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EFFECTS OF HABITAT STRUCTURE ON THE SPATIAL DISTRIBUTION OF TWO SPECIES OF TINAMOUS (AVES: TINAMIDAE) IN A AMAZON TERRA-FIRME FOREST

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Resumo. – Efeitos da estrutura do habitat na distribuição espacial de duas espécies de tinamídeos (Aves: Tinamidae) na floresta de terra-firme na Amazônia. – Nós investigamos como a distribuição espacial de duas espécies de tinamídeos (família Tinamidae) é modulada pela variação natural na estrutura de uma floresta de terra-firme, na Amazônica Central. Nós testamos como cinco componentes da estrutura da floresta (troncos mortos caídos no chão, abertura de dossel, abundância de árvores, profundidade da serapilheira e distância da água) influenciaram a distribuição espacial de Inhambu-de-cabeça-vermelha (*Tinamus major*) e Inhambu-anhangá (*Crypturellus variegatus*). Entre outubro de 2012 e abril de 2013, utilizamos 30 pontos de escuta para estimar a frequência de ocorrência das duas espécies dentro de uma área de 25 km^2 dentro de uma área de 25 km^2. Modelos lineares múltiplos indicaram que a frequência de ocorrência de Inhambu-de-cabeça-vermelhanão foi explicada por nenhum componente da estrutura da floresta. A ocorrência de Inhambu-anhangá aumentou significativamente com o aumento na abertura de dossel da floresta e a abundância de troncos mortos no chão, e diminuiu com o aumento na profundidade de serapilheira. Podemos concluir que heterogeneidade da floresta pode ser um fator importante na distribuição espacial de aves.

Abstract. – We investigated how the spatial distribution of two species of tinamous (Family Tinamidae) is modulated by the variation in the natural structure of a central Amazonian terra-firme forest. We tested whether five components of forest structure (dead fallen trunks, canopy openness, tree abundance, leaf-litter depth and distance to water) influence the spatial distribution of Great (*Tinamus major*) and Variegated Tinamou (*Crypturellus variegatus*). We used 30 listening points between October 2012 and April 2013 to estimate the frequency of occurrence of these species within a 25-km^2 area. Multiple linear models indicated that the frequency of occurrence of the Great Tinamou was not explained by any tested component of the forest structure. The occurence of the Variegated Tinamou increased significantly in areas beneath more open canopy and those with more fallen dead trunks, but diminished in areas where leaf litter was deeper. We conclude that forest heterogeneity can be an important factor influencing the spatial distribution of terrestrial birds. *Accepted 28 May 2014.*

Key words: Great Tinamou, *Tinamus major*, Variegated Tinamou, *Crypturellus variegatus,* encounter frequency, environmental heterogeneity, habitat use, structural forest components.

INTRODUCTION

Environmental heterogeneity is an important element in the patterns of habitat use by species (e.g., MacArthur & MacArthur 1961, August 1983, Karr & Freemark 1983, Khanaposhtani *et al.* 2012). Heterogeneity within forests, a result of spatial variation of the components of forest structure (*sensu* McCoy & Bell 1991), promotes and increases the volume and types of available micro-habitats, and may heighten the segregation of resource use (Tews *et al.* 2004, Bagchi *et al.* 2011, Oliveira *et al.* 2011). This segregation in resource use has been recognized as one of the mechanisms that influence spatial distributions of species and has been studied in a variety of taxons (invertebrates: Tews *et al.* 2004; amphibians and reptiles: Watling 2005, Menin *et at.* 2007; fish: Espírito-Santo *et al.* 2013; mammals: August 1983, Lambert *et al.* 2006, bats: Bernard 2001); birds are one of the best-studied groups (Bersier & Meyer 1994, Marra & Remsen 1997, Aleixo 1999, Díaz *et al.* 2005, Miranda *et al.* 2010, Bueno *et al.* 2012, Poindexter *et al.* 2012). However, the majority of studies of birds have been conducted on arboreal species.

