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Research Article

Avian distribution and life-history strategies in Amazonian terra-firme and floodplain forests

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Abstract
The diversity of avian populations in the Madre de Dios region of Peru is currently threatened by deforestation and other anthropogenic factors. In this study we assessed differences in bird species composition in two major types of tropical forests: floodplain and terra-firme forest. Abundance of groups of behaviourally similar species showed a higher presence of certain feeding guilds in either floodplain forests or terra-firme forest, whereas no difference in species richness was found. Analysis of the relative reproductive investment (RRI) of these tropical birds showed significant differences between habitats and among families and feeding guilds. Comparison of these families and feeding guilds to their relatives in temperate regions showed that neotropical birds have a smaller RRI, due to both smaller clutch sizes and lower egg mass, even when there are more broods per season. Quantification of RRI as used in this study can be useful to indicate bird species’ susceptibility to anthropogenic factors in various habitats.

Keywords: tropical birds, Neotropical forest, avian distribution, relative reproductive investment, conservation
Introduction

Deforestation and many other anthropogenic factors currently threaten tropical rainforests, the richest terrestrial ecosystem on the planet [1,2]. Human activities affect the ecological integrity of the forest by changing carbon storage, river flow, water balance, and even the amelioration of infectious diseases [2-4]. Tropical rainforests consist of various habitats, including terra-firme forest and floodplain forest, which are affected differently by anthropogenic factors [5-7]. Different land access and use of oligotrophic terra-firme forest has resulted in dissimilar trophic cascades and human activities compared to eutrophic floodplain forests. As rainforests are one of the most biodiverse habitats on the planet, many different species are affected by these anthropogenic factors [2]. Among these are around four thousand species of birds that play important roles in the various habitats as top predators, pollinators, and seed dispersers [8]. Species composition of avian populations is likely to differ between terra-firme forest and floodplain forest, and despite studies in both terra-firme forest and floodplain forest, the differences in avian populations between these habitats are still poorly understood. This novel research assesses some of these differences [9-12].

The terra-firme forest is rainforest that is not inundated or flooded by rivers and is characteristic of upland forests. These forests are noticeably taller and more diverse (>400 tree species/hectare in some areas) than floodplain forest. They are found only on dry, well-drained soils and are characterized by many tropical hardwood trees [13]. Moreover, the tall Amazonian terra-firme forests enhance a larger vertical stratification within the bird community, where species of the different layers are more likely to forage in their respective storeys and thus in narrower strata [14].

Floodplain forests, on the other hand, are flooded seasonally and have relatively rich soils from the annual replenishment of nutrients from white-water rivers. In the Amazon, vast areas of such rainforests can be found. Floodplain forests, especially those located on river banks and islands, are often short-lived due to the meandering nature of tropical lowland
rivers, which eat away at the forests' base. Tropical floodplain forests are one of the most productive ecosystems and harbour a great diversity of (tree)species, if lower on average than terra-firme forest. Although aboveground woody biomass is consistently lower than terra-firme forests, biomass accumulation is high due to deposition of nutrient-rich sediments [15]. These diverse abiotic conditions might enhance a diverse avian species composition in floodplain forests. Both terra-firme and floodplain forests are rapidly disappearing due to deforestation for development of agricultural lands, gold mining, and cattle ranching [2].

Avian diversity is likely to differ between these habitats as the incidence of flowering and fruiting is much lower in terra-firme forests than in other neotropical forest habitats, possibly influencing the abundance of specific species(guilds) like frugivores and nectarivores [16]. Other species might flourish in terra-firme forest, such as mixed-species flock insectivores, especially leaf-gleaning insectivores that congregate in food-rich areas [17].

Bird species that prefer specific habitats might be severely affected by increasing deforestation. Analysis of life-history traits could identify species that are more susceptible to these anthropogenic factors. To compare the reproductive investment of species in various guilds in the two forest types, we used the Relative Reproductive Investment (RRI) [18]. The latter value, which uses clutch size, egg mass, and the number of clutches per season in relation to female body mass, gives an indication of annual reproductive effort. This effort is a good proxy for adult mortality levels, which are hard to obtain in these kind of biotopes. Adult mortality determines a species’ vulnerability to human impact, because when adult mortality is low (and thus also the RRI is low), additional mortality due to human impact can have more severe consequences to population levels compared to species with high reproductive effort (and usually already higher adult mortality).

In this paper, we address the following questions; (a) What is the difference in avian diversity among terra-firme forests and floodplain forests, and what are the possible causes? (b) What difference in life-history-trait, especially the RRI, exists between species in terra-firme forest and floodplain forest? (c) How do these differences in life-history traits relate to birds in temperate regions, in order to present a bigger reference for these RRI values?

