Habitat use and coexistence in two closely related species of *Herpsilochmus* (Aves: *Thamnophilidae*)

Gabriel C. Costa¹*, Karol L. França¹, Tonny M. Oliveira-Junior² and Mauro Pichorim²

**Abstract:** Ecological theory predicts that species with similar niches cannot coexist on a limited resource. To allow for coexistence species would differentiate in resource use. Species that have similar ecology could coexist providing that they have different patterns of habitat use and associations with different environmental variables. In addition, similarity among species could be influenced by habitat structure and resource availability. Here, we build models of habitat use in high resolution (50 × 50 m), for two closely related species of birds in Northeast Brazil (*Herpsilochmus sellowi*–Caatinga Antwren and *Herpsilochmus pectoralis*–Pectoral Antwren). We use ecological niche factor analysis to detail the relationship between species and their habitat requirements. Our models brought new information about habitat use and how species respond to environmental variability. Habitat heterogeneity promotes the existence of distinct habitats that can be differently occupied by the species. Our analysis revealed that the two species have different strategies. *H. pectoralis* was very selective (specialist), while *H. sellowi* was habitat generalist. The use of different habitats can reduce the effect of interspecific competition to levels that allow coexistence. Our results suggest that habitat segregation as proposed by classical niche theory can explain coexistence of these two species in our study site.

**Subjects:** Conservation - Environment Studies; Ecology - Environment Studies; Biodiversity & Conservation

**Keywords:** coexistence; competition; ENFA; microhabitat use; niche overlap

---

**ABOUT THE AUTHOR**

Gabriel C. Costa is an assistant professor at Universidade Federal do Rio Grande do Norte. His major research interests are Biogeography, Macroecology and Conservation Biology. Costa strives to understand what determines the spatial distribution of biodiversity. His research programme use different approaches to disentangle the roles of ecological and evolutionary drivers of biodiversity in different taxonomic groups and from local to global scales. Costa is further motivated by using the findings of his research to create instrumental knowledge that can support conservation decisions. By understanding what factors influence how biodiversity changes across space, we can quantify, predict, mitigate and possibly manage the growing impacts caused by human activities.

---

**PUBLIC INTEREST STATEMENT**

Ecological theory predicts that ecologically similar species cannot coexist if resources are limiting. Species that have similar ecology could coexist providing that they have different patterns of habitat use. Our study looks at how two ecologically similar species of antwrens from the Brazilian Northeast are able to coexist in a small forest fragment. We built habitat use models that brought new information about how these species respond to their environment. We found that the two species have different strategies and use the habitat in different ways. One of the species was very selective on its habitat use (specialist) while the other had a broader association with the environmental parameters (generalist). The use of different habitats can reduce the effect of competition and allow coexistence. Our results suggest that habitat segregation as proposed by classical ecological theory can explain coexistence of these two species in our study site.
1. Introduction
How similar species are able to coexist has been a central question in Ecology for many decades (MacArthur, 1957; Schoener, 1974). Species coexistence in a particular region depends on the interaction of many biotic and abiotic factors (Chase, 2003). The influence of environmental factors in the selection of suitable habitats for species is the cornerstone of original ideas about the ecological niche concept (Grinnell, 1917). How species relate to their environments is fundamental to understand what determines species distribution, how species interact with each other, and consequently what drives community structure (Morris, 1988; Ortega-Huerta & Peterson, 2004). In addition, information about species habitat relationships (i.e. habitat requirements) can help in applied efforts for conservation purposes such as habitat management and studies on population viability (Ober & Hayes, 2008; Oppel, Schaefer, Schmidt, & Schröder, 2004).

Classical ecological theory predicts that two species that have a similar ecological niche cannot coexist, in which case one would competitively exclude the other (Finstad et al., 2011; Gauze, 1934; Violle, Nemergut, Pu, & Jiang, 2011). The fact that ecological similarity can hinder coexistence always raised considerable interest among ecologists (Chesson, 2000; Lack, 1945; Schoener, 1974). Closely related species show a tendency to retain ancestral traits, resulting in these species being more ecologically similar to each other than to non-related species (e.g. Niche conservatism—Donoghue, 2008; Pyron, Costa, Patten, & Burbrink, 2015; Wiens & Graham, 2005). In general, we would expect that these species also have similar habitat requirements and associations with environmental variables. However, in the case of coexistence between closely related species, classical ecological theory predicts that species would only be able to co-occur if there was a differentiation in resource use (e.g. through character displacement, Grant & Grant, 2006). In this case, when examined superficially, species that present very similar ecology would show different patterns of habitat use and associations with different environmental variables when analysed at high resolution.

In addition, patterns of similarity among species and consequently the mechanisms that explain coexistence could be influenced by habitat structure and resource availability. Some tropical forests and savannahs face strong rain seasonality, which directly affects food availability for birds (Jahn et al., 2010; Schaefer, Eshiamwata, Munyekenye, Griebeler, & Böhning-Gaese, 2006; Wikelski, Hau, & Wingfield, 2000), particularly insects (Pinheiro, Diniz, Coelho, & Bandeira, 2002; Wolda, 1980). Thus, it is expected greater availability of food resources during the rainy season when compared to the dry season (Anu, Sabu, & Vineesh, 2009; Develey & Peres, 2000; Pinheiro et al., 2002). Local species with low dispersion capacity (as Antwrens) can face difficulties in seasonal environments, forcing them to explore other food sources (Newton, 1998). This may act directly by increasing the effects of competition, which may influence the strategies of species coexistence (Develey & Peres, 2000; Langeland, L'Abée-Lund, Jonsson, & Jonsson, 1991; Werner & Hall, 1977). Therefore, seasonality may affect selection of habitats and foraging strategies in several species (Marra & Remsen, 1997).

Here, we build models of habitat use in high resolution (50 × 50 m), for two closely related species of birds in Northeast Brazil (Herpsilochmus sellowi–Coatinga Antwren, and Herpsilochmus pectoralis–Pectoral Antwren). We use ecological niche factor analysis (ENFA) to detail aspects of the relationship between the species and its habitat requirements and test hypotheses about strategies for coexistence between the two species. We predict that different habitat associations mediate the coexistence of these closely related and ecologically similar species. We also test whether seasonal variation in habitat structure and availability can influence coexistence and species interactions on habitat use. We predict that habitat differences will be more conspicuous during the dry season when resources are less abundant and the effects of competition can be more severe.