Tinamous (family Tinamidae) are a strictly Neotropical group, which are characterized by their terrestrial habits, conservative morphological characters, and limited flight capabilities, the latter aspect leading to their being widely considered as one of the most basal of living bird groups (Cabot 1992, Bertelli *et al.* 2002, Bertelli & Porzecanski 2004). Tinamous inhabit closed or open habitats in all major areas of tropical and sub-tropical Central and South America (Cabot 1992), with the greatest diversity in terms of species and life styles occurring in the Amazon Basin, where tinamous occupy a variety of forest habitats (Cabot 1992, Sick 1997). Many tinamou species of tropical forests are in decline (Lees & Peres 2006, Parry *et al.* 2007), largely due to hunting and habitat loss from the conversion of natural cover by human activities (Terborgh & Winter 1980, Thiollay 2005).

Species in this family have similar foraging habits, and appear to be generalists in the diet (Cabot 1992; Mosa 1993, 2004; Garitano-Zavala *et al.* 2003). For example, forest species, such as those in the genera *Tinamus*, *Crypturellus*, and *Nothocercus* forage mainly on the ground, eating insects, small mollusks, annelids and fruits (Cabot 1992, Sick 1997). Forest tinamous use fallen tree trunks for foraging and shelter, and nest in between the buttress roots of large standing trees, although the nest itself is a shallow depression in the soil, covered with a thin layer of leaves (McKay 1980, Cabot 1992, Sick 1997; Brennan 2009, 2010). Differences in the frequency in which different micro-habitats are used open the possibility of distributions without spatial overlap for sympatric congeneric species. This type of phenomenon has been suggested for the Undulated Tinamou (*Crypturellus undulatus*) and Brazilian Tinamou (*C. strigulosus*) by Sick (1997). The ecology of the group, due to their cryptic coloration, slow quiet movements, infrequent vocalizations and predilection for crepuscular and nocturnal activity is little known (Brennan 2004, Schelsky 2004). The basic natural history is poorly known for 40% (Schelsky 2004) of the 47 described species (Cabot 1992).

Studies analyzing the occurrence and spatial distribution of tinamou communities in a series of environments with different forest structures (Brooks *et al.* 2001, 2004; Schelsky 2004) found partial superimposition for the areas used by Great Tinamou (*T. major)* and Variegated Tinamou (*C. variegatus*). Knowledge of situations where species with similar behaviors and physical characteristics overlap in their use of a heterogeneous environment, would advance the understanding of habitat characteristics in relation to the observed patterns of use and occupation by birds.

Specifically, we investigated how the spatial variation in micro-habitats, characterized by components of the forest structure, influence the spatial distribution and frequency of habitat use by Great and Variegated Tinamou. We tested the hypotheses that the forest structure will impact the spatial distribution and micro-habitat use by two species of tinamou. We predicted that the frequency of occurrence of the species would be greater in areas with flatter dense vegetation, thicker leaf-litter, higher number of fallen dead trunks, open canopies, and close to water.

METHODS

Study area. The study was conducted in the Adolfo Ducke Forest Reserve (ADFR) in the municipality of Manaus, Amazonas State, Brazil (02°53'S, 59°58'W). The reserve has altitude of 80 – 140 m and an area of 10,000 ha (Ribeiro *et al.* 1999, Oliveira *et al.* 2008). The ADFR is composed of primary lowland Amazonian rainforest (terra-firme) (Ribeiro *et al.* 1999, Oliveira *et al.* 2008). The annual median temperature in the region is 26°C, and annual precipitation varies between 1750 and 2500 mm, with the rain peak between November and May and lowest rainfall between June and October (Oliveira *et al.* 2008). The dominant vegetation is mature evergreen lowland forest with an average canopy height of 30–40 m, with higher trees up to 55 m (Ribeiro *et al.* 1999). The topography is dominated by plateaus with closed canopy and a poorly-lit understory (Oliveira *et al.* 2008).

