Pipridae and Cotingidae (Aves: Passeriformes) lek distribution in central Amazon

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ABSTRACT

Lek polygyny represents a complex evolutionary reproductive mechanism found in approximately 1.4% of bird species, among 14 families and 138 species. Pipridae family is the better known taxa with lek reproduction system, although there are several lekking Cotingidae species. Both bird families occurs all over Amazonian rainforest, representing several lekking species. Thus, the aim of this research was to analyse spatial distribution of Pipridae and Cotingidae specie's leks in central Amazon. The study was carried out in Forest Reserve Adolpho Ducke, located in northern portion of Manaus. Lek sites were found by active search and marked with GPS device. Spatial analysis framework for point process was considered in the research, once leks can be represented as events in the continuous space. Kernel intensity, univariate and bivariate Ripley's K Function and spatial Kolmogorov-Smirnov (KS) test were used. KS test was performed in order to test whether the point pattern intensity depends on environmental covariate. The covariate was the Height Above Nearest Drainage (HAND), obtained from Shuttle Radar Topography Mission (SRTM) Digital Elevation Model (DEM). Five lekking species were found, summing 100 leks: 15 leks of *Lepidothrix serena*, 6 leks of *Dixiphia pipra*, 47 leks of *Tyranneutes stolzmanni*, 27 leks of *Lipaugus vociferans* and 5 leks of *Perissocephalus tricolor*. The results of K function suggests failure to reject the complete spatial randomness hypothesis for all species, except for *L. serena*, thus these leks has no distribution pattern in the landscape. *L. serena* shows clustering pattern in most scales. There is significant spatial co-occurrence of leks of *L. vociferans* and *T. stolzmanni* at all scales. KS test evidenced no significant spatial dependence of lekking placement on HAND for any species. Spatial statistics framework showed to be suitable for the purpose of lek distribution analysis.

Keywords: spatstat. Forest Reserve Adolpho Ducke. spatial analysis. kernel intensity. Ripley's K function.

RESUMO

Poliginia de lek é um comportamento reprodutivo complexo encontrado em aproximadamente 1,4% das espécies de aves, em 14 familias. As famílias Pipridae e Cotingidae apresentam espécies com comportamento de lek distribuídas por toda a floresta amazônica. Assim, o objetivo deste trabalho foi analisar a distribuição espacial de leks de aves dessas famílias na Amazônia central. A área de estudo foi a Reserva Florestal Adolpho Ducke, Manaus. Os leks foram encontrado por meio de busca ativa e marcados com aparelho GPS. Foram utilizadas as ferramentas de análise de processos pontuais intensidade Kernel, Função K de Ripley univariada e bivariada e o teste espacial de Kolmogorov-Smirnov (KS). KS foi utilizado para testar se as intensidades dos padões pontuais apresentam dependencia em relação a uma covariável ambiental: a Altura Acima da Drenagem Mais Próxima (HAND), obtida a partir de um MDE do SRTM. Foram encontrados 100 leks de cinco espécies diferentes: 15 de *Lepidothrix serena*, 6 de *Dixiphia pipra*, 47 de *Tyranneutes stolzmanni*, 27 de *Lipaugus vociferans* e 5 de *Perissocephalus tricolor*. Os resultados da função K sugerem que os leks de todas as espécies, exceto *L. serena*, não rejeitam a hipótese nula de completa aleatoriedade espacial e, portanto, não apresentam nenhum padrão de distribuição na paisagem. Por sua vez, os leks de *L. serena* apresentam padrão de agrupamento em diversas escalas. A função K bivariada mostrou sobreposição espacial significativa entre leks de *L. vociferans* e *T. stolzmanni* em todas as escalas. O teste KS não mostrou dependência espacial dos leks de nenhuma espécie em relação ao HAND. Os métodos de analise espacial utilizados se mostraram robustos para tal aplicação.

Palavras-chave: spatstat. Reserva Florestal Adolpho Ducke. análise espacial. intensidade kernel. Função K de Ripley.

Introduction

Leks are reproduction sites where a group of male animals of a certain species congregate and display in conjunction to females of that species. Female individuals choose one of the displaying males to receive its gametes (BRADBURY; GIBSON, 1983). Lek polygyny represents a complex evolutionary reproductive mechanism found in diverse taxa (HÖGLUND; ALATALO, 2014), ranging from invertebrates (JONES; QUINNELL, 2002) to all vertebrate classes. This reproductive behaviour is found in approximately 1.4% of bird species, among 14 families and 138 species (HÖGLUND; ALATALO, 2014). Thus, bird lekking is widely studied.

In temperate zones, lekking birds feed primarily grains and seeds (HÖGLUND; ALATALO, 2014). On the other hand, tropical lekking species are dominated by mainly frugivorous families, such as Pipridae, Cotingidae, Paradisidae and Trochilidae (KARUBIAN; DURÃES, 2013), although some Pipridae species may also be insectivorous (PRUM, 1985).