2. Materials and methods

2.1. Study site
Our study site is in the Atlantic Forest, one of the global hotspots for conservation (Myers, Mittermeier, Mittermeier, da Fonseca, & Kent, 2000). In the state of Rio Grande do Norte, the Atlantic Forest
reaches its northern limit and it is only 30 km wide, consisting primarily of lowland forests over sandy soils, usually formed by a mosaic of coastal strips (Tavares, 1960). Our sampling grid is located in an area belonging to the Brazilian Air Force, the region is locally known as “Barreira do Inferno” (Hell’s gate), hereafter named BI. The site is located in the municipality of Parnamirim, state of Rio Grande do Norte (5°55′29″S, 35°9′47″W, Figure 1(a)). The vegetation is within a system of fixed and parabolic dunes, seated on ground of sedimentary rocks (Fracasso, 2005; Rizzini, 1979).

The climate is classified as hot and humid, with the rainy season occurring between March and July (monthly average rainfall >250 mm) and dry season occurring between September and February (monthly average rainfall <100 mm), the average annual temperature is 26°C (Nimer, 1972). Precipitation variation between the rainy and dry seasons exerts great influence on the characteristics of the local flora. Several species lose their leaves during the dry season, typical of semi-deciduous forest. In a finer scale, the structure of vegetation is quite heterogeneous. About 10% of BI is bare soil, 55% dense woody shrub vegetation, 25% sparse woody vegetation, and 10% of undergrowth and/or pioneers (Fracasso, 2005). The area has a complex and heterogeneous vegetation that receives influence of elements from different Brazilian domains such as: Caatinga, Atlantic Forest and Cerrado.

Within the study area we built a sampling grid of 550 × 550 m, containing 121 sampling cells of 50 × 50 m. The size of the cells was defined based on logistic field limitations, and also to assure survey in all possible bird territories. The location of the grid was chosen based on satellite images.
of the region and local inspection of the area in order to maximize variation in vegetation structure. We built transects avoiding impacts to the habitat, trails were wide enough to ensure the passage of a person and proper installation of mist nets see Figure 1(b). Each transect crossed the centre of each cell, where it was the point of monitoring the species by mist-net and active search.

2.2. Study species

*H. pectoralis* and *H. sellowi* are two related insectivores birds morphologically similar, being the first slightly bigger (11.5–12.5 cm, 10–14 g) than the latter (10.5–11.5 cm, 7–10 g). *H. pectoralis* is classified as vulnerable to extinction (BirdLife International, 2012b) and it is distributed in the northeast of Brazil, occurring in disjunct populations at north-eastern Maranhão, east of Rio Grande do Norte and Sergipe, north-eastern Bahia and Paraíba (Pereira, Girão, Pacheco, & Brito, 2005; Ridgely & Tudor, 1994). *H. pectoralis* inhabits remnant woodlots characterized by trees over 10 m in gallery forest, wooded restinga, deciduous forest, Caatinga and secondary forest, where it utilizes all levels of forest (Zimmer & Isler, 2003; BirdLife International, 2012b). *H. sellowi* inhabits arboreal Caatinga, ecotones between Caatinga and Cerrado, semi-deciduous forest and sandbanks (Whitney, Pacheco, Buzzetti, & Parrini, 2000, BirdLife International, 2012b). This species have a wide distribution covering the states of Maranhão, Piauí, Ceará, Rio Grande do Norte, Pernambuco, Bahia, Minas Gerais and Pará (Whitney et al., 2000). In our study area these two species are syntopic. Both are not known to follow army ants and they are normally alone, but sometimes occur locally with mixed-species flocks of other insectivores and congeners (e.g. *H. rufomarginatus* and *H. atricapillus*) (Zimmer & Isler, 2003). *H. sellowi* often forages in open branches beneath canopy and in lower shrubby vegetation than *H. pectoralis* (Zimmer & Isler, 2003). We do not have previous information about competition between these two species, but we know that it occurs, at some level, in others *Herpsilochmus* (e.g. *H. gentryi*, *H. sticturus*, *H. stictocephalus* and *H. rufimarginatus*) in the Amazon, where there is an intricate process of ecological habitat partitioning (Whitney & Alonso, 1998). The high levels of syntopy among Amazonian antwrens are possible because they are excluding each other ecologically by using different resources or habitat (Bravo, Remsen, & Brumfield, 2014). Specific information about interaction between *H. pectoralis* and *H. sellowi* are completely absent. This information is important because these species are geographically restricted (both are endemic to Brazil), and has conservation concerns due to habitat under severe fragmentation.

2.3. Species occurrence data

The entire length of the grid, described above (Figure 1(b)) was sampled from January to December in the years of 2011–2012 (total of 24 months). All occurrences were assigned to a specific grid cell. We used as occurrence data-set all the cells of the grid where the species were recorded. Multiple records per cell were considered in the analysis. Therefore, cells with higher number of records had greater influence in the construction of models (Hirzel, Hausser, & Perrin, 2004). The occurrence records were obtained through capture-mark-recapture method, using mist nets (Ecotone® 18 × 3 m, mesh 19 mm and five shelves) opened ~30 min before sunrise (~5 am) and closed about 10 am, with a sampling effort of one mist net per month per cell (~14,520 total hours). Each individual captured was banded with numbered metal rings supplied by CEMAVE/ICMbio, and released at the capture site. We captured 12 individuals of *H. pectoralis* and 49 individuals of *H. sellowi* in the rainy season. In the dry season we captured 17 individuals of *H. pectoralis* and 52 individuals of *H. sellowi*. Information on the number of individuals banded and their numbers is available in the supplemental material (Table S4). Every cell with capture was assumed as used by the respective bird species. We considered this because both species have similar foraging behaviour, scanning foliage, stems and branches thoroughly and methodically through short flights and small jumps between nearby trees and bushes, not performing long flights over extensive areas (Zimmer & Isler, 2003), which could increase the chances of accidental catches in unused habitats. Besides, netting efficiently detects secretive species, is not affected by observer bias and is a good technique to study habitat segregations due to the local performance (Cintra & Naka, 2012; Karr, 1981; Whitman, 2004). We applied
similar effort among transects during each season, with one randomized visit of ~30 min per week (~6 h to survey the whole grid). The occurrence data was separated according to the season (rainy and dry). We generated separate models for each season. The occurrence records data is available in the supplemental material (Table S1).

