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THE RELATIONSHIP BETWEEN ENVIRONMENTAL STABILITY AND AVIAN POPULATION CHANGES IN AMAZONIA

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Resumen. – Relación entre la estabilidad ambiental y los cambios en las poblaciones de aves en la Amazonia. – Aunque varios autores han evaluado los efectos de alteración del hábitat sobre las comunidades de aves tropicales, ninguno ha evaluado si estas comunidades experimentan cambios poblacionales en hábitat ambientalmente estables. Nosotros evaluamos este tema usando datos de un estudio a largo plazo realizado en una región florísticamente estable de la Amazonia Peruana. Usando transectos en banda, colectamos datos sobre la presencia y abundancia de especies al final de la época de lluvias. De 262 especies de aves registradas, sólo 6 experimentaron cambios poblacionales estadísticamente significativos. El hecho de que sólo 2% de la comunidad mostró cambios poblacionales significativos sugiere que las poblaciones estables de aves prosperan en ambientes o hábitat estables. Un hecho muy importante es que las aves que dependen de los bosques tropicales no mostraron cambios poblacionales, fortaleciendo nuestro argumento de que los ambientes y hábitat estables conducen a comunidades faunísticas estables. Se examinan patrones a gran escala con el fin de ayudar a interpretar nuestros resultados.

Abstract. – Although several authors have addressed the effects of habitat alteration on tropical bird communities, none have addressed the magnitude of population changes in environmentally stable habitats. We address this topic using long-term data from a floristically stable region of the Peruvian Amazon. We collected data on species presence and abundance using strip transects at the termination of the high water season. Of 262 species of birds recorded, only 6 species had population changes that were statistically significant. The fact that only 2% of the community showed significant population changes suggests stable avian populations thrive in stable environments or habitats. More importantly, species dependent upon tropical forest did not show population changes, strengthening our argument that stable environments or habitats lead to stable faunal communities. Broad-scale patterns are examined to help interpret our results.

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Key words: Tropical forest, stability, population change, Neotropical birds, Amazonia.

INTRODUCTION

Environmental stability implies increased predictability and less variability within a given environment relative to another (Leigh 1990). Tropical lowland rainforest is often considered more stable than tropical or subtropical environments, as productivity, temperature and humidity are relatively constant throughout the year (Karr & Freemark 1983, Brooks 2003). However, while stable environments yield a sufficient supply of resources for species to exist, environmental stability itself is difficult to measure (Leigh 1990).

While tropical communities are shaped by many factors (Brooks 2003), a strong characteristic of environmental stability is increased species diversity (Levins 1968, MacArthur 1972, May 1973). Diminished abundance of individual species is the compensatory mechanism or ecological trade-off for high diversity (Brooks 2003). Nonetheless, complex and species rich communities depend on a stable environment and consequently are more sensitive to human disturbance (May 1973).

Given such threats of human disturbance, long-term preservation of biodiversity is a primary objective of conservation biology (Robinson 1999). Monitoring population changes in vertebrate communities is the first step to identify causative factors of species increases and declines over time. Unfortunately, most field studies are of a shorter duration, and consequently long-term monitoring studies are rather limited (Turner 1996, Robinson 1999, 2001). However, some studies have been able to address long-term changes in vertebrate communities by comparing historical data and notes from the literature to more recently collected data (e.g., Renjifo 1999; Robinson 1999, 2001; Schmidly 2002), or by comparing pristine sites to disturbed sites (e.g., Bodmer & Brooks 1997, Brooks & Begazo 2001).

Even though long-term population monitoring studies of Neotropical vertebrates do exist, comparison among such studies is severely hampered by lack of standardized methodologies (Terborgh *et al* 1990). Stouffer & Bierregaard have investigated the effects of forest fragmentation on Amazonian birds over time, but their analyses are restricted mostly to individual species (Stouffer & Bierregaard 1993) or ecological guilds (e.g., Stouffer & Bierregaard 1995). Hill *et al.* (1997) investigated the effects of hunting upon tropical game species over time; this is one of the few, if not only, long-term studies that addresses population fluctuations of an entire tropical assemblage, but the focus is upon game species (primarily mammals) rather than an avian community.