Experimental design. Sampling of forest structure components and sound recording of the study species occurred in 30 pre-established plots systematically placed along six trails, of 5 km in length (Oliveira *et al.* 2008). All plots were separated by at least 1 km. The plots were non-linear 250 x 2 m and followed undulations in the level of the terrain (Magnusson *et al.* 2005). As the plots follow the isocline, variation in elevation within the plot is negligible (Magnusson *et al.* 2005). This allows inclusion of elevation as a predictor variable.

Bird surveys. Species occurrence was surveyed at listening points (Gregory *et al.* 2004), placed at the center of each of the 30 permanent plots. Species surveys occurred during a series of five extended (12–15 days) field visits made between October 2012 and March 2013. Bird surveys during these visits were conducted between 05:30 and 10:00 h daily.

Auditory sampling began with 10 min of passive listening at each listening point. This was followed by two sequences of 1-min call broadcasting followed by 2 min of passive listening over a sample regime totaling 6 min in each of the species. A total of 22 min of sampling occurred in each of the 30 plots. The same effort was used in each of the five visits for bird surveys.

The recordings of calls used in the playback experiments were made in areas close to the study area (Naka *et al.* 2008) without the use of filter or any treatments. The loudspeaker was positioned 30 cm above the forest floor, and pointed in four directions (north, south, east, and west) for 30 s each with the order decided randomly. Response calls were recorded with directional microphones (Sennheiser ME66) and a digital recorder (Sony ICD-PX720) for later identification. Playback volume was standardized at all points at a level similar to that of the target species' vocalizations. The order, in which each species call was presented, was selected randomly to minimize the potential effects of inter-species dominance hierarchies on vocalization likelihood. The duration of playback and passive observation was the result of a series of pilot field studies in which the field methodology was progressively refined. Preliminary field tests, using a digital recorder and a portable loudspeaker, indicated the maximum distance, at which the two tinamou species could be identified by ear by RSG was ~ 100 m. The species detection within the radius of listening observer was considered indicative of occurrence and use of environment by the species. It was considered unlikely the same individual bird would have been recorded at more than one listening station (Vispo 1995, Johnson *et al.* 2011).

Forest structural component sampling. Data on the elevation of each permanent study plot were collected in 2000 by a topographic surveyor. Distances of the plots to water were calculated from a detailed topographic map of the area. For both components more details are available at the PPBio website (http://ppbio.inpa.gov.br).

In April 2013, the number of fallen dead trunks with a DBH > 20 cm were counted in a 10-m wide sector (5 m on each side of the central trail) of each 250-m study non-linear plot, because such trunks may offer refugia from predator attack and also places for nesting. We also recorded forest canopy openness using a Spherical Crown Densiometer (Concave - Mode C - Robert E. Lemon, Forest Densiometer - Bartlesville, OK, USA) in the same month. Measurements were obtained from four readings (north, south, east, and west) at points at 10 m intervals along each plot; the median value was calculated and used as an index of canopy openness for each plot.

Tree abundance was recorded in February 2007 and March 2009. Since there was no high frequency of mortality in the area (Toledo *et al.* 2012), we believe that the tree density in 2013 was similar to those from previous years. A hierarchical sampling design based on tree DBH was established within the permanent plots following Castilho *et al.* (2006), with total number of trees used as an index of abundance. Mean leaf-litter depth was calculated for each plot using data collected seven times a year between 2007 and 2013 (March, April, May, August, October, November). All samples followed the same protocol, measuring the maximum depth of leaf-litter with a ruler. Depth measurements were made every 5 m along the central line of each plot, and the median per plot values were calculated. This value provided an index of leaf-litter density. More details are available at the PPBio database (http://ppbio.inpa.gov.br).

Data analysis. A Spearman correlation matrix was constructed to learn if significant correlations existed between the forest structure components (independent variables). In those cases where independent variables were significantly correlated, these were not used together in the statistical model. Multiple linear models were used to evaluate the effect of each structural component on plot use frequency by Great and Variegated Tinamou. Tests for normality and distribution of residuals were made for all variables. To verify potential problems of residual analysis and multicollinearity in multiple linear models we used the graphic method called partial residual plot (Fox 2002). All tests were performed using program R 2.15.2 (R Development Core Team 2013).