Spatial allocation of bird lek sites may be favoured by many factors. Once lek displays requires high calories input for males (COWLES; GIBSON, 2014), leks could take place nearby areas with locally high food density (BALMFORD, 1991; THÉRY, 1992).

Other factors may constraint lek spatial distribution, such as places where topography or lightning effects minimizes predation risks, female hotspot distribution (ALONSO; ÁLVAREZ-MARTÍNEZ; PALACÍN, 2012) and also by specific light conditions for performing courtship (UY; STEIN, 2007; ANCIÃES; PRUM, 2008), contrasting with environmental background. It is reported that lek location in slopes changes along the day (THÉRY, 1990) due to changes in ambient light condition (ENDLER; THERY, 1996). However, there is no displacement in lek territories locality in central

Amazon, indicating that there is evidence for geographical variation in lekking behaviour (MEDEIROS, 2012).

In this sense, Pipridae family is the better known taxa with lek reproduction system and it is characterized by strong sexual divergence and complex courtship (SNOW, 2010), although there are several lekking Cotingidae species (OMENA JR; MARTINS, 2013; NOSSA, 2008). Both bird families occurs all over Amazonian rainforest, representing several lekking species. Thus, the aim of this research was to analyse spatial distribution of Pipridae and Cotingidae specie's leks in central Amazon.

Material and Methods

Study Site

The study site in central Amazon forest was located in the Forest Reserve Adolpho Ducke (RFAD), in northern region of Manaus, Brazil (Figure 1). This reserve is administered by National Institute for Amazonian Research (INPA) and accounts with a 100 km^2 tropical humid *terra firme* protected rainforest with uniform canopy (HOPKINS, 2005). Annual precipitation varies from 1,750 mm to 2,500 mm, with rainy season occurring from November to May and dry season from June to October. Mean temperature is 26 °C with annual amplitude of 3 °C (OLIVEIRA et al., 2011).

Topography is highly irregular and undulated with plateaus reaching altitudes of 140 m above sea level (RIBEIRO, 1999). Soils are strongly influenced by topography. Clay soils are dominant in plateaus, with decreasing clay fraction along slopes, resulting in sandy soils in lower terrains (OLIVEIRA et al., 2011).

About 350 birds species are found in Ducke reserve. Among plants, 96 terrestrial herbs species, distributed in 16 families are found in the reserve (OLIVEIRA et al., 2011). Herb plants play important role for Pipridae and Cotingidae nutrition, mainly those of

Melastomataceae family, which accounts, for example, for 60% of *Lepidothrix serena* Pipridae input calories (KRIJGER et al., 1997). There are abrupt changes in herbaceous vegetation only within a few metres from stream borders and most species presents wide distribution along soil and altitudinal gradients (DRUCKER; COSTA; MAGNUSSON, 2008).

RFAD has a 64 km^2 grid with 1x1 km trails covering the entire reserve, except a 1 km border. The area under study accounted for 3,000 ha inside RFDA, in which sampling efforts were made in 5 x 6 km trails, as shown in Figure 1.

Spatial analysis of leks distribution

Field survey was conducted during July and August 2011. Active search of the leks was made by means of registering main vocalization of the species along transects in the RFDA studied grid. All leks found had coordinates marked with GPS device and notes were taken, such as number of males, topography and species.

GPS points of the leks were imported in open source Geographic Information System (GIS) QGIS, where they were joined with a table containing the exact name of the GPS point and the corresponding lek species. This database was exported as shapefile in WGS84 UTM zone 20S coordinate system (EPSG: 32720) and analysed with "spatstat" package (BADDELEY; TURNER, 2004) in R environment.

As lek observations are reported as locations, not counts in transects or grid cells, and may occur at the same site for a long time, as found by Medeiros (2012), they are best described as point locations in continuous space (RENNER et al., 2015). This characteristic motivates the use of point process approach for spatial analysis of lek distribution.