Although several authors have addressed the effects of habitat alteration on tropical bird communities (e.g., Stouffer & Bierregaard 1993, 1995; Renjifo 1999, Robinson 1999), none have addressed the magnitude of population changes in environmentally stable habitats. We have studied the bird community described herein intensively, with our combined efforts exceeding 70 observation-years. While we have addressed the role of size assortment in structuring this community (Brooks 2003), community ecology of various frugivorous assemblages (Brooks 1997; Brooks *et al.*1999, 2001, 2004), and the role of harvest rates in attributing species loss (Brooks *et a*l. 1999, Brooks & Begazo 2001), we have failed to address population changes in this community over time. In this paper, we address whether populations of species in this community change in a stable environment and habitat, from data collected over 9 years (1995–2003). Defining environmental stability itself is highly debated because it is so difficult to measure. However, one of the main predictions of environmental stability is that populations living within stable environments tend to change little. Our objectives herein are to test that prediction with bird populations

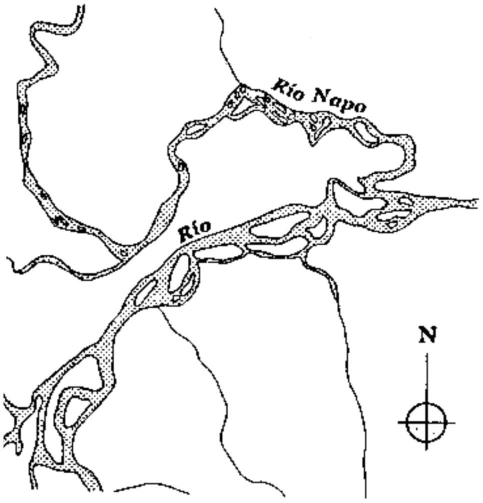

FIG. 1. Study region in the Peruvian Amazon.

living in an environment deemed stable historically, tropical lowlands.

METHODS

Field methods. The study site is ideal to test hypotheses involving stable environments, as the forest is quite stable floristically with timbering not being a major threat. One of the forests surveyed on our study site represents the highest known diversity of trees in the world (Gentry 1988).

The study site was located 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). Mean annual temperature in the region is 26°C, ranging from 22°C in July to 31°C.in November (Salati 1985). Annual rainfall ranges 2500–3000 mm per year, with low-water season generally ranging from June–October (Johnson 1976, Brooks pers. observ.). Plant species in the region have been described (e.g., Remsen & Parker 1983) as 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.).

Eight broad categories of habitat were sampled: mainstem Amazonian river, wider tributaries with open cover, narrow tributaries with closed canopy, oxbow lake-dense sawgrass cover, oxbow lake-blackwater with water hyacinths, Amazonian Islands, lowland tropical forest and associated edge, and lowland tropical forest canopy (Table 1). For analytical purposes, these habitats were lumped into one of the following categories: riverine edge, lake edge, forest edge, and forest (Table 2).

Sampling protocols were detailed in Brooks (1998), but are briefly summarized here. Sampling took place at the termination of the high-water season (May–early June) in 1995, 1998 and 2003. We collected data on species presence and abundance using strip transects, recording birds that could 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 (Brooks *et al.* 1999, 2001). The number of transects for each habitat varied per sample year, but averaged 3.6 transects/habitat (Table 1), with a mean transect length of 1.7 km (Brooks 1998). An effort was made to use several transects in each habitat to reduce the risk of over- or underestimating species abundances due to higher or lower yields along certain transects. Unknown species were identified using Hilty & Brown (1986) and the unpublished checklist of Parker *et al.* Selected voucher recordings were deposited in the Bioacoustics Laboratory at Texas A&M University.

Analyzing population trends. A population of a given species was considered to change if the

TABLE 1. Number of transects sampled in each habitat.