2.4. Environmental variables

For each cell of the grid, we characterized the vegetation structure and bird habitat by measuring a series of environmental variables (detailed below). The variables were measured at four different locations within each grid cell (Figure 1(c)) and the average values for each cell were used in the analysis. To characterize cell heterogeneity we also compute the variance for each cell. We measured: (1) Flower availability: number of plants with flower in 1 m radius of each grid cell sampling point (Figure 1(c)) (this measure captures only the number of plant individuals with flower and not total flower abundance); (2) Fruit availability: number of plants with fruit on 1 m radius of each grid cell sampling point (Figure 1(c)) (this measure captures only the number of plant individuals with fruits and not total fruit abundance); (3) Leaf litter: we sifted and weighted (in grams) the leaf litter contained in a 1 m² quadrat using portable scales. This measure was repeated for all four sampling points within each grid cell (Figure 1(c)); (4) Canopy cover: estimated using digital photos (used camera Fujifilm Finepix 3000 and imaging software, Can eye v. 6.3 (https://www4.paca.inra.fr/can-eye/Download) to extract the percentage of canopy cover; (5) Canopy height: maximum tree height (in metres) found within a 1 m radius of each grid cell sampling points (measured or estimated using a measuring tape and 1 m long stakes that were stacked together); (6) Tree richness: number of morphospecies within 1 m radius (we differentiate morphotypes of plants based on their morphological characteristics, primarily leaves and stem, only plants with a diameter at breast height (DBH) greater than or equal to 3 cm were considered as trees; (7) Density of trees: number of plants with DBH greater than 3 cm in 1 m radius; (8) Density of shrubs: number of shrubby plants in 60 cm radius. We measured shrub density using a vertical rod of 50 cm attached to a horizontal rod of 60 cm (L shape device). The vertical rod was placed to the ground and spun 360°. Each touch of the horizontal rod on a plant, with DBH smaller than 3 cm, was counted as one occurrence of shrub; (9) DBH: average of the five largest DBHs (in cm) in a 1 m radius. In case there was no plant with DBH higher than 3 cm this variable was considered as zero at the sampled point; (10) Altitude: altitude (metres above sea level) obtained at the centre of each cell with Garmin 76CSx GPS device (it was the only variable measured at a single point in each cell).

Variables 5–10 did not vary seasonally and were measured only once. These variables are general descriptors of habitat structure and complexity. These variables may be related to species requirements relative to nesting sites, shelter, foraging perches, etc. Variables 1–4 were collected in both seasons. These variables are related to habitat structure and complexity and also capture the strong seasonality in the region. They are also a general proxy for insect abundance, which is an important resource for insectivorous birds. We do not have data on insect abundance variation in our study site. However, some studies in nearby regions with similar precipitation seasonality dynamics suggest that insect abundance has a peak in the rainy season, which is also reflected in fruit and flower availability (Vasconcellos et al., 2010). Each variable was sampled in four points within the grid cell (and averaged out for each cell), being 12 m away in each direction of the cell centre (Figure 1(c)). Altitude was measured only once at the centre point of each cell. Mean and variance values of each variable measured in the grid are available in the supplemental material (Tables S2 and S3). After preliminary ENFA runs (see ENFA details below), we observed extremely high eigenvalues for some factors calculated for H. pectoralis. These high values suggest that there is influence of correlated predictor variables in the analysis. We built a correlation matrix of our variables and identified nine variables (dbh, canopy cover, canopy cover variation, flower availability variation, fruit availability variation, leaf litter variation, density of shrubs variation, density of trees, tree richness) that if removed would minimize the overall collinearity of our data-set. These variables were removed of the
model and there were no more extremely high eigenvalues. Our final models were run with the following variables: altitude, canopy height variation, dbh variation, flower availability, fruit availability, leaf litter, density of shrubs, density of trees variation, tree density variation, and tree richness variation. We checked for deviations of normality using Shapiro–Wilks normality test in R Core Team (2015). All variables were normally distributed and following analysis were run with untransformed data.

2.5. Statistical analysis
For the variables that were measured in both seasons we test whether there was differences in the mean values across the grid between seasons using analysis of variance (ANOVA). We also performed a \(F\)-test to compare variances to test whether there were differences in the heterogeneity of the grid between seasons.

2.5.1. ENFA
The ENFA compares, in the multidimensional space of ecological variables, the distribution of ecological conditions where the focal species was observed to the whole ecological space available in the study area (Hirzel, Haussler, Chessel, & Perrin, 2002). Species are usually non-randomly distributed in the environment, occurring in more frequency near optimum conditions. This can be quantified by comparing the environment where the species was observed with what is available throughout a specific region. ENFA searches for directions in the ecological space so that (1) the difference between the conditions used on average by the species and the conditions available in the study area (defined as marginality—\(M\)) is maximized and (2) the ratio between the variance of available conditions and the variance of conditions used by the species (defined as specialization—\(S\)) is maximized (Basille, Calenge, Marboutin, Andersen, & Gaillard, 2008). \(M\) and \(S\) are uncorrelated factors, with the major information contained within the first factors (Hirzel et al., 2002). \(M\) is the first axis extracted from the analysis and it represents the ecological distance between the species optimum and the mean habitat within the reference area. \(M\) is defined as the absolute difference between environmental mean \((m_E)\) and species mean \((m_S)\), divided by 1.96 standard deviations \((\delta_E)\) of the environmental distribution:

\[
M = \frac{(m_E - m_S)}{1.96\delta_E}
\]

ENFA produces a score matrix where the coefficients related to the marginality factor (first axis) indicate the correlation between each environmental variable and the factor. The greater the absolute value of the coefficient, the higher the environmental variable contributes to the marginality. Positive score values indicates that the species is associated with high values of the environmental variable, while negative score values shows that the species is associated with low values of the environmental variable. \(M\) scores for each variable can be summarized in a global marginality index \((M_G)\), which is calculated as:

\[
M_G = \sqrt{\sum_{i=1, V} [M_i]^2} / 1.96
\]

where \(M_i\) are the coefficients of the marginality factor and \(V\) is the number of variables. \(M_G\) takes into account all the environmental variables and summarizes how much the species habitat differs from the available conditions. A low value (close to 0) indicates that the species tends to occupy average conditions throughout the study area, whereas a high value (close to 1) indicates a tendency to live in habitats that are different from the environment mean.

