RESOURCE SEPARATION IN A NAPO-AMAZONIAN TINAMOU COMMUNITY

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Resumen. – Repartición de recursos en una comunidad de tinamúes en Napo-Amazónico. – Investigamos la posibilidad de separación ecológica en tinamúes Amazónicos (Tinamiformes) en una localidad ubicada en la región de intersección del Napo y el Amazonas, en el norte de la Amazonía Peruana (aprox. 02°45'S, 72°55'W). Los datos han sido reunidos desde noviembre de 1993 durante los periodos 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 recorridos 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 el hábitat (N = 5) y el tiempo de actividad (N = 4). Se usó una matriz de nicho para evaluar el solapamiento entre las especies comunes. Adicionalmente, las especies comunes se comparan con "grupos nulos" de especies raras que podrían potencialmente colonizar la región, pero que son raras o ausentes. Se encontró un solo caso de solapamiento global (8%), lo que indica una separación ecológica espacial y temporal. El bosque tropical de *terra firme* que es explotado de forma acelerada alberga más de la mitad de todas las especies y mantiene al menos el doble de la diversidad encontrada en la mayoría de los otros hábitat.

Abstract. – We investigate the possibility of ecological separation in Amazonian tinamous from a site in the Napo-intersect region of the northern Peruvian Amazon (approx. 02°45'S, 72°55'W). Data have been collected since 1993, mainly during the terminal periods of high and low waters 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) and time of activity (N = 4). A niche matrix is used to assess overlap among common species. Additionally, the common species are compared to "null groups" of rare species that could potentially colonize the region, but are rare or absent. Only a single case of overlap occurred overall (8%), indicative of spatial and temporal ecological separation. *Terra firme* rainforest that is being harvested at rapid rates harbors half of all species and supports at least twice the diversity, compared to most of the other habitats. *Accepted 6 January 2004.*

Key words: Tinamou, community ecology, Amazonian game birds, Neotropical game birds.

INTRODUCTION

Neotropical game birds are of paramount importance in their ecosystem as a protein source for local people, as seed dispersing/predating agents in shaping the tropical habi-tats they live in, and as bioindicators of environmental integrity (Strahl & 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 sus-
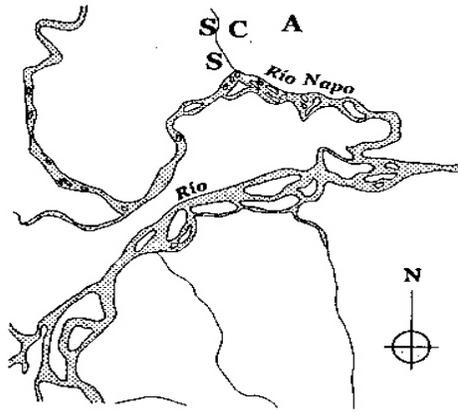
FIG. 1. Study sites in the region. S = Sucusari Tributary, C = Camp, A = ACEER.

tainable harvest studies, with few studies focusing upon community organization processes.

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 tinamou communities. Habitat separation (e.g., Cody 1974) helps alleviate the chance for competition in bird communities, 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, 2003), and habitat separation (Terborgh 1985) driven by microhabitat preference (Rosenberg 1990) or competitive exclusion (Robinson & Terborgh 1995,

Brooks 1997). As can be expected, a suite of these factors is typically the driving force of ecological separation (Brooks 1999, Brooks *et al.* 2001).

When studying temporal separation in a guild of Amazonian game birds, Brooks *et al.* (2001) found that habitat association and temporal activity were stronger indicators of ecological separation than body size and strata. Similarly, 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. Activity patterns of most Neotropical birds are largely constrained by phylogeny (e.g., strigids, nyctibiids, caprimulgids). Nonetheless there are some exceptions such as Neotropical game birds 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 tinamou community 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 species.

METHODS

Fieldwork. Sampling took place in the Napo-intersect region, where the Napo river drains into the Amazon river in Peru (approx. 02°45'S, 72°55'W; Fig. 1). The three sites sampled were located next to one-another, bordered to the west by the Sucusari tributary (1st

TABLE 1. Sampling days at Sucusari tributary, Camp and ACEER sites.

Sites	11/93	10/94	5/95	10/95	5/96	10/96	3/97	10/97	5/98	10/98	6/03	Mean number of days/trip
Sucusari	1	1	1	4	4	4	4	4	4	3	3	2.90
Camp	4	3	4	4	4	1	4	3	3	3	3	3.45
ACEER	9	2	2	2	2	2	4	2	2	2	2	2.81

TABLE 2. Number of encounters/species/sampling period.