RESULTS

Forest structural components. The elevation of the plots varied between 46 and 105 m (mean ± SD = 75.67 ± 20.56 m, n = 30). The number of dead fallen trunks varied between 8 and 40 (22.83 ± 7.54, n = 30). The mean percentage of canopy openness varied between 1.4 and 4.52% (2.86 ± 0.74%, n = 30). The abundance of trees varied between 565 and 1184 per plot (775.60 ± 134.62, n = 30). Mean leaf-litter depth varied between 1.77 and 2.88 cm (2.38 ± 0.29 cm, n = 30). Distance from plot to nearest water varied between 18 and 579 m (214.10 ± 160.98 m, n = 30). There was a significant correlation between terrain elevation and distance to water (Table 1). We selected the variable distance to water as the preferred micro-habitat descriptor to be included in the multiple linear model analysis.

TABLE 1. Spearman correlation coefficients (ϱ) and associated probability (*P*) (significance: ** $P < 0.001$) for the forest structural components in 30 permanent plots in Adolpho Ducke Forest Reserve, Central Amazonia, Brazil.

Structural components	Abundance of fallen dead trunks	Canopy openness	Leaf-litter depth	Elevation	Distance to water	Tree abundance
Abundance of fallen dead trunks	1					
Canopy openness	-0.22	1				
Leaf-litter depth	0.19	0.07	1			
Elevation	-0.21	-0.06	-0.24	1		
Distance to water	-0.06	0.05	-0.32	0.80**	1	
Tree abundance	-0.04	0.10	0.001	0.24	0.21	1

TABLE 2. Correlation coefficients and significance (*P)* for each structural forest component in 30 permanent plots in Adolpho Ducke Forest Reserve, Central Amazonia, including multiple linear models for Great and Variegated Tinamou.

Structural components	Great Tinamou		Variegated Tinamou	
	Estimated	*P* Value	Estimated	*P* Value
Distance to water	-0.002	0.21	0.0001	0.99
Abundance of fallen dead trunks	-0.044	0.10	0.055	**0.04**
Canopy openness	-0.041	0.88	0.7708	**0.008**
Leaf-litter depth	0.0003	0.86	-0.0002	0.87
Tree abundance	2.918	0.67	-2.1	**0.006**

Effects of forest structure components on the frequency of records of Great and Variagated Tinamou. The frequency of encounter rates for both species is shown in Fig. 1. The Great Tinamou occurred at 60% (n = 18) of the listening posts and the frequency of encounter per post varied between 0 and 3 during the entire sample time. The frequency of encounter was not significantly influenced by variation in the abundance of fallen dead trunks, canopy openness, tree abundance, leaf-litter depth or distance to water (Table 2; $F = 0.98$, r^2 (adjusted) = –0.002, $DF = 24$, $P = 0.447$; Fig. 2). The Variegated Tinamou had a greater spatial distribution than the Great Tinamou and was recorded at 29 of the 30 (97%) listening posts, with encounter rates varying between 0 and 5 per post during the sampling time (Fig. 1). The frequency of occurrence of the Variegated Tinamou increased significantly with the increase in canopy openness and with the abundance of dead fallen trunks, and diminished with the increase in the depth of leaf-litter [Table 2; $F = 3.56$, r^2 (adjusted) = 0.306, $DF = 24$, $P = 0.015$, Fig. 3].

DISCUSSION

We added new evidence to the existing body of knowledge which suggests that heterogeneity in tropical forests can influence the spatial distribution of bird species (e.g., Karr &