**Methods**

**Study area**
This study was conducted within the Madre de Dios region of Peru at 18 sites of similar size: Fauna Forever House (AFF-House), Amazon Rainforest Conservation Center (ARCC), Rio Azul Ranger Station (AZUL), El Gato Homestay (BAL), Bozovitch Concession (BOZ), Chuncho Clay Lick (CHUN), Los Amigos Research Center (CICRA), Explorer’s Inn (EI), Limon Concession (LIMON), Malinowski Ranger Station (MALI), Campamento Pampa (PAMPA), Las Piedras Biodiversity Station (PIE), Reserva Amazonica Lodge (RA), Saona Lodge (SAONA), Sachavacayoc Centre (SC), Tambopata Ecolodge (TPL), Tambopata Research Center (TRC) and Wasai Lodge (WASAI). All of the sites are rainforest areas in the Amazon Basin, and six of them are located within the protected area complex of the Tambopata National Reserve and Bahuaja Sonene National Park (Fig. 1).
Fig. 1: Map of sampling sites in the Madre de Dios region, Peru. All of the sites are within the Amazon Basin and six are within the protected area complex of the Tambopata National Reserve and Bahuaja Sonene National Park.

Distribution of avian populations using mist-netting
Eighteen sites with either floodplain or terra-firme forest were studied (Appendix 1), six of which are located within the protected area complex of the Tambopata National Reserve and Bahuaja Sonene National Park. Each site sampled with mist-nets covers a representative area of about 2,500 ha.

Birds were sampled by using mist-nets, which was justified as it allows similar and simultaneous sampling of various sites. Three mist-nets (each 12 m long, 3.5 m high, 5 shelves, and mesh size 36 mm) were placed consecutively (in a straight line) to provide a total net length of 36 m per sample point. At each site, sample points were located 50-300 m (mean 200 m) apart, for a total of 3-42 points per site. Sampling was spread over a five-year period (2009-2014), with 3-73 sample days per site. Intervals when no data was collected varied among sample periods at sites, and some sites were only sampled once during the aforementioned five-year period. During a mist-net operation at a site, nets were opened at three sample points simultaneously for the first few hours after dawn for three days. Netting-days were not always consecutive, due to weather conditions (sampling did not occur on rainy or very windy days). Open mist-nets were checked at least every half hour, and all captured birds, with the exception of hummingbirds, were banded with a numbered ring. After banding, female birds (based on plumage, cloacal protuberance and brood patch) were weighed. New captures and recaptures were recorded, although recaptures on the same day were released immediately.

Mist-nets focus on understory birds, but do not sample birds randomly [19-22]. As the effectiveness of mist-nets differs among different species, in this study only the capture rates of groups of behaviourally similar species were compared [19-21]. Therefore birds were
divided into guilds based on previous ecological classification [14,16,21,23]. Guilds included army ant followers (AA), solitary insectivores (I), solitary insectivore-frugivores (IF), mixed-species insectivore flocks (MFI), solitary frugivores (F), solitary frugivore-insectivores (FI), mixed-species insectivore-frugivore flocks (MFIF), and small vertebrates and large insects (SVLI) (Appendix 2 & 3).

Analysis
Capture rates were used as an index of abundance and presented as captures/1,000 net-hours, where a net-hour refers to 12 m of net open for one hour. Recaptures of birds during the same day were excluded. Species richness of the different habitats was determined with the program EstimateS (http://viceroy.eeb.uconn.edu/estimates/), using the classic formula for Chao 1 & Chao 2. Non-parametric richness and diversity estimators (MM Means, Jackknife, Chao, Bootstrap, ICE, Shannon and Simpson) were also assessed with EstimateS. Species richness estimators based on incidence data were Chao 2 and ICE, where the latter calculated the proportion of ‘infrequent’ species that were not ‘unique’. Jackknife 1 and 2 used both incidence and abundance data: Jackknife 2 used both ‘uniques’ and ‘duplicates’ and Jackknife 1 only ‘uniques’, but in combination with observed amount of species either corrected for repeated samples in incidence data. Chao 2 only used different factors for repeated sampling compared to Jackknife 2. Chao 1 and Bootstrap used abundance data again with ‘uniques’ and ‘duplicates’, but the Bootstrap estimator is based on the frequency distribution of the species found [24]. Diversity of species was assessed through the Shannon [25] and Simpson index [26].

Chi-square test of independence was performed to determine habitat specialists in terra-firme and floodplain forest. For analysis of capture rates between terra-firme forest and floodplain forest, which occurred per feeding guild, independent t-tests were conducted in SPSS (Version 16.0).

