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Evidence for longitudinal migration in a 'sedentary' Brazilian flycatcher

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Abstract

The digitalization of museum collections and concurrent rise in citizen science initiatives is ushering in an era of unprecedented availability of primary biodiversity data. These changes permit a reappraisal of phenological patterns of tropical species. Here I explored spatio-temporal variation in the distribution patterns of an ostensibly sedentary endemic Brazilian flycatcher, the Ash-throated Casiornis (*Casiornis fuscus*), using both specimen data from museums and sighting records and rich media data from citizen science initiatives. I found compelling evidence for partial intratropical longitudinal migration to Amazonia and the Cerrado biomes from the species' core range in the semi-desert Caatinga biome and adjacent ecotones. These records from outside of the Caatinga were distributed between April and October during the height of the dry season, although the Caatinga is not entirely vacated at this time. This pattern of partial migration leads to a doubling of the species' range size and strongly suggests that the species is a breeding near-endemic of the Caatinga biome. This pattern was potentially previously occluded by significant biases in specimen collection between biomes, giving a false sense of abundance in the Brazilian Amazon.

Key words: Migratory bird, precipitation, Pará, secondary habitats, suboscine, eBird, WikiAves

Our knowledge of patterns of migratory phenology of the birds of the New World is increasing rapidly (Faaborg et al. 2010), but understanding these patterns is complicated because many South American migrants include non-migratory subspecies, populations, or individuals (Chesser 2005), and some individuals may migrate in some years, but not others (Jahn et al. 2010). Patterns of migration in the New World are not limited to Nearctic and austral migrants, but also include intratropical migrants whose movements are limited to tropical environments, often between seasonal environments such as savannahs in response to wet and dry seasons. Identifying 'partial' migration, i.e., when some birds of the same population migrate and others do not, is difficult with limited data, but partial migration is known to be a widespread phenomenon (Lack 1944, Newton 2010, Jahn et al. 2012).

Tyrant-flycatchers (Tyrannidae) accounting for about one third of austral migrants (Chesser 1994). The two species of flycatchers in the genus *Casiornis* are sister to the genus *Myiarchus* and closely-related to *Sirystes* (Chaves et al. 2008). Rufous Casiornises (*C. rufus*) are apparently resident over a substantial swathe of dry forest habitat in central and southern South America, including northern and eastern Bolivia, south-central Brazil, Paraguay, and northern Argentina, albeit with some austral migration into dry-forest and non-forest habitats in Amazonia where some may also breed (Chesser 1994, Vasconcelos et al. 2006). Ash-throated Casiornises (*C. fuscus*) are Brazilian endemics restricted to northeast Brazil in southern Amazonia from the

lower river Tapajós, south to northeast Mato Grosso in the drainage of the upper Xingu river, and east to the Atlantic coast encompassing the entire Caatinga biome and a substantial portion of the Cerrado (Scholes and Boesman 2016). The species is found in both wooded and shrubby Caatinga with equal frequency (Santos 2004), in addition to Cerrado, but their habitat preferences in Amazonia are poorly known. Ridgely and Tudor (1994) indicated that the species frequented campina enclaves in Amazonia. Unlike Rufous Casiornises, 'poorly-known' (sensu Parker et al. 1996) Ash-throated Casiornises are considered sedentary (Sick 1993, Parker et al. 1996, Ridgely and Tudor 1994, Scholes and Boesman 2016). The assumption of residency in Ash-throated Casiornises has never been tested. Considering that many other sympatric species in strongly seasonal regions of north-east Brazil are also partial or full migrants (e.g., Ruiz-Esparza et al. 2011) and considering that its sister species the Rufous Casiornis is known to be an austral migrant, then some form of migratory movement in Ash-throated Casiornis would not be unexpected.

Here, I conduct a review of the spatiotemporal distribution of Ash-throated Casiornises, stimulated by my own field experience of apparent seasonality in records in north-eastern Amazonia, making full use of primary biodiversity data from diverse sources and extensive recent field survey data.