In this sense, lek records are a set of point locations y={y1, y2, . . . , yn} in a two-dimensional area A, where locations where
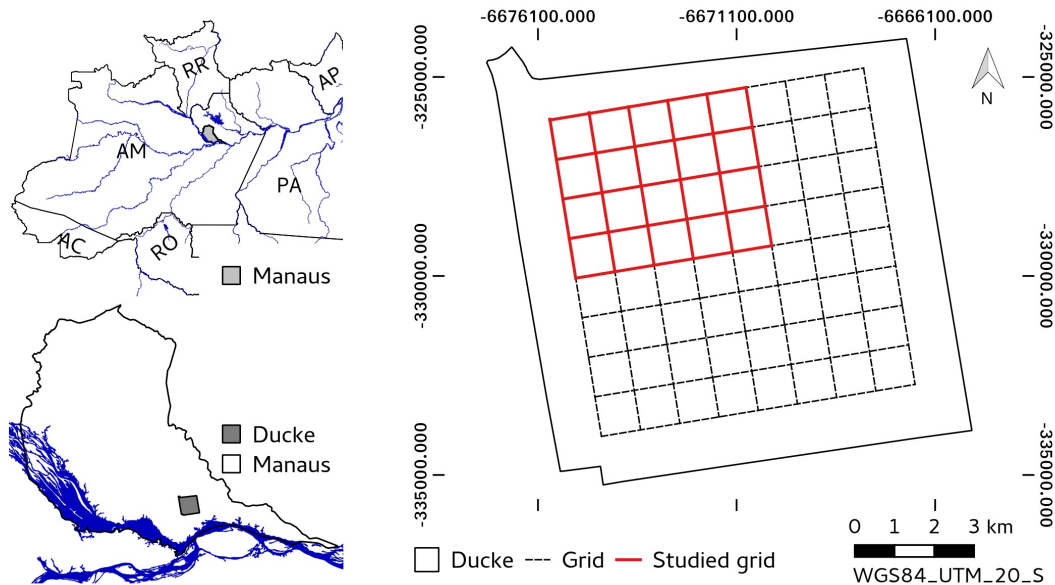
Figure 1 – Location map of the studied area. 5 x 6 km transects are highlighted in red over Ducke Reserve grid.

presences are recorded (yi) are out of the control of the researcher, as the total number of presence points n (WARTON; SHEPHERD et al., 2010). So, points are stochastically generated events in A, assuming its stationarity and isotropy (CÂMARA; CARVALHO, 2004).

First order effects analysis of the spatial distribution of the leks was made by means of Kernel intensity estimation. Kernel estimation is an exploratory tool which provides a global view of the studied phenomena in the study region, such as cluster of events. It is calculated as:

$$\hat{\lambda}_\tau(y) = \frac{1}{\tau^2} \sum_{i=1}^{n} k\left(\frac{d(y_i, y)}{\tau}\right), d(y_i, y) \leq \tau$$

(1)

where, τ is a bandwidth defined by the user and k is a Kernel function defined as:

$$k(h) = \frac{1}{2\pi\tau} exp\left(-\frac{h^2}{2\tau^2}\right)$$

(2)

where, h is the distance between a

certain point in A and the observed event.

The kernel estimation is highly sensitive to the bandwidth or smoothing factor because it determines the search radius. Three bandwidth sizes were considered (100 m, 500 m, 1000 m) in order to explore clustering differences among smoothest intensities $\hat{\lambda}_\tau$.

To access spatial inhomogeneity, dependence or clustering of events at multiple scales, a widely accepted tool is the Ripley's K function (MOUNTRAKIS; GUNSON, 2009). Another useful tool for exploring spatial patterns is the Nearest Neighbour distance G function, which it is dependent on each point location, thus it is suitable for small scales (CÂMARA; CARVALHO, 2004).

Ripley's K function is a second order exploratory tool and defined for univariate process as:

$$\lambda K(h) = E(x)$$

(3)

where, λ is the intensity and x is the number of events within a distance h of a randomly chosen event.

4

K(h) univariate estimative can be described as:

$$\hat{K}(h) = \frac{A}{n^2} \sum_{i}^{n} \sum_{j,i\neq j}^{n} \frac{I_h(d_{ij})}{w_{ij}} \qquad (4)$$

where, if $I_h(d_{ij}) <= $ h the value of the function is 1, else is 0, and w is the edge correction.

However, Ripley's K function can also de used for bivariate data, as shown in Equation 5 and Equation 6 (DIXON, 2002). Bivariate K function analysis is useful for ecological purposes, such as investigating spatial association between males and females of a species (VARGA; KYTÖVIITA, 2011) or co-occurrence of different species in the same area (SCHNEIDER; MEADOR; COVINGTON, 2015). In this study, it was applied to test association of leks between different species.

$$\lambda K_{ij}(h) = E(x_{ij}) \qquad (5)$$

where, λ is the intensity and x_{ij} is the number of type j events within distance h of a randomly chosen type i event.

$$\hat{K}_{ij}(h) = (\hat{\lambda}_1 \hat{\lambda}_j A)^{-1} \sum_{k} \sum_{l} w(i_k, j_l) I(d_{i_k j_l} < h) \qquad (6)$$

where, $d_{i_k j_l}$ is the distance between the kth location of type i and the lth location of type j, $w(i_k, j_l)$ is the fraction of the circumference of a circle centred at the kth location of process i with radius $d_{i_k j_l}$ that lies inside the study area.