To get a comprehensive and comparable measure of reproductive investment, life-history traits like clutch size ($\bar{c}$), number of clutches per season ($N_c$) and egg mass ($m_{\text{egg}}$), divided by the female body mass ($m_{\text{female}}$) were used to assess the Relative Reproductive Investment (RRI) according to the following formula: $\text{RRI} = (\bar{c} \times N_c \times m_{\text{egg}}) / m_{\text{female}}$ [18]. Values were assessed for every individual species, to compare differences among habitats, between feeding guilds and phylogenetically related groups. For comparison with outlier values, data of life-history traits of West-European birds were included among phylogenetically related groups and among feeding guilds as well. Mann-Whitney U tests and Independent t-tests (SPSS, Version 16.0) were conducted to assess significant differences in life-history traits between related groups.

Results
Avian diversity in terra-firme and floodplain forests
After a total of 11,205 mist-net hours, 188 and 118 bird species were found in floodplain and terra-firme forests respectively. The species accumulation curves for the floodplain forest and terra-firme forest are presented in Figure 2. The x-axis is scaled by the number of accumulated samples and compares species density between the forest types. The species accumulation curves for the two habitats did not approach an asymptote, but the rate of accumulation of species with increasing sample numbers is decreasing (Fig. 2).
The floodplain forest has fewer species at comparable levels of sample accumulation. The number of species at 64 pooled samples (the maximum sample size of terra-firme forest) was 118 and 109.4 species for terra-firme forests and floodplain forest respectively. Accordingly, the observed species accumulation curve of the floodplain forest was within the 95% confidence intervals of the corresponding species accumulation curve of terra-firme forest, indicating no significant difference in species richness between floodplain forest and terra-firme forest.

![Fig. 2: Species accumulation curves.](image)
Grey line represents species richness in terra firme forest, black line in floodplain forest. Continuous lines surrounded by dashed lines represent cumulative number of species and confidence intervals of the respective habitats.

More samples were taken from floodplain forests, with more observed species than in terra-firme forest (Table 1). Non-parametric species richness estimators for incidence and abundance data estimated the species richness of the two habitats (Table 1). The differences between the highest and lowest species estimators were 71.47 for floodplain forest (n=353), 47.11 for floodplain forest (n=64) and 42.29 for terra-firme forest.

A total of 90 unique bird species were present in floodplain forest, and 20 unique species in terra-firme forest; 98 species were present in both habitats. Of course, a higher species richness in floodplain forest was found due to the greater number of samples; at the maximum sample size of terra-firme forest (n=64), species richness of almost all estimators, except for Chao 2, were higher in terra-firme forest. Diversity estimators were higher in terra-firme forest at all sample sizes (Table 1).

Estimation of preference of various bird species for specific habitats occurred by comparing abundance data in floodplain and terra-firme forests. Habitat associations were detected in 60 species (Appendix 4), chi-square tests showed that 30 species preferred floodplain forest and 30 terra-firme forest.

Preferences of certain feeding guilds for floodplain forest and terra-firme forest were estimated: solitary frugivore-insectivores (FP=3; TF=0) and mixed species flock insectivores (FP=7; TF=3) had more habitat specialists present in floodplain forest. Habitat specialists of solitary insectivores (FP=4; TF=17) preferred terra-firme forest.
Table 1: Species richness estimators. Number of samples and individuals, species observed and species richness (MM means, Chao 1, Chao 2, Jackknife 1, Jackknife 2, Bootstrap and ICE) and diversity (Shannon and Simpson) estimate values for floodplain and terra-firme forests.

<table>
<thead>
<tr>
<th></th>
<th>Floodplain Forest</th>
<th>Terra Firme Forest</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>No. of samples</strong></td>
<td>353</td>
<td>64</td>
</tr>
<tr>
<td><strong>No. of Individuals</strong></td>
<td>3,285</td>
<td>711.3±0.29</td>
</tr>
<tr>
<td><strong>S_{obs}</strong></td>
<td>188</td>
<td>79.4±1.28</td>
</tr>
<tr>
<td><strong>Unique species</strong></td>
<td>90</td>
<td>19.9±0.03</td>
</tr>
</tbody>
</table>

**Richness**

<table>
<thead>
<tr>
<th></th>
<th>MM Means</th>
<th>Chao 1</th>
<th>Chao 2</th>
<th>Jackknife 1</th>
<th>Jackknife 2</th>
<th>Bootstrap</th>
<th>ICE</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Floodplain Forest</strong></td>
<td>192.3</td>
<td>224.74±14.88</td>
<td>242.41±20.75</td>
<td>236.86±7.88</td>
<td>263.77</td>
<td>210.07</td>
<td>231.46</td>
</tr>
<tr>
<td><strong>Terra Firme Forest</strong></td>
<td>144.68</td>
<td>147.68±16.86</td>
<td>160.74±21.04</td>
<td>151.91±8.10</td>
<td>175.53±15.33</td>
<td>128.42±7.51</td>
<td>156.51</td>
</tr>
</tbody>
</table>