Species	11/93	10/94	5/95	10/95	5/96	10/96	3/97	10/97	5/98	10/98	6/03	Mean number of encounters/trip
Common												
Tinamus major	1	1	1	1	-	3	3	3	1	2	-	1.45
Crypturellus undulatus	2	-	-	-	-	4	-	3	3	2	4	1.63
Crypturellus variegatus	-	-	-	-	1	1	1	3	1	1	1	0.81
Rare												
Crypturellus soui	1	-	-	1	-	-	-	-	-	1	-	0.27
Crypturellus. cinereus	-	-	-	-	-	-	-	2	1	1	1	0.45
Crypturellus bartletti	-	-	-	-	-	-	-	2	1	-	-	0.27
Tinamus guttatus	1	-	-	-	-	-	-	-	-	-	-	0.09
Tinamus tao	-	-	-	-	-	1	-	-	-	-	-	0.09

site), to the southeast by the Napo Camp (2nd site), and to the northeast by the ACEER (Fig. 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 & Parker 1983).

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 3.05 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.

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 & Brown (1986) and Parker *et al.* (undated). Species that could not be identified with confidence were excluded from the data. Taxonomy (Tables 2 and 3) follows Stotz *et al.* (1996). Selected voucher recordings were deposited in the Bioacoustics Laboratory at Texas A&M University.

Analyses. It is important that species that are pervasive or common in the community be considered serious candidates for current competition. While rare species represent an important part of the community, their low abundance results in them having 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 6 of the 11 sampling periods, with an average encounter rate (= number of individuals/8 sampling periods) 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 tinamou community. Specifically, we will compare cell occupation by common species in relation to rare species. 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 species, this would suggest that ecological separation is occurring through more relaxed packing of species within the community.

RESULTS

A total of three species were common, and five were rare (Table 2). The niche matrix produced a total of 20 cells, attributed by five parameters for habitat, and four for activity (Table 3). Of these, four species occupied a single cell (one common, three rare), three species occupied two cells (one common, two

TABLE 3. Niche matrix reflecting habitat and activity patterns of individual species. Species keys: bold font = common species, normal font = rare species, Tg = *Tinamus guttatus*, Tt = *T. tao*, Tm = *T. major*, Cb = *Crypturellus bartletti*, Cc = *C. cinereus*, Cs = *C. soui*, Cu = *C. undulatus*, Cv = *C. variegates*.

	Riverine forest	*Terra firme*	Forest edge	Secondary forest	Varzea
Diurnal during morning	Cc	-	-	-	**Cu**
Diurnal during afternoon	Cc	Tg	Cs	Cs	**Cu**
Crepuscular	-	**Tm**, Tt, **Cv**	**Tm**	-	-
Nocturnal	Cb	**Tm**	**Tm**	-	-

rare), and one (common) species occupied four cells.

A total of six cells (30%) were occupied total by the common species pool; when the rare pool is added, 12 cells (60%) were occupied total. Only a single case of overlap is recognized: the Great Tinamou (*Tinamus major*; common) overlaps one-fourth of its niche cell breadth with the Variagated Tinamou (*Crypturellus variegates*; common) and the Gray Tinamou (*T. tao*; rare), suggesting that only a portion of the realized niche overlaps for the Great Tinamou. In sum, the amount of ecological overlap (8%) in this Amazonian tinamou community is very low when considering parameters of habitat association and activity.

DISCUSSION

Other factors besides competition that may influence the composition of Neotropical avian communities include predation, parasitism and disturbance (Begon & Mortimer 1986). Predation will affect different species in different ways, though it appears to have the most severe impact on nesting birds and their brood (Lack 1947). However, there are often tradeoff relationships between factors such as nest exposure, crypsis of incubating hen, voice intensity of begging chicks, and clutch size (Lack 1947). This decreases the likelihood of one species receiving a higher nest predation rate than another, since all spe-

cies should theoretically reach an evolutionary stable strategy if the community is at equilibrium (Maynard Smith 1977).

While it initially seems apparent that all species should have an equal probability of infestation by parasitic diseases, this is not necessarily the case. For example, parasite banks of some species are restricted to the soil, and consequently species such as tinamids that are primarily terrestrial or consume their food mostly on the ground may have higher parasite loads, which could in turn affect abundance of individual species in the community.

Disturbance manifested through habitat alteration will benefit some open habitat specialists such as tyrannids, but negatively affects forest-dwelling species such as several of the tinamids. Indeed, it is important to note that one-half (50%) of all species in this study were associated with primary *terra firme* rainforest. This is relevant, as primary *terra firme* rainforest harbors a diverse array of organisms, such as the little-known tinamou communities we are so anxious to preserve, and is currently being harvested at unprecedented levels throughout the tropics (e.g., Myers 1984).

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