K function is useful for comparing the observed spatial points ($\hat{K}(h)$) with a complete randomly generated set of events ($\bar{K}(h)$). This complete spatial randomness (CSR) condition (a homogeneous Poisson Process) often serves as a null hypothesis in spatial statical analysis, because the points are completely unpredictable and have no trend or association with anything else.

The homogeneous Poisson process of intensity $\lambda > 0$ has the properties:

- The number N($X \cap$ A) of points falling in any region A is a Poisson random variable;

- the expected number of points falling in A is E[N($X \cap$ A)]=λ*area(A);

- if A_1 and A_2 are disjoint sets, then N($X \cap A_1$) and N($X \cap A_2$) are independent random variables;

- given that N($X \cap$ A) = n, the n points are independent and uniformly distributed in A.

Point process under CSR is defined as:

$$K = \pi\tau^2 \qquad (7)$$

where τ is a distance bandwidth.

By a Monte Carlo approach with 1000 simulations, upper and lower envelope values for CSR were calculated. Any distance at which estimated $\hat{K}(h)$ falls outside simulation envelops indicate significant departure from CSR. If above the upper lines, it denotes clustering, and below means over-dispersal.

Environmental covariate dependence test

In order to test whether the point pattern intensity depends on environmental covariate, a spatial Kolmogorov-Smirnov (KS) test was applied. This test consists in to compare the observed and expected distributions of the values of some function T. First, a real-valued function $T(x, y)$ is defined at all locations (x, y) in A. This function is evaluated at each of the data points. Then, this empirical distribution of values of T is compared with the expected distribution of values of T under CSR.

The environmental covariate used for KS test was the Height Above Nearest

Drainage - HAND (RENNÓ et al., 2008). HAND is a terrain model based on Digital Elevation Data (DEM) which normalizes topography according to the local relative heights found along the drainage network (NOBRE et al., 2011). It was generated in TerraHidro plugin[1], an open source platform for hydrological modelling developed by INPE's Image Processing Division (DPI). A 30 m Shuttle Radar Topography Mission (SRTM) DEM was used in the model, obtained from United States Geological Survey (USGS) online database[2].

HAND was considered for the analysis because it is strongly correlated with soil water conditions in Amazon and it is a good terrain descriptor (RENNÓ et al., 2008). As Pipridae and Cotingidae birds are primarily frugivorous, the leks were supposed to be found in regions whose water and slope conditions favours herbs communities, such as Melastomataceae family light-dependent plants (ELLISON et al., 1993). The interaction of Melastomataceae herbs and Pipridae birds is well reported in literature (KRIJGER et al., 1997; GOMES; MARCELIANO; JARDIM, 2008), as well as the role of some Pipridae and Cotingidae species as seed dispersors (TELLO, 2003; ARTEAGA; AGUIRRE; MOYA, 2006; FOSTER, 2014).

Results

Five lekking species were found, three from Pipridae family and two from Cotingidae family. Registered Pipridae species were *Dixiphia pipra* (white-crowned manakin), *Lepidothrix serena* (White-fronted manakin) and *Tyranneutes stolzmanni* (Dwarf tyranneutes). Among Contigidae there were: *Lipaugus vociferans* (Screaming Piha) and *Perissocephalus tricolor* (Calfbirds).

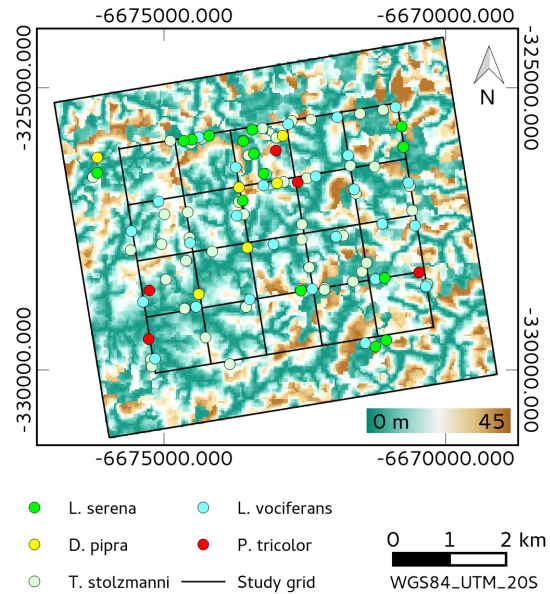In total 100 leks were registered during fieldwork (Figure 2): 15 of *L. serena*, 6

Figure 2 – Leks location in the study site. Background map is the Height Above Nearest Drainage (HAND), which units are in metres.

of *D. pipra*, 47 of *T. stolzmanni*, 27 of *L. vociferans* and 5 of *P. tricolor*.