The following \(V-1\) axis are \(S\) axis and are defined as the ratio of the standard deviation of the environmental distribution \((\delta_E)\) to that of the focal species \((\delta_S)\):
where $S$ measures how narrow is the distribution of ecological space occupied by the species in relation to the distribution of ecological space available in the whole study area. Therefore, $S$ measures how specialized in particular conditions a species may be (niche breadth). ENFA score matrix shows coefficients for each variable in each $S$ axis, similarly to the described above for $M$. $S$ scores for each variable can be summarized in a global specialization index ($S_G$), which is calculated as:

$$S_G = \sqrt{\sum_{i=1}^{V} \frac{\lambda_i}{V}}$$

where $\lambda_i$ are the eigenvalues of each $S$ axis. $S_G$ ranges from 1 to infinity. Because this range of values may be difficult to interpret we define Tolerance—$T = 1/S_G$, ranging from close to zero to one. Higher values of $T$ than suggest that a species is less selective in the ecological space it occupies (i.e. more tolerant or more generalist), and lower values of $T$ suggests a species that is more selective in the ecological space it occupies (i.e. less tolerant or more specialized). A randomly chosen set of cells is expected to have a tolerance of 1, that is, any value below 1 indicates some form of specialization.

For each species in each season we used MacArthur’s broken-stick distribution criteria (MacArthur, 1957) to decide the number of factors to be included in the analysis. This method compares the distribution of the eigenvalue to the distribution of MacArthur’s broken-stick model. The factors that have eigenvalues that are larger than what would have been obtained randomly are retained (Hirzel et al., 2004).

These parameters ($M$, $S$, $T$) have been used to describe species habitat relationships and to test hypotheses about coexistence and niche segregation among related species. For example, sympatric species of panda showed distinct patterns of environmental requirements based on values of marginality and tolerance, and niche segregation in these species was mediated by different habitat selection (Qi, Hu, Gu, Li, & Wei, 2009). In our study system we expect that different habitat associations will facilitate species coexistence. Therefore we expect species to show differences in the marginality and or tolerance parameters of ENFA. In addition, we expect that these differences will be more conspicuous in the dry season where competition for resources may be stronger. We run ENFA in the software Biomapper vs 4.0 (Hirzel et al., 2004).

3. Results

3.1. Spatial and temporal variation of the sampling grid

We can observe that vegetation is highly variable in the space, especially considering variables that represent vegetation structure, such as canopy height, dbh and tree density. There is a gradient ranging from sites with high canopy and large trees through a vegetation of intermediate size structure to regions of predominantly more bushy, fewer trees, composed predominantly of sparse small plants, (Figure 2(a)–(c)). Furthermore, dbh and tree density showed strong correlation ($r = 0.83$). Elevation is negatively correlated with vegetation height ($r = -0.43$), tree density ($r = -0.31$) and dbh ($r = -0.35$). Thus, in areas of higher altitude, we tend to find low values of canopy height, dbh and tree density. On the other hand, in lower elevations, we found high values of canopy height, dbh and tree density. The opposite case is found at lower elevations, where there is a tendency to find, in general, larger vegetation, with high values of canopy height, dbh and tree density (Figure 2(a)–(d)). This heterogeneity in the grid is fundamental to potential habitat selection of the focal species. The different habitat structures may be differentially preferred by the species, with parts of the grid being more or less suitable for the species.
Some variables not only show a strong spatial variation but also vary temporally between rainy and dry seasons. Regarding temporal variation, we found that flower and fruit availability and the amount of leaf litter were more homogeneously distributed during the dry season. Furthermore, flower and fruit were less available, and there were smaller amounts of leaf litter during the same period (Figure 3, Table 1). Contrary to our expectation, canopy cover maintained a similar pattern in both seasons (Table 1, Figure 3(g)–(h)).

3.1.2. ENFA
For all our ENFA analyses (both species in both seasons), three axes were selected using MacArthur’s broken-stick criteria (i.e. the axis of marginality and the first two axis of specialization). These axes accounted for most of the explained variance (Tables 2 and 3). In the dry season ENFA showed a global marginality value of 0.73 for *H. pectoralis* and 0.4 for *H. sellowi*. In the dry season global tolerance was 0.16 for *H. pectoralis* and 0.415 for *H. sellowi*. In the rainy season global marginality value for *H. pectoralis* was 0.68 and for *H. sellowi* was 0.285. In the rainy season global tolerance was 0.39 for *H. pectoralis* and 0.774 for *H. sellowi* (Tables 2 and 3).
Figure 3. Maps of seasonal environmental variables.

Notes: Warm colours represent higher values of the variable in that grid cell. Maps were placed side by side to show the differences between seasons. Left panel figures are the rainy season and right panel figures are the dry season. (a) and (b) Leaf litter: mean weight of leaf litter contained in a 1 m² quadrat. (c) and (d) Fruit availability: mean number of plants with fruit on 1 m radius of each grid cell sampling point. (e) and (f) Flower availability: mean number of plants with flower on 1 m radius of each grid cell sampling point. (g) and (h) Canopy cover: mean percentage of canopy cover. See Methods for details on how variables were measured.

Table 1. Mean and standard deviation (SD) across the grid for variables that were measured in both seasons. Results of analysis of variance (Anova) and F-tests comparing mean and variance of variables across the grid.

| Variable                  | Mean ± SD  | F_{anova} | P_{anova} | F_{f-test} | P_{f-test} |
|---------------------------|------------|-----------|-----------|------------|------------|
|                           | Rainy      | Dry       |           |            |            |
| Flower availability (N)   | 2.37 ± 1.43| 0.44 ± 0.70| 178.3     | <0.001     | 4.21       | <0.001     |
| Fruit availability (N)    | 2.68 ± 1.63| 0.51 ± 0.49| 196.9     | <0.001     | 11.17      | <0.001     |
| Leaf litter (grams)       | 616.44 ± 246.12| 477.19 ± 164.62| 26.76     | <0.001     | 2.23       | <0.001     |
| Canopy cover (%)          | 50.77 ± 18.34| 47.46 ± 17.80| 2.03      | 0.156      | 1.06       | 0.74       |
Table 2. ENFA scores, percentage of specialization explained by each factor, marginality and tolerance indexes for *H. pectoralis* in the dry and rainy seasons. Scores represent correlations between ENFA factor and the corresponding environmental variable. Factor 1 explains 100% of the marginality. Three factors were retained using the broken-stick heuristics. The percentage of specialization explained by each factor in each season is reported.