METHODS

Data acquisition. I used the digital database VertNet (www.vertnet.org/) to search for Ash-throated Casiornis specimens, and this information was augmented with specimen data from the Museu Paraense Emílio Goeldi, Belém, Brazil (MPEG), which has the largest collection of bird specimens from northeast Amazonia and the Caatinga biomes. Searches were made for both *Casiornis fuscus* and its synonym *Casiornis fusca*. We obtained geographical coordinates of specimen collection locations from the original sources, or if unlisted from Paynter and Traylor (1991). This search of museum holdings was accompanied by a search for data on Ash-throated Casiornis 'presence only' data on the two richest sites for citizen-science bird data in Brazil: sighting records archived on eBird http://ebird.org/ and images at WikiAves (www.wikiaves.com.br). I only retained records with accurate location (to the municipality) and date information (to the day). For image-based records from WikiAves, the Exif data associated with the images was taken as verification of the date of a record. Conversely, images lacking Exif data were coded separately and considered to lack date verification. Multiple registrations from the same location from the same day were discarded (i.e. more than one individual mentioned on an eBird checklist or more than one photograph or specimen per site per day). I carefully checked photographic records from Amazonia and the Cerrado in areas of seasonal overlap with austral migrant Rufous Casiornises and discarded those where identification was either ambiguous or erroneous, i.e. where no contrast was visible in the image between the rufous head and browner back and nape. I did not include sound recordings because few were available in online databases and confusion with occasionally sympatric Rufous Casiornises was possible.

I incorporated images and sightings posted through 25 January 2016 in my analysis. A complete list of records and associated metadata is listed in Supplemental Table S1.

Sources of bias. Different data sources present different sources of bias and care needs to be taken in their interpretation. Specimen records and digital vouchers are less likely to be prone to identification error than sight records (e.g. Lees & Martin 2015) but only complete checklist data or targeted surveys can provide robust data on species absences (Munson et al. 2010). Despite the risk of misidentification with unvouchered sight records I have opted to include eBird data in the analysis in order to a) increase the sample size and b) check for spatio-temporal variation in observer effort that is not possible without complete survey data. State level filters within the eBird platform mean that extralimital records will have to be vetted by moderators and documentary material will typically be required before records are 'accepted' into the database (Sullivan et al. 2014) which provide safeguards against extralimital misidentification.

Analysis of spatio-temporal distribution. To facilitate visualization of seasonal variation in *Casiornis* distribution, I constructed distribution maps for discrete periods throughout the annual cycle and also examined continuous variation in spatio-temporal distribution by plotting longitude against the ordinal date (day number: 1-366). The main breeding season for birds in the Caatinga is December-March during the wet season (Santos 2008). Given the expectation that Ash-throated Casiornises would be nesting at this season I treated records from December-March as representing wet / breeding season records. The opposite 4 months on the calendar (June–September) were

considered the peak dry / non-breeding season. The remaining 4 months (April-May and October-November) separating these two periods were designated as the migration period, following the rationale of Lees & Martin (2015). This treatment of records resulted in three approximately equal-length seasons. I included all records of specimens, photographs and sight records within these analyses. In order to check for potential spatio-temporal bias in observer activity I also examined the distribution of all complete checklists submitted to eBird from within a minimum convex polygon encompassing the entire geographic distribution of the Ash-throated Casiornis across the corresponding three seasons.

Given that the species occupies regions with pronounced rainfall seasonality, I overlaid the records onto data on precipitation rates for that season extracted from the maps of New et al. (2002) and compared season trends with rainfall data extracted from the Brazilian National Institute of Meteorology (INMET: http://www.inmet.gov.br/portal/). I plotted mean annual rainfall data (1960-1990) from Petrolina in Pernambuco (in the central part of the Caatinga biome that experiences a pronounced dry season) against the spatio-temporal distribution of records of Ash-throated Casiornises. To calculate a broad range size estimate between seasons, I generated 100% Minimum Convex Polygons (single minimum convex hull function) around all points in QGIS Open Source Geographic Information System (QGIS Development Team, 2016). To quantify associations between the regional (Caatinga, Cerrado, and Amazonia) and seasonal (breeding, non-breeding, and wintering) distributions of Ash-throated Casiornises, I constructed a contingency table with the total records for each category and performed both a G-test and Pearson's chi-squared test to test a null hypothesis that region and

season were independent using the JMP (SAS Institute, Cary, NC) software. I compared mean latitudes and longitudes of Ash-throated Casiornises during the breeding and non-breeding periods using unpaired *t*-tests with JMP. In addition, to illustrate patterns of longitudinal displacement at a finer scale, I plotted the day number of each record against its longitude.