Habitats	1995	1998	2003	Mean
Mainstem Amazonian River	5	4	4	4.3
Wider tributaries with open cover	4	5	4	4.3
Narrow tributaries with closed canopy	5	6	6	5.6
Oxbow Lake-dense sawgrass cover	1	1	2	1.3
Oxbow Lake-blackwater with water hyacinths	2	2	2	2.0
Amazonian Islands	1	1	1	1.0
Lowland tropical forest and associated edge	9	9	8	8.6
Lowland tropical forest canopy	2	2	2	2.0

following assumptions were met: 1) the population change was steady without any dipping or peaking from the general slope of the plotted data, 2) the population data were not derived from only a single sample, and 3) the population for 1995 was at least five times the amount of 2003 to be considered a population decrease, or vice-versa for a population increase.

The overall avian community would be deemed “highly unstable” if $\geq$ 75% of the community showed significant population changes, “moderately unstable” if 50% of the community showed significant population changes, and “relatively stable” if $\leq$ 25% of the community showed significant population changes. These parameters were established to equitably delineate chance of community instability at three levels. Chi-square tests were performed to determine how many species showing population change trends were statistically significant.

RESULTS AND DISCUSSION

We recorded a total of 262 species (complete list available from corresponding author upon request). Of the 13 species meeting the assumptions of population change, 6 (2% of the community) of these population changes were statistically significant: 2 population increases, and 4 decreases (Table 2).

The fact that only 2% of the community showed significant population changes suggests stable avian populations thrive in stable environments or habitats. More importantly, only a single species, the White-throated Toucan (*Ramphastos tucanus*), was associated with tropical forest, and none of the species occurred solely in tropical forest. Thus, species dependent upon tropical forest did not show population changes, strengthening our argument that stable environments or habitats lead to stable faunal communities. Below we examine more broad-scale patterns to help explain changes for the six species that showed significant population increases and decreases.

Ecological patterns. If we examine dietary patterns, both species showing population increases were frugivores (Table 2). Of the four species showing population decreases, two were frugivores, and a single species in omnivore and granivore categories (Table 2). Frugivores are the most abundant group for both population increases and decreases. This is likely to be a reflection of species whose populations fluctuate with seasonality of fruit blooms (e.g., Terborgh 1986).

If we examine patterns of habitat association, four of the species (66%) were associated with more than one habitat type (Table 2). Both of the species showing population increases occupied riverine edge, and one of these was also associated with forest edge

TABLE 2. Population changes for individual species 1995-2003. Units of measurement represent individuals/yr.

	1995	1998	2003	Chi-Sq.	Diet[a]	Habitat[b]
Population increases						
Snowy Egret (*Egretta thula*)	0	1	7	NS	P	R
Canary-winged Parakeet (*Brotogeris versicolorus*)	0	0	260	< 0.001	F	R, E
Short-tailed Parrot (*Graydidascalus brachyurus*)	0	2	37	< 0.001	F	R
Amazon Kingfisher (*Chloroceryle amazona*)	3	6	11	NS	P	R, L
Chestnut Jacamar (*Galbalcyrhynchus leucotis*)	0	0	5	NS	I	E
Plum-throated Cotinga (*Cotinga maynana*)	1	1	6	NS	F	R, L
Social Flycatcher (*Myiozetes similis*)	0	2	6	NS	I	R
Crested Oropendola (*Psarocolius decumanus*)	4	4	14	NS	O	R
Population decreases						
Red-bellied Macaw (*Ara manilata*)	5	2	0	NS	F	R
Blue-headed Parrot (*Pionus menstruus*)	15	12	1	< 0.025	F	R, L
White-throated Toucan (*Ramphastos tucanus*)	17	8	2	< 0.05	F	F, E
Yellow-rumped Cacique (*Cacicus cela*)	28	7	6	< 0.01	O	R, E
Lined Seedeater (*Sporophila lineola*)	25	5	0	< 0.001	G	L

[a] Diet: F = Frugivore, P = Piscivore, I = Insectivore, O = Omnivore, G = Granivore.