Kernel intensity estimation of the leks of all five species is shown in Figure 3. It evidences the smoothing effects of bandwidth τ size. In this research, 100 m, 500 m and 1000 m search radius were used inside a 3,000 ha area (5 km x 6 km).

Higher intensity values are found with 100 m bandwidth, reaching $3.1e^{-05}$ (Figure 3c), in the point placement. Considering 1000 m bandwidth, maximum intensity values ranges from $5e^{-07}$, when only five events were registered (Figure 3b), to $1.3e^{-06}$ (Figure 3c), with 47 events.

Spatial regularity of lek placements seem to occur in *L. vociferans* and *T. stolzmanni*, while some clustering is observed for the other species. It does not imply that the leks are organised into identifiable "clusters", which was statistically measured by means of Ripley's K function. It is important to highlight the small number of leks of both *D. pipra* and *P. tricolor*, which biases this
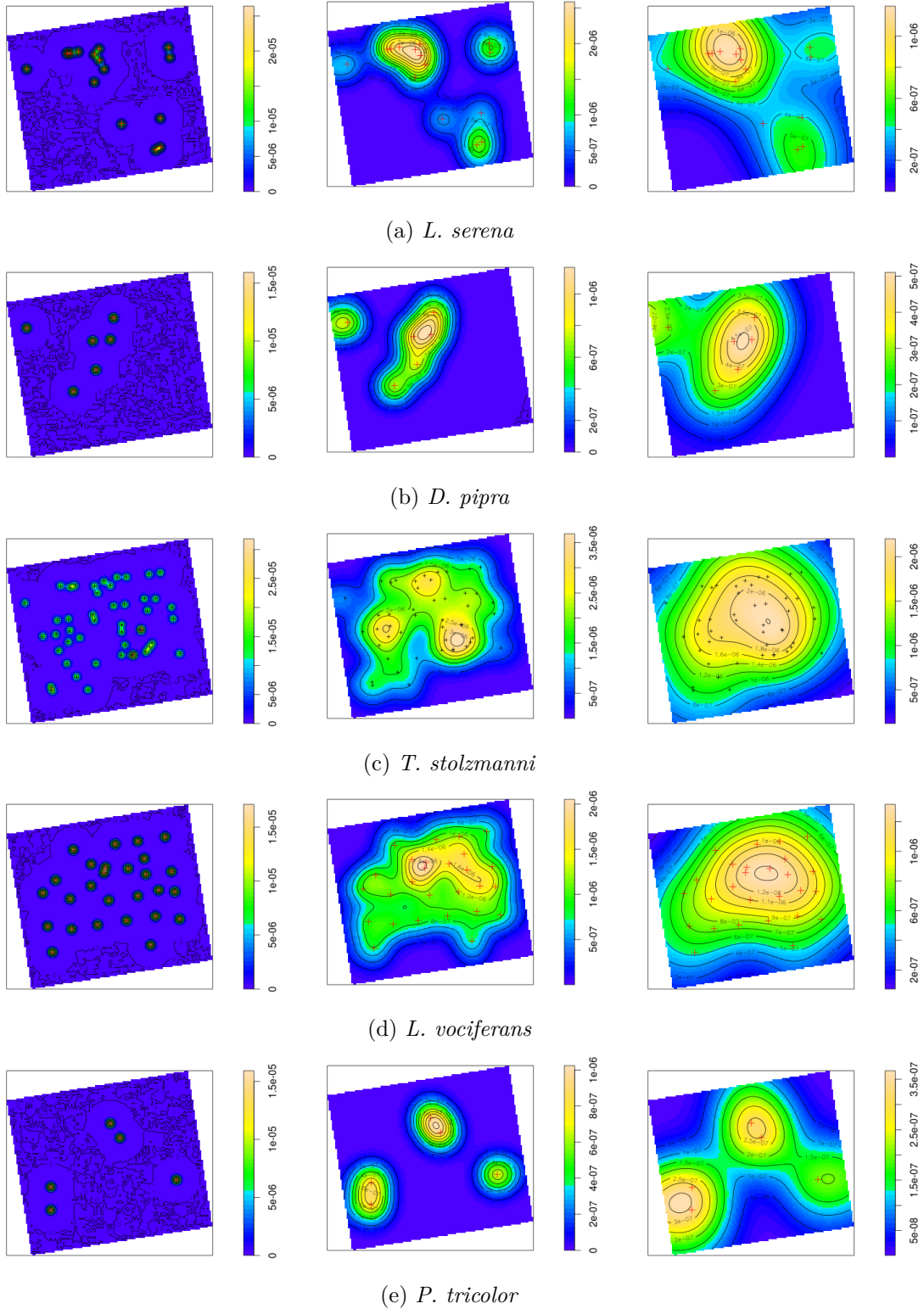

(a) *L. serena*

(b) *D. pipra*

(c) *T. stolzmanni*

(d) *L. vociferans*

(e) *P. tricolor*

Figure 3 – Kernel intensity estimation for all species evidencing smoothing effect with increase bandwidth τ. $\tau = 100$ m in left column, $\tau = 500$ m in middle column and $\tau = 1000$ m in right column. Red dots are the leks placements in the landscape.