Field surveys and habitat preference data. To understand the habitat preferences of Ash-throated Casiornises in Amazonia, I relied on both contemporary and historic field survey data. Three recent field surveys of avian biodiversity across all *terra firme* land-cover types in the state of Pará provided data on avian habitat preferences. These included variably disturbed primary forests, secondary forests of varying ages, plantations, and arable and pastoral agriculture. Two of these studies, in Paragominas (Lees et al. 2012) and the Santarém region (Lees et al. 2013), were conducted under the auspices of the Sustainable Amazon Network (RAS, http://www.redeamazoniasustentavel.org/) and the other was conducted in the municipalities of Moju and Tailândia for a study of the impact of oil palm plantations on avian communities (Lees et al. 2014, 2015). Surveys in the municipality of Paragominas (1.9 Mha) located in northeast Pará state, 300 km southeast of Belém, were conducted between 28 July and 20 November 2010 and again between 18 and 29 May 2011. Surveys were conducted in the municipalities of Santarém-Belterra-Mojui dos Campos (hereafter Santarém) in the region between the Tapajós and Curuá-Una rivers, bordered to the north by the Amazon River, from 16 October 2010 to 8 February 2011. Surveys in the municipalities of Moju and Tailândia along the east bank of the Rio Tocantins ~90 km south-southwest of Belém were conducted from 11 September to 1

October 2013. During these surveys, 196 transects were surveyed in Paragominas, 165 in Santarem, and 50 in Moju-Tailandia (Supplemental Table S2). For all surveys, two repetitions of three fixed-width (75 m) 15-min point counts were carried out in each 300-m transect sited at 150-m intervals. All birds seen or heard during these surveys were recorded, repetitions ensured that temporal variation in avian vocal activity was minimized. Point Counts were sound-recorded using solid state recorders to facilitate error checking. For further detail about methods, see Lees et al. (2012, 2013, 2015).

The Parker et al. (1996) databases attributes only one habitat choice 'tropical dry forest' for the Ash-throated Casiornis, a habitat which is unavailable to the species in Amazonia. Historic specimens often have poor location data that limit inferences about habitat preferences (Remsen 1995), but, by comparing the 'companion fauna' collected on the same date from the same collecting locality, some insight into habitat affinities might be gained. Given the lack of data on habitat preferences for Ash-throated Casiornises in Amazonia I obtained data from VertNet and the MPEG catalogue by searching for all species collected on the same day and locality as specimens of Ash-throated Casiornises within the biome. I then used the species composition to make inferences about the habitat where specimens were collected (considering only samples that included at least 10 specimens collected for the day and location in question). I used the Parker et al. (1996) databases to attribute habitat preferences for each species and calculated the percentage of species not associated with 'tropical lowland evergreen forest' (the dominant vegetative physiognomy in Amazonia) for each collecting locality and looked at the total incidence of each habitat type. Only one individual per species per day was used to calculate percentage habitat occupancy if

multiple individuals per species were collected. It is quite possible that a bird collector might visit multiple habitat types within the course of a single day's collecting effort but any co-collected species not occurring in 'tropical lowland evergreen forest' is indicative that any Ash-throated Casiornes may have been frequenting habitats other than 'tropical lowland evergreen forest'.

RESULTS

Seasonal distribution of the Ash-throated Casiornis. My systematic search recovered 102 specimen records, including 49 retrieved from VertNet from seven North American institutions and 53 from the collection of the MPEG (collected from 1884 to 2013). To these were added 69 observational records from eBird (observed from 1995-2015) and 251 images archived on WikiAves (taken from 2003 to 2016). Once duplicate images and specimens from the same site and same day were removed, I was left with 417 independent data points for analysis. There were some spatial biases in the distribution of information by source for the different biomes with a more uniform distribution of specimen records between the three principle biomes (Caatinga = 37, Cerrado = 36, and Amazonia = 25; Fig. 1a) than for images archived on WikiAves (Caatinga = 170, Cerrado = 57, and Amazonia = 9) or eBird (Caatinga = 35, Cerrado = 23, and Amazonia = 5), indicating both better contemporary sampling of the arid region of northeast Brazil (Figs. 1b, 2, (Supplemental Fig. 1) and intense historical collecting effort in eastern Amazonia. In addition to records from the three biomes, there were also 30 from transitional Atlantic Forest-Caatinga (Fig. 2), but the species never seems to penetrate far into this well-sampled biome, and these records may relate to birds in Caatinga-like vegetation in the Atlantic Forest biome.