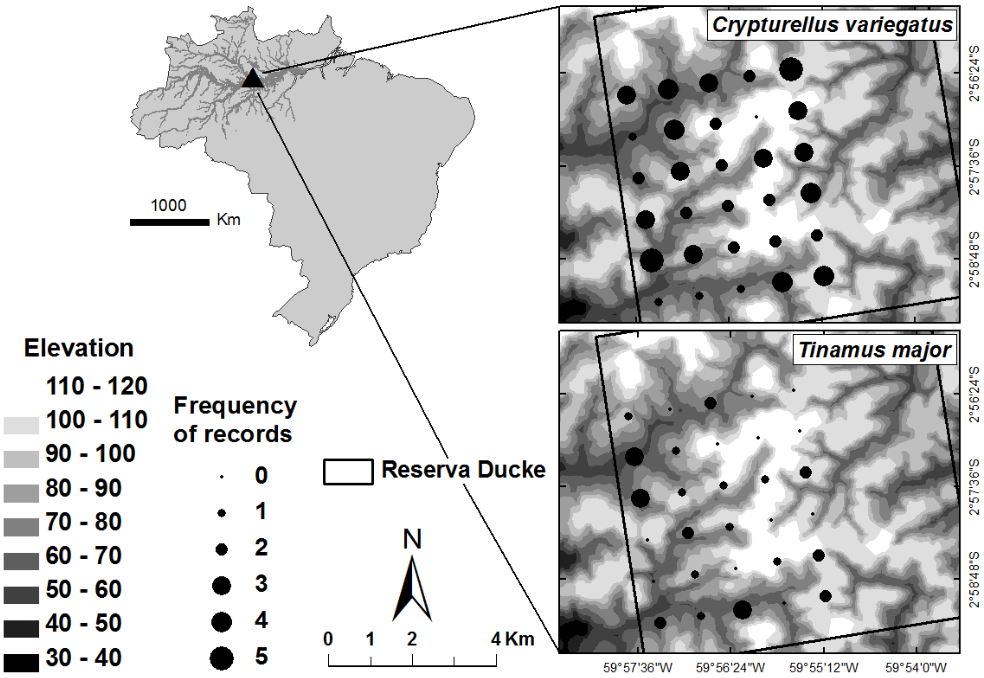

FIG. 1 Frequency of records for Great and Variegated Tinamou in 30 sample plots, in Adolpho Ducke Forest Reserve, Manaus, Brazil.

Freemark 1983; Terborgh 1985, 1990; Pearman 2002, Cintra & Naka 2012). Our study is the first one to investigate, using simultaneous observation and call playback, the effect of heterogeneity on the spatial distribution of tinamou species. Spatial variation in structural components of terra-firme forest influenced the frequency with which two species of the same family used the studied microhabitats.

The frequency of habitat use by the Great Tinamou was similar in all localities within the terra-firme forest. The spatial variation in the measured forest structural components, which act as proxies for the spatial variation between microhabitats and its extent, had no effect on the spatial distribution of the Great Tinamou, nor in the frequency with which it used micro-habitats. This is probably because this large-bodied species requires a much larger home-range area for its biological needs. In fact, there is a direct relationship between body size and the size of area used by individuals of a species (Schoener 1968, Holling 1992) as well as in the manner in which they perceive differences in habitat patch size or the availability of resources required for basic survival (Ziv 2000, Haskell *et al.* 2002).

Previous studies have demonstrated differences in habitat use by the Great Tinamou, according to different structural vegetation forms (secondary forest, terra-firme and seasonally-flooded forest, várzea) (Brooks 2004, Schelsky 2004). This suggests that the species perceives the differences in the characteristics of the habitat at a level greater than the fine-scale special variation measured by the structural components of a terra-firme forest (e.g., Wiens 1976, Kotliar & Wiens 1990, Tews *et al.* 2004). The Great Tinamou is larger than the