| Variable                  | Factor 1 Dry | Factor 1 Rainy | Factor 2 Dry | Factor 2 Rainy | Factor 3 Dry | Factor 3 Rainy |
|---------------------------|--------------|----------------|--------------|----------------|--------------|----------------|
| Altitude                  | -0.354       | -0.52          | 0.09         | 0.225          | 0.2          | -0.16          |
| Canopy height variation   | 0.107        | -0.18          | 0.087        | 0.373          | -0.402       | -0.353         |
| DBH variation             | -0.011       | -0.097         | -0.451       | -0.845         | 0.366        | 0.121          |
| Flower availability       | -0.254       | 0.005          | 0.836        | -0.171         | 0.185        | -0.081         |
| Fruit availability        | -0.34        | 0.003          | -0.168       | -0.048         | -0.503       | -0.465         |
| Leaf litter               | 0.609        | 0.48           | 0.142        | -0.045         | 0.264        | -0.615         |
| Density of shrubs         | 0.251        | 0.504          | 0.139        | 0.249          | -0.44        | -0.049         |
| Density of trees variation| -0.121       | -0.195         | -0.086       | -0.013         | 0.337        | -0.401         |
| Tree density variation    | 0.485        | -0.406         | 0.085        | 0.008          | -0.033       | -0.267         |
| Tree richness variation   | -0.354       | -0.52          | 0.09         | 0.225          | 0.2          | -0.16          |
| Eigenvalues               | 106.8        | 4.34           | 190.7        | 33.38          | 26.27        | 10.98          |
| % variance explained      | 32.1         | 7.5            | 57.2         | 57.7           | 7.9          | 19             |
| Marginality               | 0.73         | 0.68           | -            | -              | -            | -              |
| Tolerance                 | 0.16         | 0.39           | -            | -              | -            | -              |

Table 3. ENFA scores, percentage of specialization explained by each factor, marginality and tolerance indexes for *H. sellowi* in the dry and rainy seasons. Scores represent correlations between ENFA factor and the corresponding environmental variable. Factor 1 explains 100% of the marginality. Three factors were retained using the broken-stick heuristics. The percentage of specialization explained by each factor in each season is reported.

| Variable                  | Factor 1 Dry | Factor 1 Rainy | Factor 2 Dry | Factor 2 Rainy | Factor 3 Dry | Factor 3 Rainy |
|---------------------------|--------------|----------------|--------------|----------------|--------------|----------------|
| Altitude                  | 0.058        | -0.448         | 0.104        | -0.066         | 0.025        | -0.581         |
| Canopy height variation   | -0.218       | -0.595         | 0.103        | 0.219          | 0.186        | 0.199          |
| DBH variation             | -0.112       | -0.24          | -0.431       | -0.835         | -0.777       | 0.321          |
| Flower availability       | -0.334       | 0.321          | 0.817        | -0.131         | -0.449       | -0.14          |
| Fruit availability        | -0.565       | 0.276          | -0.281       | -0.087         | 0.265        | -0.239         |
| Leaf litter               | 0.017        | 0.088          | 0.093        | -0.475         | 0.24         | -0.625         |
| Density of shrubs         | 0.653        | 0.401          | 0.146        | 0.023          | 0.087        | 0.194          |
| Density of shrubs variation| -0.191      | 0.195          | -0.047       | -0.005         | -0.123       | 0.098          |
| Tree density variation    | -0.204       | -0.049         | 0.118        | 0.008          | 0.094        | -0.082         |
| Tree richness variation   | 0.058        | -0.448         | 0.104        | -0.066         | 0.025        | -0.581         |
| Eigenvalues               | 12.68        | 2.41           | 22.81        | 3.39           | 6.03         | 2.32           |
| % variance explained      | 24.3         | 16.1           | 43.7         | 22.6           | 11.5         | 15.5           |
| Marginality               | 0.4          | 0.285          | -            | -              | -            | -              |
| Tolerance                 | 0.415        | 0.774          | -            | -              | -            | -              |
4. Discussion

In lower resolutions the environment of fixed dunes of BI has been described as largely heterogeneous in vegetation structure (Fracasso, 2005). Our results show that this heterogeneity is also noticeable in high resolution (50 × 50 m cells) and limited extent (550 × 550 m). Much of the spatial variation we found may be associated with variation in altitude due to the presence of sand dunes of different sizes. This peculiarity of the terrain may imply differences in soil composition, and availability of water and nutrients (variables not studied). Sites with low altitude possibly have soils with different composition than dunes tops (sandy soil, sandbank). In turn, different soil compositions can reflect different patterns of absorption and retention of water and nutrients.

In addition to spatial variation, our sampled grid also shows temporal variation in some variables. The availability of flower, fruit and leaf litter decreased between the rainy and dry seasons. The abundance of these resources may be directly or indirectly correlated with the availability of insects, the main food source for the species studied. Flower, fruit and leaf litter may be important attractions for insects in their various stages of development, and respond similarly to drought and rainfall regime (Anu et al., 2009; Develey & Peres, 2000; Wolda, 1978). Thus, the reduced availability of flower, fruit and leaf litter can be important indicators of diminishing resources and consequently increased competition between the two species during the dry season. In fact, our results showed very different habitat associations across seasons (discussed below). This temporal variation can be explained by climatic seasonality, which is mainly determined by the pattern of rainfall in the region (Nimer, 1972). However, we did not notice a marked variation in the percentage of canopy cover between these periods (overall average rainy and dry 50% 47%, Figure 3). One possible explanation for this is that 2011 was an “El Niño” year and presented atypical rainfall (2,061 mm), well above the average over the last 10 years (1,740 mm). This increased water availability may have been enough to prevent major leaf decay and explain why canopy cover is similar in both seasons (Figure 3).