Examination of records revealed a consistent pattern of seasonality in the spatial distribution in eastern Brazil. From December to March records were clustered around the Caatinga biome, with a few outlying individuals in adjacent areas of the Cerrado in transitional habitats (Figs. 2 and 3) and no birds recorded further west than 45ºW. Between June and September, the records show a westward expansion into much of the northern Cerrado biome south to 16ºS and west to include a huge swath of eastern Amazonia as far as 56ºW. Many individuals remain within the Caatinga during this season (Fig. 3) indicating that not all members of the population undertake dispersive movements. There was a significant westward expansion in the area occupied by the species during the non-breeding season (wintering and migration season - mean latitude = 6.80ºS, SD = 3.55º, mean longitude = 43.45ºW, SD = 4.81º n = 163) compared to the breeding season (mean latitude = 7.91ºS, SD = 3.1º, mean longitude = 40.02ºW, SD = 1.77º n = 131). This difference in mean longitude was significant ($t_{288.24}$ = 2.8, $P < 0.0001$), but the difference in latitude was not ($t_{37.85}$ = -8.1, $P = 0.99$). This represents an annual doubling in the area occupied by the species from a breeding season extent of 1,133,000 km^2 to a wintering distribution of 2,295,000 km^2 as defined by 100% minimum convex polygons. This westward movement occurs during the dry season in southern Amazonia and the driest and hottest time of the year in the Caatinga (Figs. 2 and 3). Considering only complete checklists (n = 5336) from eBird there was no evidence for significant spatial or temporal biases with checklists submitted evenly across the region between seasons (Supplemental Fig. 1). There were insufficient complete checklists recording Ash-throated Casiornes (n = 57) to test for any seasonal redistribution within the Caatinga biome. There was no evidence for a strong temporal

bias in specimen data either; the total number of specimens of all bird collected in the state of Pará and deposited in MPEG did not vary greatly between the three time periods (breeding $N = 8273$, wintering $N = 9447$, migration $N = 8764$).

The null hypothesis that seasonal records were independent of the regions where they were recorded was rejected ($\chi^2_1 = 112.8$, $P < 0.001$; $G = 5.9$, $P = 0.01$, $N = 410$). This supports the hypothesis of spatiotemporal variation in the presence of Ash-throated Casiornises in different biomes. Sample size of birds of known sex were small ($N = 53$), but I found the sex ratios of birds collected in the three principle biomes were similar (Caatinga: M = 12, F = 4; Cerrado: M = 12, F = 4; and Amazonia: M = 15, F = 7).

Field surveys and habitat associations. Ash-throated Casiornises were recorded on five occasions in Paragominas during surveys between 13 August and 10 October (e.g. Supplemental Fig. 2). Four detections were in young (>20 years old) secondary forest transects and one in a heavily logged primary-forest transect (Supplemental Table S2). There were no sightings during fieldwork in Santarém, and none during quantitative work in Moju-Tailândia, although one bird was seen and photographed (Supplemental Fig. 3) there at the edge of a natural campina formation on 14 September 2013.