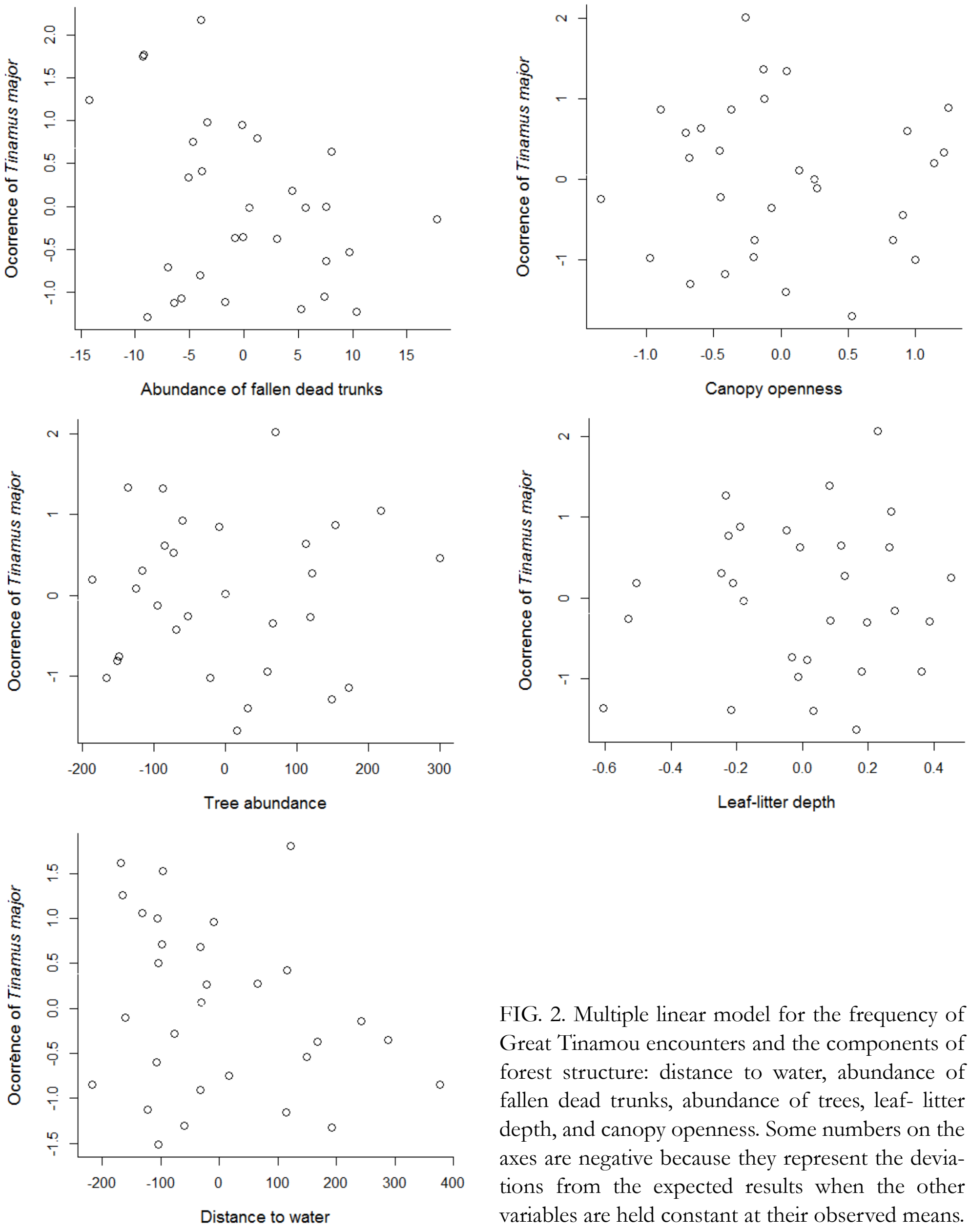

FIG. 2. Multiple linear model for the frequency of Great Tinamou encounters and the components of forest structure: distance to water, abundance of fallen dead trunks, abundance of trees, leaf- litter depth, and canopy openness. Some numbers on the axes are negative because they represent the deviations from the expected results when the other variables are held constant at their observed means.

Variegated Tinamou (Cabot 1992) and may have greater energetic requirements, as reflected in larger home ranges (Kelt & Vuren 1999, Brown 2007). Nevertheless, territory size can be influenced by other causes, such as the amount of resources and effectiveness in defense. This difference in size could explain the need of the Great Tinamou to explore a