The difference in habitat use between H. pectoralis and H. sellowi is clear in the ENFA analysis and reflected in the values of marginality and tolerance for both species. Our results show that H. pectoralis has a narrower niche breadth (much lower values of tolerance) and select a well-differentiated habitat than the available average (higher marginality) when compared to H. sellowi. This result is consistent in both seasons. For instance it is clear from the ENFA biplots (Figure 4) that for H. pectoralis the distance between the centroid of the species niche (darker grey polygons in Figure 4) and the centroid of the available habitat (origin of the plot), was quite high, resulting in a marked marginality (X-axis, Figure 4(a) and (c)). Therefore, the environmental optimum of H. pectoralis was clearly shifted away from the mean available conditions in the sampling grid. This result was consistent across seasons. In the specialization axis we can see that H. pectoralis show lower ranges of values in the Y-axis, indicating that the species is using a much more narrow set of environmental conditions when compared to H. sellowi (Table 2, Y-axis Figure 4(a) and (c)). Our results show that H. sellowi was more generalist (much higher tolerance) than its conspecific. Considering the environmental conditions of the sampling grid, H. sellowi seems to be selecting habitats with features closer to the average of the values available in the environment (lower marginality values). ENFA biplot shows that the distance between the centroid of the ecological niche and the centroid of the available habitat was smaller when compared to H. pectoralis, hence the lower marginality (X-axis, Figure 4(b) and (d)). Therefore, the optimum of the species was not so different from the mean available conditions in the sampling grid. In the specialization axis we can see that the species show high values of specialization indicating a wide niche breadth (Table 3, Y-axis Figure 4(b) and (d)). In general, the values of marginality and tolerance for both species were quite different, indicating that they have different relationships with the set of available variables. One caveat of our analysis is that the number of H. pectoralis individuals captured was lower than H. sellowi. It is possible that H. pectoralis higher habitat specialization may be an artefact of its lower sampling. However, our results and field observations suggest that indeed H. pectoralis is more selective, and we do not expect that our results would change with more individuals sampled.
In addition to the differences on the comparison between species we also build ENFA models across seasons. There were no markedly differences in the general use of habitat between seasons. In both seasons *H. pectoralis* showed higher marginality and lower tolerance than that found for *H. sellowi*. Overall our ENFA models showed that *H. pectoralis* is more specialized in habitat use in the grid (lower tolerance, higher marginality) when compared to *H. sellowi* that is more generalist in its habitat use (higher tolerance, lower marginality). These different strategies of both species are also reflected in a broader scale (e.g. whole geographical distribution). It is a well-established general ecological pattern that niche breadth correlates to geographical range distribution (Slatyer, Hirst, & Sexton, 2013).

*H. pectoralis* has a narrower habitat niche breadth and also show a narrower and more punctual geographical distribution. On the other hand, *H. sellowi* has a much wider geographical range (BirdLife International, 2012a, 2012b).

Body size is another ecological trait that is generally associated with niche breadth, where species with larger body sizes tend to be more generalist (Brandl & Brandl, 2001; Costa, Vitt, Pianka, Mesquita, & Colli, 2008; Pyron, 1999). Our results did not follow this trend; *H. pectoralis* is about 40% heavier than *H. sellowi* (max 14 g versus max 10 g) and had a narrower habitat niche breadth. One possible explanation for this result could be that *H. pectoralis* being larger and likely dominant in its antagonistic relationship with *H. sellowi*, dominates habitat of higher quality leaving *H. sellowi* to be distributed in peripheral wider distributed and less optimal habitat throughout the grid. Our results suggest that *H. sellowi* is primarily distributed in areas with less density of trees and more shrubs, these areas are in fact more common throughout the grid. On the other hand, *H. pectoralis* is more associated with habitats that are not very common in the grid, particularly areas of more dense
arboreal vegetation. These different habitat selection strategies between species can be critical to assure coexistence. Previous work focusing on coexistence showed that generalist species can occupy habitats unused or underutilized by specialists facilitating coexistence (e.g. Morris, 1996). In case regions with higher density of trees consists of better quality territories, the fact that H. pectoralis, is dominating this portion of the grid, may suggest a competitive advantage against H. sellowi. This hypothesis can be tested in future studies by collecting data on territory sizes and nest success parameters in different regions of the grid.

5. Conclusions
Our ENFA models brought new information about habitat use and how species respond to environmental variability. Through our study we could also better understand the possible mechanisms promoting coexistence between species. First, our environment maps revealed high spatial and temporal heterogeneity in a fine resolution. This heterogeneity allows for distinct habitats that can be differently occupied by the species. Our analysis showed that the species have different strategies in habitat use, H. pectoralis was very selective (specialist), and H. sellowi was more generalist in the selection of habitat. Our results suggest that habitat segregation as proposed by classical niche theory is the main mechanism explaining coexistence of these two species. Thus, spatial niche segregation may be a reflection of competitive interactions between species. The use of different habitats can reduce the effect of interspecific competition to levels that allow coexistence.

Supplementary material
Supplementary material for this article can be accessed here http://dx.doi.org/10.1080/23311843.2016.1264126.

Acknowledgements
We are grateful to Barreiro do Inferno Launch Centre - Brazilian Air Force for permission to access the study area, and to Brazilian Centre for Research and Conservation of Wild Birds (CEMAVE) for supplying the aluminium leg bands. We thank A. Fadigas, M. Marini and two anonymous reviewers for comments on earlier versions of the manuscript. The staff of the Laboratory of Ornithology of UFRN helps in the field works, especially Guilherme S. Toledo de Lima, Phoeve Macário, Priscilla S. Amorim de Araújo, José V. Fernandes de Lima, Thaynira P. F. Câmara, Danilo Valdenor de Oliveira and Elaine D. Bandeira.

Funding
This work was partially supported by the Brazilian Research and Technological Development Council [CNPq Process 474945/2010-3] and GCC thanks CNPq [grant numbers 201413/2014-0, 302776/2012-5 and 563352/2010-8].

Author details
Gabriel C. Costa¹
E-mail: costagc@mac.com
ORCID ID: http://orcid.org/0000-0002-6777-6706

Tonny M. Oliveira-Junior²
E-mail: tonnybas@hotmail.com
ORCID ID: http://orcid.org/0000-0002-4266-242X

Mauro Pichorim²
E-mail: mauropichorim@yahoo.com.br
ORCID ID: http://orcid.org/0000-0002-9340-9010

¹ Centro de Bicências, Departamento de Ecologia, Universidade Federal do Rio Grande do Norte, Campus Universitário Lagoa Nova, Natal, Rio Grande do Norte 59072-970, Brazil.
² Centro de Bicências, Departamento de Botânica e Zoologia, Universidade Federal do Rio Grande do Norte, Campus Universitário Lagoa Nova, Natal, Rio Grande do Norte 59072-970, Brazil.

References
Anu, A., Sabu, T. K., & Vineesh, P. (2009). Seasonality of litter insects and relationship with rainfall in a wet evergreen forest in South Western Ghats. Journal of Insect Science, 9, 1–10. http://dx.doi.org/10.1673/031.009.4601

Basille, M., Colenge, C., Marboutin, E., Andersen, R., & Gaillard, J. M. (2006). Assessing habitat selection using multivariate statistics: Some refinements of the ecological-niche factor analysis. Ecological Modelling, 211, 233–240. http://dx.doi.org/10.1016/j.ecolmodel.2007.09.006

Birdlife International. (2012a). Herpsilochmus pectoralis. The IUCN Red List of Threatened Species (Version 2015.2). Downloaded on July 22, 2015, www.iucnredlist.org.