Eight specimens of Ash-throated Casiornis from eastern Amazonia were collected with at least 10 other individual birds on the same day ($N = 8$ companion faunas, 119 individuals, 111 species, Supplemental Table S3). These companion faunas were typically species not associated with Amazonian *terra firme* primary forest habitats (Parker *et al.* class ‘tropical lowland evergreen forest’) which are the dominant land-cover in the biome (mean = 36.18%, SD = 21.58, range = $N = 8$). Most of the birds

co-collected with Ash-throated Casiornses in Amazonia were habitat generalists (*N* =119, mean number of habitat frequented = 3.11, SD = 1.33, Supplemental Table S3). The commonest habitat association across the 119 individuals was 'secondary forest' (*N* = 57), followed by 'tropical lowland evergreen forest' (*N* = 41), 'gallery forest' (*N* = 38) and 'river edge forest' (*N* = 33). Of the habitat specialists, thirteen species were restricted to 'tropical lowland evergreen forest, three species were found only in 'flooded tropical evergreen forest' - Silvered Antbird (*Sclateria naevia*), Amazonian Black-tyrant (*Knipolegus poecilocercus*), and Yellow-crowned Elaenia (*Myiopagis flavivertex*), and one to 'palm forest' - Sulphury Flycatcher (*Tyrannopsis sulphurea)* (Supplemental Table S3).

DISCUSSION

My results suggest that the assumption of residency of Ash-throated Casiornises in the ornithological literature (e.g., Sick 1993, Ridgely and Tudor 1994, Parker et al. 1996, Scholes and Boesman 2016) is not supported by a spatiotemporal analysis of records. Pending more detailed fieldwork across the species range, I provisionally consider Ash-throated Casiornises to be partial longitudinal migrants within the tropics, that may likely prove to be a breeding endemic of the Caatinga biome (and adjoining areas of transitional Cerrado-Caatinga vegetation). I found no evidence for the occurrence of this species in Amazonia outside of the period from April to October, suggesting that Ash-throated Casiornises are only seasonal visitors to this biome, whereas at least some individuals are present year-round in the Caatinga. Given extensive historical and contemporaneous sampling of both Amazonia and the Cerrado (e.g., Lees and Martin 2015, Supplemental Fig 1.), I do not believe these results reflect

differences in observer effort. This hypothesis is further reinforced by the well-documented presence of Rufous Casiornises in savannah enclaves in Amazonia during the period from December to March (e.g., four specimens in the MPEG: #4724 and #54405, #54406 and #54407 from Monte Alegre, Pará state, collected in February 1909 and January 1999) when Ash-throated Casiornises appears to be absent and which suggests that temporal sampling biases are not responsible for the absence of the latter species at this time.

Many Ash-throated Casiornises remain in the Caatinga biome during the driest period of the year (June-September, Fig. 3) although detailed autecological studies would be necessary to uncover any within-biome movements. Migration to Amazonia during the southern hemisphere winter is a life history strategy used by at least 24 species of austral migrants which breed mainly outside of Amazonia and winter extensively within it (Chesser 1994). Some species of austral migrants migrate to the Caatinga biome from breeding areas in the Southern Cone of South America (e.g., Ruiz-Esparza et al. 2011) principally during the austral winter between March and July. However, I am aware of only one bird species, Lined Seedeaters (*Sporophila lineola*), that breeds in this biome and largely migrates out of it during the austral winter. Silva (1995) demonstrated that one population of Lined Seedeater migrates northwest from their breeding range in the Caatinga to their non-breeding range on the Guiana Shield (Silva 1995).

Both austral and Neotropical-Nearctic migrants are often restricted to edge, river island, and non-forest habitats in the Neotropics (e.g., Karr 1976, Chesser 1997). This pattern was formerly attributed to competitive exclusion by resident species in ‘primary’

rainforest habitats (e.g., Willis 1966, Keast 1980). However, such behavior may also reflect species' evolutionary histories and thus be a cause rather than a consequence of their migratory behavior (Levey and Stiles 1992). As such, it should not come as a surprise that Ash-throated Casiornises may avoid primary rainforest in Amazonia. The vegetative structure of open habitat enclaves, scrubby varzea, or the increasingly dominant young secondary forests and abandoned pastures mirrors that of their inferred breeding grounds in the Caatinga, a habitat structure to which they may be better adapted to forage in. That Ash-throated Casiornes were recorded in 20% of young secondary forests in Paragominas (Supplemental Table 2) and was the most common habitat associated with their 'companion fauna' in Amazonia suggests that these successional habitats may be an important wintering area for the species.