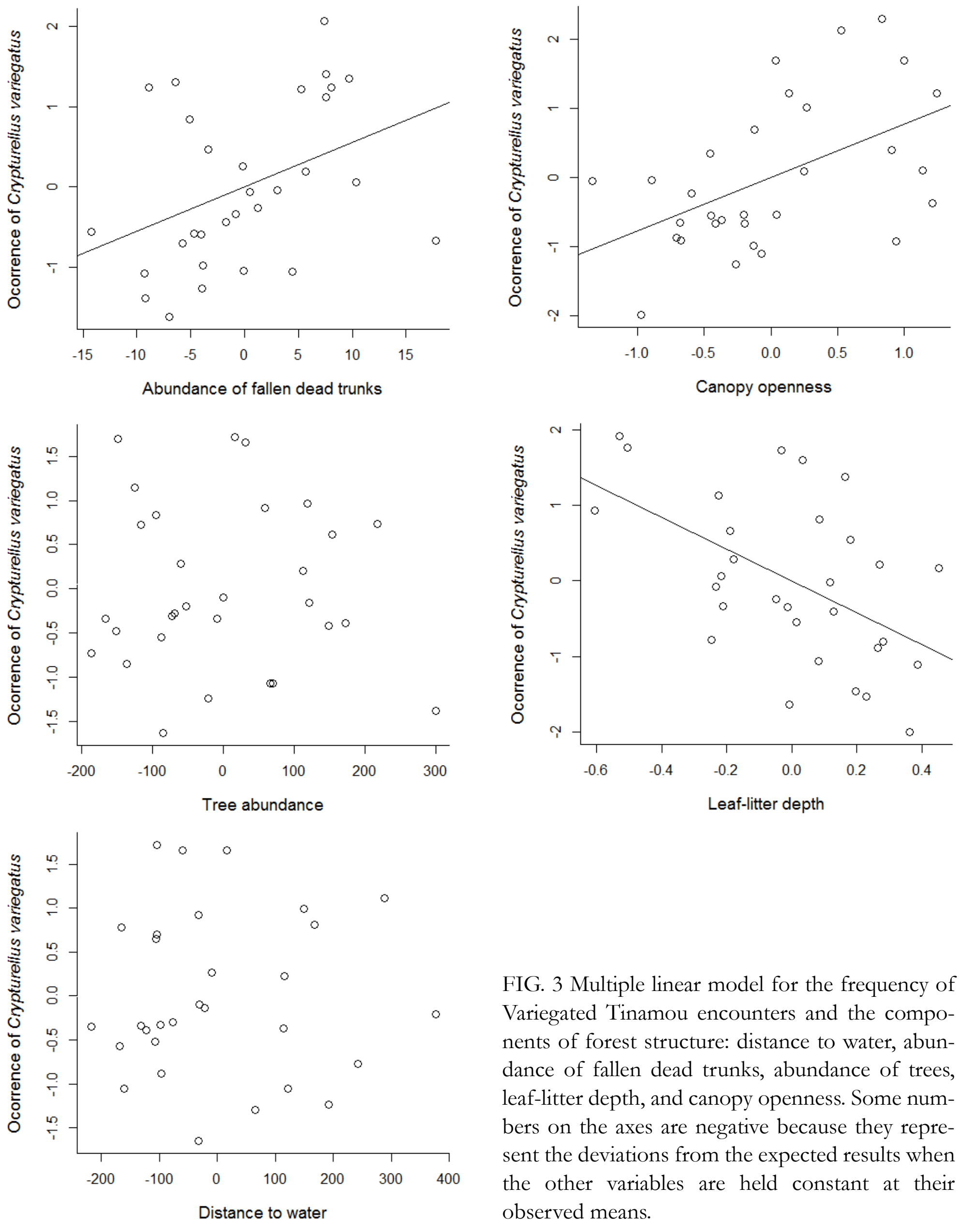

FIG. 3 Multiple linear model for the frequency of Variegated Tinamou encounters and the components of forest structure: distance to water, abundance of fallen dead trunks, abundance of trees, leaf-litter depth, and canopy openness. Some numbers on the axes are negative because they represent the deviations from the expected results when the other variables are held constant at their observed means.

larger area overall and thus encompass a greater range of habitats, leading to both lower frequency within the forest and less habitat selectivity.