"clustering" effect.

In light of that, only *L. serena* shows significant clustering pattern in leks distribution, from 100 m to 1600 m. It is evidenced by comparing the estimated K function for observed leks with K function for estimated CSR with 1000 Monte Carlo simulations, that is shown in Figure 4a.

The hypothesis of CSR of lek spatial distribution for the other four species is not rejected (Figure 4), as the K function for observed leks does not falls outside simulation envelops. The analysis of K function evidences no trends of clustering or dispersion in leks placement in the landscape.

Spatial association was found only between leks of *L. vociferans* and *T. stolzmanni* by means of the Bivariate Ripley's K function analysis (not shown), which was suggested by the analysis of Kernel intensity. The co-occurrence of leks of these two species was significant at all scales.

Kolmogorov-Smirnov test for spatial dependence of points against Height Above Nearest Drainage (HAND) showed no significant influence of the environmental covariate in lek distribution of any species. KS D statistics and *p*-value are shown in Table 1. The KS test uses the maximum vertical deviation between the two curves as the statistic D. The lowest D value is for *L. serena* and can be observed in Figure 5a.
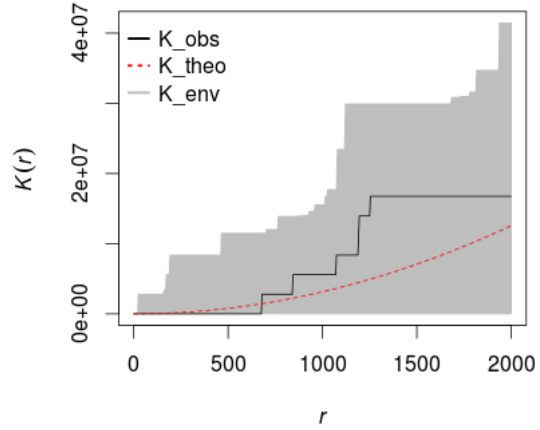
Observed and expected (CSR) probabilities distribution of values of *T* function considering HAND are shown in Figure 5.

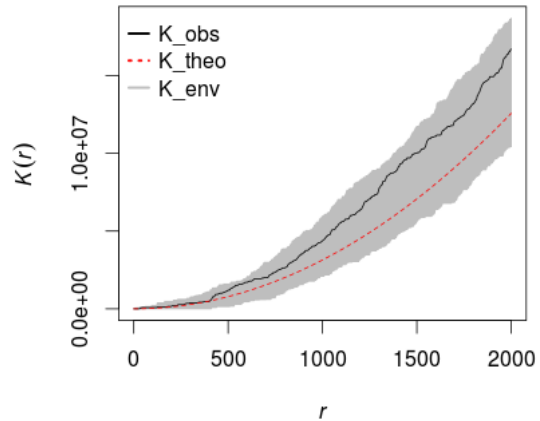Table 1 – D statistic and *p*-value obtained from KS test of leks with HAND covariate.

	D	*p*-value
L. serena	0.11409	0.9772
D. pipra	0.41795	0.1836
T. stolzmanni	0.12039	0.4676
L. vociferans	0.17815	0.3193
P. tricolor	0.33715	0.5182
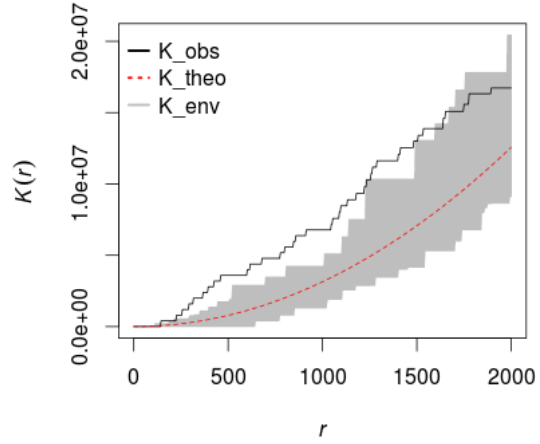
(a) *L. serena*