The formulation of this hypothesis for partial migration in Ash-throated Casiornis was grounded in historic specimen records and contemporary sighting data and digital vouchers. It seems possible that a strong historic bias in collecting activity in Eastern Amazonia and a lack of fieldwork in the Caatinga biome contributed to the notion that eastern Amazonia forms part of the core range of this species. This would have hampered the discovery of seasonality in the species, in conjunction with the pervasive notion of residency in tropical birds. Ornithologists should continue to critically re-examine spatiotemporal patterns in the distribution of tropical birds and expect to find more evidence for partial migration in ostensibly 'sedentary' species, which may substantially alter perception of their conservation status. Care should be taken to check for any discrepancy between the spatio-temporal distribution of vouchered and un-

vouchered records, particularly in the case of cryptically-similar species (Lees and Martin 2015).

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Figure Legends

Figure 1. Distribution of records of museum specimens a) and observational records (eBird and WikiAves) b) of Ash-throated Casiornis by time period between biomes.

Figure 2. Variation in longitudinal position (y-axis) of Ash-throated Casiornis records during the annual cycle (x-axis) and mean annual precipitation rates (z-axis) at Petrolina. Triangles represent specimen records, circles are sight records on eBird, and squares are images on WikiAves. Green/dark gray denotes records from Amazonia, orange/mid gray from the Cerrado, black from the Atlantic Forest, and yellow/light gray from the Caatinga.

Figure 3. Spatio-temporal variation in the distribution of records of Ash-throated Casiornis between the breeding, wintering and migration seasons overlain on a map of Brazilian biomes and mean precipitation rate (mm) data for the months of February (breeding), August (non-breeding) and November (migration).

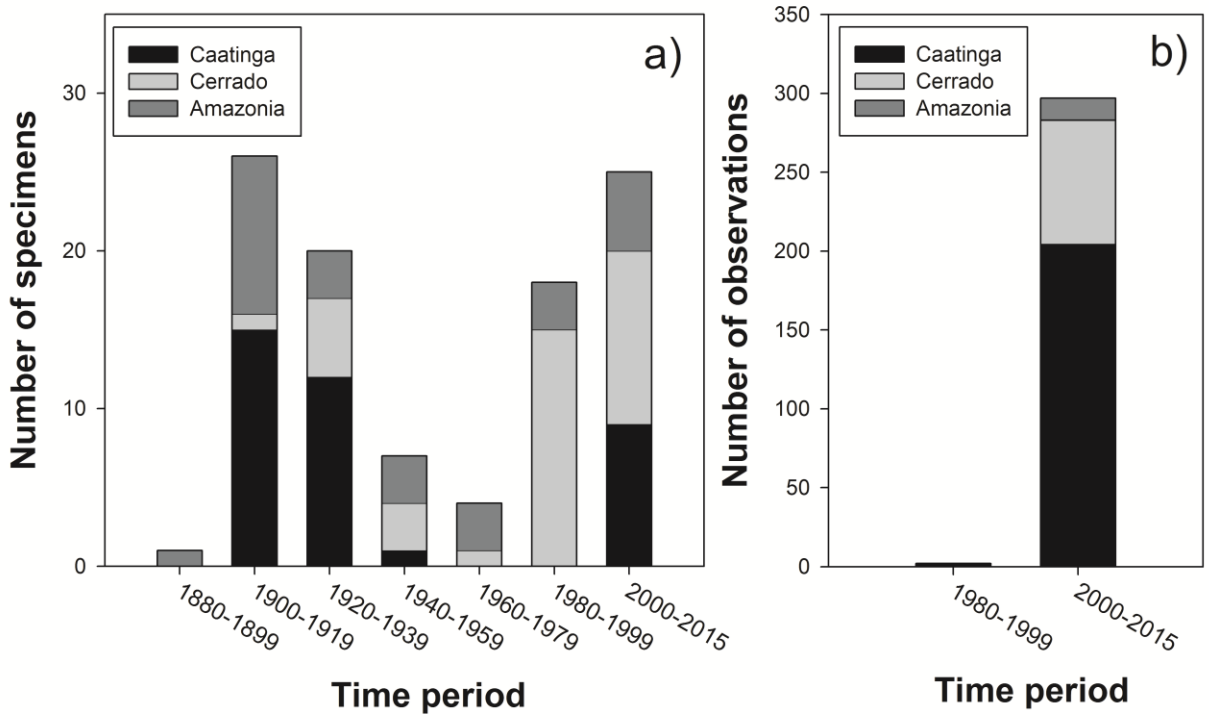

Figure 1.

