Myers 1984). However, a more serious threat to multiple species in this region, especially large cracids, is severe overhunting. Nonetheless, preliminary data suggest that overhunting is being curbed in this region. What was an intensively hunted site for two to three decades can now be considered a moderately hunted site. Although still a very subtle pattern, more residual game species are increasingly abundant in the past five years, most dramatically over the last two years. For example, larger species of primates that are more preferred by hunters are being

recorded with increasing regularity (DMB and LPV, unpubl. data), suggesting more sustainable levels of game harvest through lower rates of take.

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