[b] Habitat: R = Riverine Edge, L = Lake Edge, E = Forest Edge, F = Forest.

(Table 2). Of the four species showing population decreases, two species occupied riverine edge, two species occupied forest edge, two species occupied lake edge, and only a single species occupied forest (Table 2).

Riverine edge was the most frequently used habitat for species showing population change, with forest edge and lake edge being used by fewer species. As mentioned above, it is not too surprising that forest is used by fewer species showing population change, as this habitat is more stable over time in areas where timbering is not intensive, such as our study region. In contrast, edge habitats are much more prone to seasonal disturbance due to weather patterns and other events; consequently one would expect more population fluctuations in these habitats (Remsen & Parker 1983).

Taxonomic patterns. If we examine taxonomic patterns, half of the six species with significant population changes were psittacids. Canary-winged Parakeet (*Brotogeris versicolorus*) and Short-tailed Parrot (*Graydidascalus brachyurus*) showed population increases, whereas Blue-headed Parrot (*Pionus menstruus*) showed a population decrease (Table 2). Psittacids are challenging to sample because they can travel great distances on a daily basis (Munn 1992). However, this variation in abundance is also tied to other factors, including seasonal and annual fluctuations in fruit and resource abundance, overharvest of parrots for protein or the pet trade, and palm tree harvest (Terborgh 1986, Begazo 1997, Brooks & Begazo 2001).

Species turnover. Punctuated species turnover as it relates to beta-diversity might play a role in rapid population increases for species such as Canary-winged Parakeet (Table 2). For example, sister-taxa Tui Parakeet (*B. sanctihomae*) and Cobalt-winged Parakeet (*B. cyanoptera*) were the dominant *Brotogeris* at the study site, with 155 and 146 individuals recorded, respectively, from 1993–1998. Canary-winged Parakeet was not nearly as abundant during the same period, but approximately 150 individuals were recorded east of our study site, along the Amazon River from Iquitos to the Colombia/Brazil border in May 1996; in contrast only two Tui Parakeet and no Cobalt-winged Parakeet were recorded along the same length of river (D. Brooks unpubl.). During surveys in 2003 when record numbers (260) of Canary-winged Parakeet were obtained at the study site, only 24 and 2 individuals of Tui Parakeet and Cobalt-winged Parakeet were recorded, respectively.

The dynamics of species turnover within assemblages, while not well understood, are undoubtedly important factors in structuring tropical communities, as they drive change in species composition over time. This raises the importance of accomplishing studies of even longer duration that address community change over time. By achieving studies of longer duration we will be better equipped to unravel puzzling questions that cannot be answered using short-term data.

Conservation implications. Of the species showing significant population declines, Blue-headed Parrot and White-throated Toucan (half of those showing declines) are potential protein sources. Moreover, these two species plus a third species, Yellow-rumped Cacique (*Cacicus cela*) (75% of those species showing declines), are used to make feather ornamentation by Amerindians (Brooks 2001).

Stattersfield *et al.* (1998) provide avian conservation priorities in 41 regions of South America, with the Upper Amazon-Napo Lowlands (UANL) being one of these regions. Although Stattersfield *et al.* (1998) provide the UANL region with a "high" priority rank, it is surpassed by other regions that received "urgent" and "critical" ranks. The "high" priority rank estimates no more than 5% of range-restricted species to go extinct in the UANL region over the next century, compared to 5–30% for the "urgent" category, and > 30% for the "critical" category.

It is important to note that we only addressed population changes in pristine habitat herein, rather than resiliency of these species to forest destruction; the main factor leading to local extinction of most tropical avifaunas (J. Tello pers. com.). Regeneration of tropical forest and its inhabitants subsequent to deforestation takes hundreds of years, and the resulting forests never return to their original form during recovery (e.g., Renjifo 1999, Robinson 1999).

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