Birdlife International. (2012b). Herpsilochmus sellowi. The IUCN Red List of Threatened Species (Version 2015.2). Downloaded on July 22, 2015, www.iucnredlist.org.

Brandle, M., & Brandl, R. (2001). Distribution, abundance and niche breadth of birds: Scale matters. Global Ecology and Biogeography, 10, 173–177. http://dx.doi.org/10.1046/j.1466-822x.2001.00213.x

Bravo, G. A., Remsen, J., & Brumfield, R. T. (2014). Adaptive processes drive ecomorphological convergent evolution in antwrens (Thamnophilidae). Evolution, 68, 2757–2774. http://dx.doi.org/10.1111/evo.12506

Chase, J. M. (2003). Community assembly: When should history matter? Oecologia, 136, 489–498. http://dx.doi.org/10.1007/s00442-003-1311-7

Chesson, P. (2000). Mechanisms of maintenance of species diversity. Annual Review of Ecology and Systematics, 31, 343–366. http://dx.doi.org/10.1146/annurev.ecolsys.31.1.343

Cintra, R., & Naka, L. N. (2012). Spatial variation in bird community composition in relation to topographic gradient and forest heterogeneity in a central Amazonian rainforest. International Journal of Ecology, 2012, Article ID 435671.
Costa, G. C., Vitt, L. J., Pianka, E. R., Mesquita, D. O., & Colli, G. R. (2008). Optimal foraging constrains macroecological patterns: Body size and dietary niche breadth in lizards. Global Ecology and Biogeography, 17, 670–677. http://dx.doi.org/10.1111/j.0962-8898.2008.001255.x

Develey, R. F., & Perez, C. A. (2003). Resource seasonality and the structure of mixed species bird flocks in a coastal Atlantic forest of southeastern Brazil. Journal of Tropical Ecology, 16, 33–53. http://dx.doi.org/10.1017/s0266467703001255

Donoghue, M. J. (2008). A phylogenetic perspective on the distribution of plant diversity. Proceedings of the National Academy of Sciences, 105, 11549–11555. http://dx.doi.org/10.1073/pnas.0801962105

Finsdahl, A., Godt, T., Jonsson, B., Bellier, E., Hesthaven, T., Jensen, A. J., ... Foldvik, A. (2011). Competitive exclusion along climate gradients: Energy efficiency influences the distribution of two salmonid fishes. Global Change Biology, 17, 1703–1711. http://dx.doi.org/10.1111/j.1365-2486.2011.02727.x

Fracasso, P. (2005). Sistemas de dunas do parque das dunas e barreira do inferno/Natal (RN): Levantamento geológico e geo-físico, elaboração do modelo determinístico e avaliação do impacto ambiental. (Doctoral dissertation). Universidade Federal do Rio Grande do Norte, Natal, RN.

Gauze, G. F. (1934). The struggle for existence, by G. F. Gause. Baltimore, MD: Lippincott Williams and Wilkins. http://dx.doi.org/10.5962/bhl.title.4489

Google Earth. (2010). Centro de Lançamento Barreira do Inferno. 5°55′24″ S and 35°10′09″ W. Google Earth. May 27, 2010.

Grant, R. &; Grant, B. R. (2006). Evolution of character displacement in Darwin’s finches. Science, 312, 224–226. http://dx.doi.org/10.1126/science.1128374

Grinnell, J. (1917). The niche-relationships of the California thrasher. The Auk, 34, 427–433. http://dx.doi.org/10.2307/4122721

Hirzel, A. H., Hauser, J., Cheissel, D., & Perrin, N. (2003). Ecological-niche factor analysis: How to compute habitat-suitability maps without absence data? Ecology, 83, 2027–2036. http://dx.doi.org/10.1890/0012-9658(2002)083[2027:EFACHT]2.0.CO;2

Hirzel, A. H., Hauser, J., & Perrin, N. (2004). Bimapper 4.0. Division of Conservation Biology, University of Bern. Retrieved from http://www.unil.ch/bimapper

John, A. E., Levey, D. J., Mamani, A. M., Saldivas, M., Alcaba, A., Ledezma, M. J., ... Hilario, F. (2010). Seasonal differences in rainfall, food availability, and the foraging behavior of Tropical Kingbirds in the southern Amazon Basin. Journal of Field Ornithology, 81, 340–348. http://dx.doi.org/10.1111/j.1540-9994.2010.01814.x

Karr, J. R. (1981). Surveying birds with mist nets. Studies in Avian Biology, 6, 62–67.

Lack, D. (1946). The ecology of closely related species with special reference to cormorant (Phalacrocorax carbo) and Shag (P. aristotelis). The Journal of Animal Ecology, 14, 12–16. http://dx.doi.org/10.2307/1395

Langeland, A., L’Abee-Lund, J. H., Jonsson, B., & Jonsson, N. (1991). Resource partitioning and niche shift in arctic char Salvelinus alpinus and brown trout Salmo trutta. The Journal of Animal Ecology, 60, 895–912. http://dx.doi.org/10.2307/1945445

MacArthur, R. H. (1957). On the relative abundance of bird species. Proceedings of the National Academy of Sciences, 43, 293–295. http://dx.doi.org/10.1073/pnas.43.3.293

Marra, P. P., & Remsen Jr., J. (1997). Insights into the maintenance of high species diversity in the neotropics: Habitat selection and foraging behavior in understory birds of tropical and temperate forests. Ornithological Monographs, 48, 1248–1262. http://dx.doi.org/10.2307/4157547

Morris, D. W. (1988). Habitat-dependent population regulation and community structure. Evolutionary Ecology, 2, 253–269. http://dx.doi.org/10.1007/BF02214286

Morris, D. W. (1998). Coexistence of specialist and generalist rodents via habitat selection. Ecology, 77, 2352–2364. http://dx.doi.org/10.2307/2657377

Myers, N., Mittermeier, R. A., Mittermeier, C. G., da Fonseca, G. A. B., & Kent, J. (2000). Biodiversity hotspots for conservation prioritization. Nature, 403, 853–858. http://dx.doi.org/10.1038/35052051

Newton, I. (1998). Population limitation in birds. San Diego, CA: Academic press.

Nimer, E. (1972). Climatologia da região Nordeste [Climatology of the Northeast region]. Revista Brasileira de Geografia., 3, 3–51.