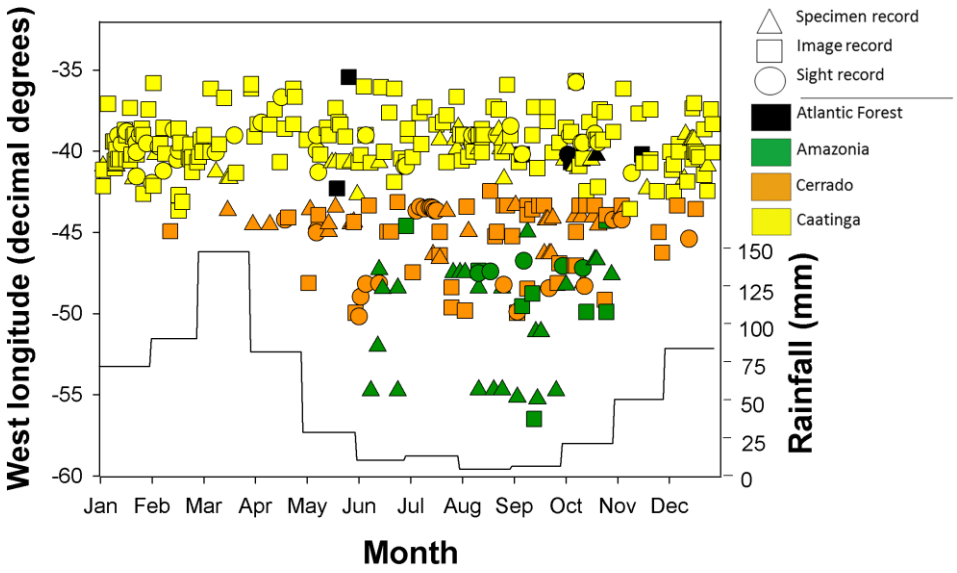

Figure 2.

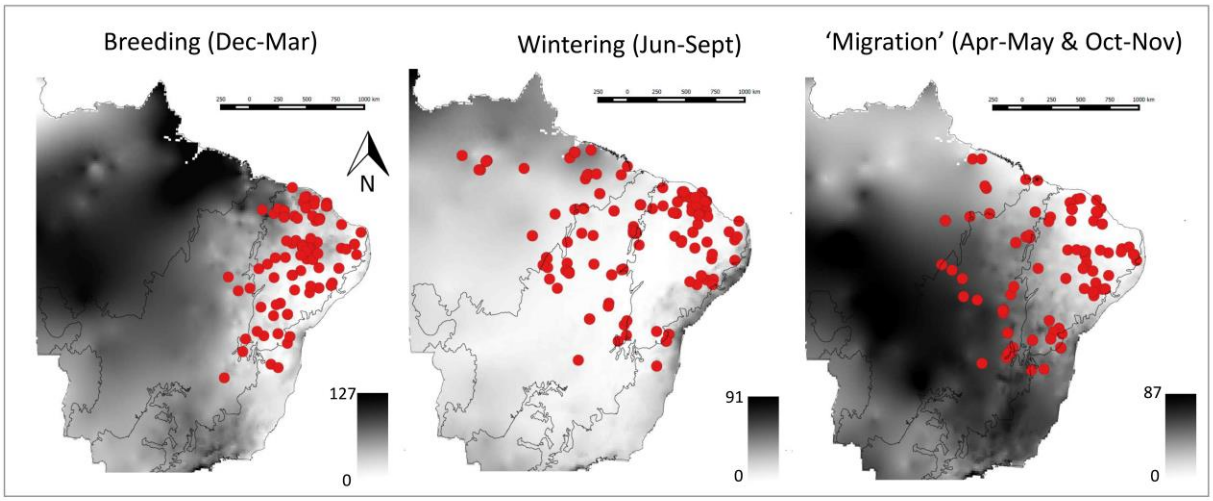

Figure 3.