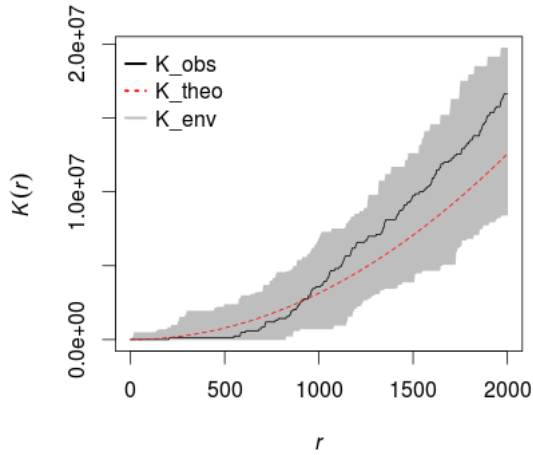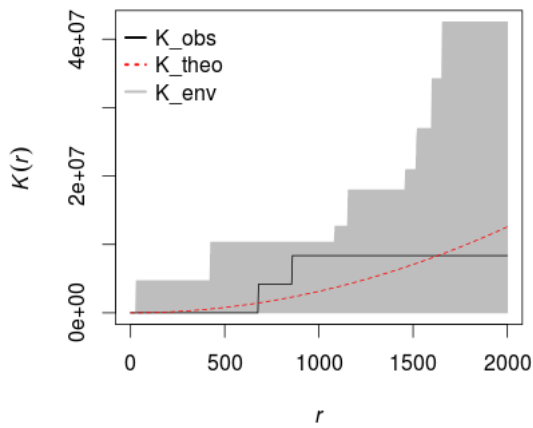(b) *D. pipra*

(c) *T. stolzmanni*

Figure 4 – K function showing acceptance of CSR null hypothesis. K_obs is the observed K for the events, K_theo is the K function under CSR and K_env are upper and lower envelope values for CSR.
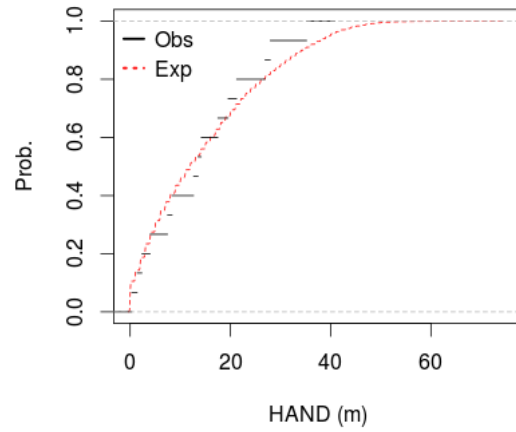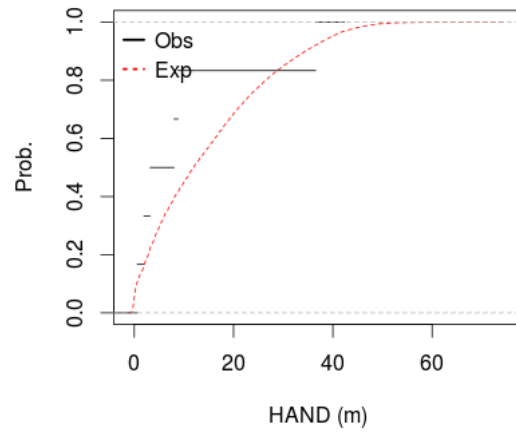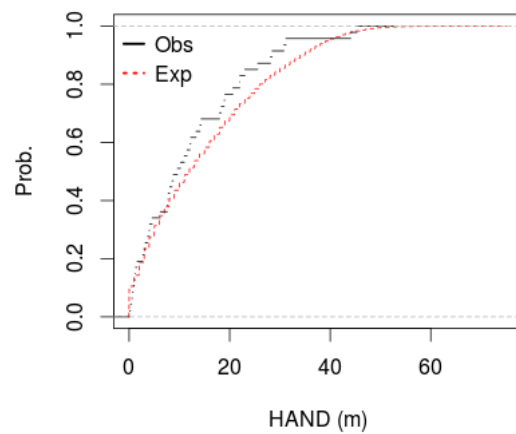
(d) *L. vociferans*

(e) *P. tricolor*

Figure 4 – K function showing acceptance of CSR null hypothesis, continued. K_obs is the observed K for the events, K_theo is the K function under CSR and K_env are upper and lower envelope values for CSR.
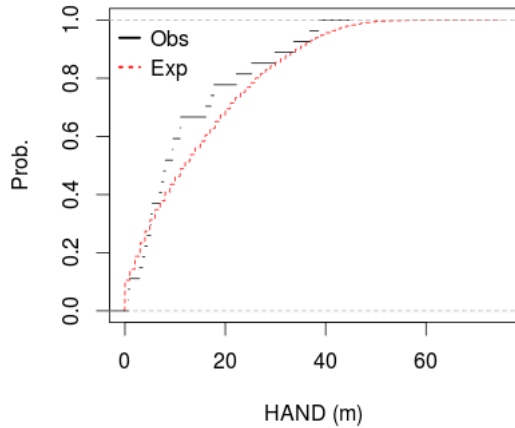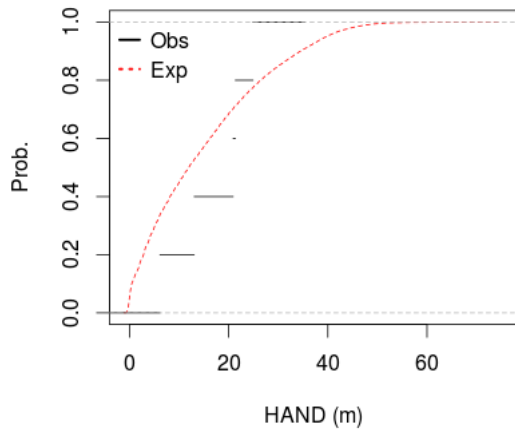