Ober, H. K., & Hayes, J. P. (2008). Influence of vegetation on bat use of riparian areas at multiple spatial scales. Journal of Wildlife Management, 72, 386–406. http://dx.doi.org/10.2193/2007-193

Oppel, S., Schaefer, H. M., Schmidt, V., & Schröder, B. (2004). Habitat selection by the pale-headed brush-finch (Atilopetes pallidicollis) in southern Ecuador: Implications for conservation. Biological Conservation, 118, 33–40. http://dx.doi.org/10.1016/j.biocon.2003.07.006

Ortego-Huerta, M. A., & Peterson, A. T. (2004). Modelling spatial patterns of biodiversity for conservation prioritization in North-eastern Mexico. Diversity and Distributions, 10, 39–54. http://dx.doi.org/10.1111/j.1366-9516.2004.00121.x

Pereira, G. A., Girão, W., Pacheco, G. L., & Brito, M. T. (2005). Primeiro registro documentado de Herpsilochmus pectoralis sclater, 1857 no Estado da Paraíba, Brasil (First documented record of Herpsilochmus pectoralis sclater, 1857 in the State of Paraíba, Brasil). Atualidades Ornitológicas, 127, 29–32.

Pinheiro, F., Diniz, I. R., Coelho, D., & Bandeira, M. P. S. (2002). Seasonal pattern of insect abundance in the Brazilian Cerrado. Austral Ecology, 27, 132–136. http://dx.doi.org/10.1046/j.1442-9993.2002.01165.x

Pyron, M. (1999). Relationships between geographical range size, body size, local abundance, and habitat breadth in North American suckers and sunfishes. Journal of Biogeography, 26, 549–558. http://dx.doi.org/10.1046/j.1365-2699.1999.00303.x

Pyron, R. A., Costa, G. C., Patten, M. A., & Burbink, F. T. (2015). Phylogenetic niche conservatism and the evolutionary basis of ecological speciation. Biological Reviews, 90, 1248–1262. http://dx.doi.org/10.1111/brv.12195

Qi, D., Hu, Y., Gu, X., Li, M., & Wei, F. (2009). Ecological niche modeling of the sympatric giant and red pandas on a mountain-range scale. Biodiversity and Conservation, 18, 2127–2141. http://dx.doi.org/10.1007/s10531-009-9577-7

R Core Team. (2015). R: A language and environment for statistical computing. Vienna: R Foundation for Statistical Computing. http://www.R-project.org

Ridgely, R. S., & Tudor, G. (1994). The birds of South America. Austin, TX: University of Texas Press.

Rizzini, C. T. (1979). Tratado de fitogeografia do Brasil São Paulo [Brazilian treaty of Phytogeography]. São Paulo: Editora da Universidade de São Paulo.

Schafer, H. C., Eshiamwata, G. W., Munyekenye, F. B., Griebeler, E., & Böhning-Gaese, K. (2006). Monthly survival of African Sylvia warblers in a seasonally arid tropical environment. Ibis, 148, 411–424. http://dx.doi.org/10.1111/j.1474-919X.2006.00544.x
Schoener, T. W. (1974). Resource partitioning in ecological communities. Science, 185, 27–39. http://dx.doi.org/10.1126/science.185.4145.27

Slatyer, R. A., Hirst, M., & Sexton, J. P. (2013). Niche breadth predicts geographical range size: A general ecological pattern. Ecology Letters, 16, 1104–1114. http://dx.doi.org/10.1111/ele.2013.16.issue-8

Tavares, S. (1960). Estudos geobotânicos no Rio Grande do Norte [Geobotanical studies in Rio Grande do Norte]. Arquivo Instituto de Pesquisas Agronômicas, 5, 39–51.

Vasconcellos, A., Andreazze, R., Almeida, A. M., Araujo, H. F., Oliveira, E. S., & Oliveira, U. (2010). Seasonality of insects in the semi-arid Caatinga of northeastern Brazil. Revista Brasileira de Entomologia, 54, 471–476. http://dx.doi.org/10.1590/S0085-56262010000300019

Violle, C., Nemergut, D. R., Pu, Z., & Jiang, L. (2011). Phylogenetic limiting similarity and competitive exclusion. Ecology Letters, 14, 782–787. http://dx.doi.org/10.1111/ele.2011.14.issue-8

Werner, E. E., & Hall, D. J. (1977). Competition and habitat shift in two sunfishes (Centrarchidae). Ecology, 58, 869–876. http://dx.doi.org/10.2307/1936222

Whitman, A. A. (2004). Use of mist nets for study of Neotropical bird communities. Studies in Avian Biology, 29, 161–167.

Whitney, B. M., & Alonso, J. A. (1998). A new Herpsilochmus Antwren (Aves: Thamnophilidae) from northern Amazonian Peru and Adjacent Ecuador: The role of edaphic heterogeneity of terra firme forest. The Auk, 115, 559–576. http://dx.doi.org/10.2307/4089406

Whitney, B. M., Pochecho, J. F., Buzzetti, D. R., & Parrini, R. (2000). Systematic revision and biogeography of the herpsilochmus pileatus complex, with description of a new species from Northeastern Brazil. The Auk, 117, 869–891. http://dx.doi.org/10.1642/0004-8038(2000)117[0869:SRABOT]2.0.CO;2

Wiens, J. J., & Graham, C. H. (2005). Niche conservatism: Integrating evolution, ecology, and conservation biology. Annual Review of Ecology, Evolution, and Systematics, 36, 519–539. http://dx.doi.org/10.1146/annurev.ecolsys.36.102803.095431

Wikelski, M., Hau, M., & Wingfield, J. C. (2000). Seasonality of reproduction in a neotropical rain forest bird. Ecology, 81, 2458–2472. http://dx.doi.org/10.1890/0012-9658(2000)081[2458:SOR]2.0.CO;2

Wolda, H. (1978). Seasonal fluctuations in rainfall, food and abundance of tropical insects. The Journal of Animal Ecology, 47, 369–381. http://dx.doi.org/10.2307/3789

Wolda, H. (1980). Seasonality of tropical insects. The Journal of Animal Ecology, 49, 277–290. http://dx.doi.org/10.2307/4289

Zimmer, K., & Isler, M. L. (2003). Caatinga antwren (Herpsilochmus sellowi) and Pectoral antwren (Herpsilochmus pectoralis). In J. del Hoyo, A. Elliott, J. Sargatal, D. A. Christie, & E. de Juana (Eds.), Handbook of the birds of the world alive, 2014. Barcelona: Lynx Edicions.