The frequency of habitat use by the Variegated Tinamou is related to the spatial variation in the number of fallen dead trunks, canopy openness, and leaf-litter depth. This suggests the species uses some sub-sets of the available micro-habitat array more frequently than others. Some structural forest components had distinct effects on the use frequency by the Variegated Tinamou.

Our prediction that the use frequency by the Variegated Tinamou would be higher in areas with a more open canopy is supported. These areas have a forest understory that receives more light, permitting greater and more constant growth of understory vegetation in comparison to less well-lit areas (Nicotra *et al.* 1999, Montgomery & Chazdon 2002, Richards & Coley 2007), which attracts more herbivorous arthropods (Moore *et al.* 1988, Basset *et al.* 2001). The use of better illuminated areas of the understory by the Variegated Tinamou is probably related to the greater availability of food items, such as invertebrates, fruits, seeds, buds, and young leaves (Schubart *et al.* 1965, Cabot 1992, Sick 1997). Use of areas of dense cover may expose foraging individuals to increased risk of predation by hawks, bush dogs, jaguarundis, and spotted cats (Murray & Gardner 1997, Zuercher *et al.* 2005, Calleia *et al.* 2009, Tófoli *et al.* 2009, Melnyk *et al.* 2013). It is possible that a balance exists between time spent foraging in such areas and frequency of foraging, to reduce vulnerability to predators and at the same time use areas with the most favorable conditions for foraging (e.g., Lima & Dill 1990, Masse *et al.* 2013).

The prediction that variation in spatial abundance of logs influenced the use frequency by the Variegated Tinamou was also supported. Areas with greater abundance of dead trunks appear to be places of refuge and nesting sites for tinamou. They are probably places in which foraging tinamous are more likely to encounter potential prey items as invertebrates live within decomposing wood (McKay 1980, Cabot 1992). These locals tend to be more humid, especially in the dry season, when the majority of terrestrial birds in the Ducke Reserve are nesting (Cintra & Naka 2012).

We believed that the occurrence of the Variegated Tinamou would be positively associated with areas of greater leaf-litter depth, since arthropod abundance in leaf-litter increase with deposit depth (Lieberman & Dock 1982, Adis 1988, Sayer *et al.* 2010). A relationship between the spatial variation in leaf-litter layer depth has been shown to influence the distribution of a wide variety of understory birds in the Ducke Reserve (Cintra & Cancelli 2008, Cintra & Naka 2012), and in other tropical forests (Pearson 1977, Pearson & Derr 1986). Our results suggest that the Variegated Tinamou preferentially uses those parts of the forest with the lowest depth of leaf-litter. Tinamous are generally opportunistic foragers with a generalized diet (Schubart *et al.* 1965, Cabot 1992, Sick 1997). Their more frequent use of areas with thin leaf-litter cover might be explained by augmenting prey detection and catching of food items (such as small fruits, seeds, and invertebrates), and the latter would be more evident where a shallow leaf-litter layer makes these items more detectable on the forest floor. Moreover, tinamous walk very slowly on the forest floor without calling, using the beak to sweep the layers of leaf-litter (Cabot 1992). These actions produce rustling noises which could alert predators to the presence of tinamous. Areas with shallow layers of leaf-litter may be preferred as less noise will be generated during foraging, reducing the risk of predation.

Our study has shown that different tinamou species respond in distinct ways to natural variation in habitats, suggesting that the heterogeneity of the central Amazonian terra-firme forest has an important, perhaps species-specific, role in affecting the spatial distribution of birds (Terborgh 1985, Aleixo 1999, Cintra *et al.* 2006). The lack of correlation between the frequency of microhabitat use by the two species and variation in some structural forest components suggests that only some of the variables in forest structure affect the species' habitat use. The number of records for Great and Variegated Tinamou during our study appear proportional to the natural densities of the species calculated by previous studies at ADRF (Soto 2013) and in a nearby area (Johnson *et al.* 2011). The lower numbers of the Great Tinamou compared to the Variegated Tinamou could reflect their lower natural density in the forest vs. the latter species. However, we assume that at least some portion of the forest structure is important for understanding the spatial niche between the two species.

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