(a) *L. serena*

(b) *D. pipra*

(c) *T. stolzmanni*

Figure 5 – Spatial Kolmogorov-Smirnov test of CSR based on HAND.

(d) *L. vociferans*

(e) *P. tricolor*

Figure 5 – Spatial Kolmogorov-Smirnov test of CSR based on HAND, cont.

HAND ranges from 0 to 45 m, thus the observed probability of lek distribution of all species evidences no preference for any height, once probability of 1 are about 40 m for all species.

Discussion

Spatial analysis of leks distribution of mainly frugivorous birds in RFDA was conducted in this research. As far as it is known, this spatial approach for lek studies has not been previously reported in the literature. In light of that, despite spatial statistics provides suitable tools for point processes modelling (UPTON; FINGLETON et al., 1985), only recently it has been used in ecology field as a natural way for analysing species data (WARTON; SHEPHERD et al., 2010; RENNER et al., 2015).

The lekking species found in the survey presents different habitat, diet and foraging behaviour. *L. serena*, *D. pipra* and *T. stolzmanni* are found in understore *terra firme* forests. In turn, *L. vociferans* and *P. tricolor* habits the midstore and canopy level of Amazonian rainforests (RIDGLEY; TUDOR, 1994).

Kernel intensity provided an overview of lek placements, showing that only *T. stolzmanni* and *L. vociferans* are found on the entire study site. In this sense, different patterns of lek distribution were expected for each species.

Exploring different Kernel bandwidths, intensities range would lead to visual misinterpretation of the phenomena, suggesting some lek clusters both in *D. pipra* and *P. tricolor*, mainly when considering 500 m search radius τ. The small size of sampling causes this effect, because a few number of points closer to each other will form a hotspot. It highlights the importance of resorting another spatial tools for point process analysis, as Kernel intensity's role is merely exploratory.

Except *L. serena*, none of the species shows strong statistical evidence against CSR condition, suggesting that all the leks are randomly distribute in the landscape. From this result, it would be expected that KS test also could not provide useful information about the dependency of lek placement on HAND. More specific covariates for each species could be used in a future work, considering biological aspects for lek modelling. While *L. serena* main feed are Melastomataceae seeds (KRIJGER et al., 1997), it is reported that *L. vociferans* acts as important *Ficus pertusa* s.l. tree (Moraceae) dispersal, swallowing the entire fig (TELLO, 2003).

T. stolzmanni is also an important seed dispersal in some landscapes (ARTEAGA; AGUIRRE; MOYA, 2006; FOSTER, 2014), but more generalist than the other species.

Laurance (2004) reports high abundance of *L. serena* in road-disturbed intermediate regrowth sites, suggesting optimal foraging sites where forest dynamics is greater, due to the presence of light dependent plants. Despite *L. serena* is the only species with clustering of leks, KS evidenced that HAND does not influence its distribution (p-value = 0.9772). It makes sense, once possible feed-source herbaceous plants are widely distributed along altitudinal and soil gradients (DRUCKER; COSTA; MAGNUSSON, 2008).

Although not significant, K function evidences some dispersion trend for *L. vociferans* leks until approximately 900 m, when K_obs is lower than K_theo.

Finally, lek association of *T. stolzmanni* and *L. vociferans* was described in the studied area by means of non-spatial statistics tests (MEDEIROS; PAVANELLI; ANCIÃES, 2012) and it is now confirmed with a more robust spatial approach. Such spatial co-occurrence of leks of species with distinct habitats have not been reported anywhere else and is also of interest for future research.

Final Considerations

This study used spatial statistics for point process framework to analyse distribution of five species of Pipridae and Cotingidae families leks in Adolpho Ducke Forest Reserve, Manaus. As far as it is known, this spatial approach have not been previously reported in the literature for lekking studies and its robustness showed to be suitable for this purpose.

It was not found strong statistical evidence against complete spatial randomness of lek distributions, meaning that there is no apparent factors influencing their placements in the landscape, except those leks of *L. serena*. In the same way, HAND model has no significant effects in lek distribution for any of the five species.

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