**Diversity**

<table>
<thead>
<tr>
<th></th>
<th>Shannon Index</th>
<th>Simpson Index</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Floodplain Forest</strong></td>
<td>4.16</td>
<td>26.79</td>
</tr>
<tr>
<td><strong>Terra Firme Forest</strong></td>
<td>3.98±0.08</td>
<td>25.82±3.5</td>
</tr>
</tbody>
</table>

Fig. 3: Abundance per sampling effort of various feeding guilds compared between floodplain (FP) and terra-firme forest (TF). See Table 2 for abbreviations of feeding guilds. Fault bars indicate Standard Error, **= P<0.01.
Abundances for the various feeding guilds per 1,000 mist-net hours (Fig. 3) showed significant differences among certain guilds. Significantly more present in floodplain forests were frugivores (Independent t-test, \( P=0.005 \)) and insectivore-frugivores (Independent t-test, \( P=0.002 \)), and a trend was shown by army-ant followers (Independent t-test, \( P=0.053 \)). An opposite trend was found with insectivores (Independent t-test, \( P=0.072 \)), which were more abundant in terra-firme forests.

**Life-history traits of tropical bird populations**

Average values of the specific life-history traits used to calculate the relative reproductive investment (RRI) have been estimated for the species in various families and feeding guilds (Table 2; Appendix 5 & 6).

<table>
<thead>
<tr>
<th>Table 2: Average value (with standard error) for specific life-history traits of tropical birds, in various feeding guilds, used in the calculation of the relative reproductive investment.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Feeding guilds based on classification in Henriques et al. [16]. AA = army ant followers, F = solitary frugivores, FI = solitary frugivore-insectivores, I = solitary insectivores, IF = solitary insectivore-frugivores, MFI = mixed species insectivore-frugivore flocks, MFIF = mixed species insectivore-frugivore flocks, N = nectarivores, SVLI = small vertebrates and large insects.</td>
</tr>
<tr>
<td></td>
</tr>
<tr>
<td>---</td>
</tr>
<tr>
<td>AA</td>
</tr>
<tr>
<td>F</td>
</tr>
<tr>
<td>FI</td>
</tr>
<tr>
<td>I</td>
</tr>
<tr>
<td>IF</td>
</tr>
<tr>
<td>MFI</td>
</tr>
<tr>
<td>MFIF</td>
</tr>
<tr>
<td>N</td>
</tr>
<tr>
<td>SVLI</td>
</tr>
</tbody>
</table>

Birds of different feeding guilds in the tropics all had similar clutch sizes and number of broods per season, so the difference in RRI was the result of egg and female body mass. For nectarivores, mostly hummingbirds, egg mass and female body mass were small. For frugivores these values were higher than in insectivores, resulting in an average lower RRI for frugivores than for insectivores (Table 2 & 3).

Estimation of the relative reproductive investment (RRI) has been calculated based on several life-history traits (Appendix 2 & 3). RRI was calculated per individual species and was combined per family and per feeding guild (Appendix 5 & 6). In the tropical regions, there was a broad range of RRI-values (0.253-0.814) among families with significant differences (Kruskal-Wallis: \( P=0.001 \)). Among feeding guilds a trend was present (Kruskal-Wallis: \( P=0.079 \)). In temperate regions significant differences were found in RRI-values both among families (Kruskal-Wallis: \( P<0.001 \)) and feeding guilds (Kruskal-Wallis: \( P<0.001 \)) (Appendix 5 & 6).

RRI among bird species with a preference for floodplain forest or terra-firme forest within feeding guilds was compared (Table 3). Only frugivores showed a significant higher RRI in floodplain forest compared to similar species in terra-firme forest (\( P=0.016 \); independent t-test) (Table 3). For comparison of life-history traits and RRI between the tropical and temperate region, families and feeding guilds present in both regions were compared (Table 4).
Table 3: Comparison of RRI from habitat specialists within feeding guilds. Average values (with Standard Error) and P-values for independent t-test and Mann Whitney U test are shown. See Table 2 for abbreviations of feeding guilds.

<table>
<thead>
<tr>
<th></th>
<th>Floodplain forest</th>
<th>Terra firme forest</th>
<th>T-test</th>
<th>Mann-Whitney U-test</th>
</tr>
</thead>
<tbody>
<tr>
<td>F</td>
<td>0.724(0.074)</td>
<td>0.345(0.079)</td>
<td>P=0.016</td>
<td></td>
</tr>
<tr>
<td>FI</td>
<td>0.614(0.029)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>I</td>
<td>0.642(0.085)</td>
<td>0.633(0.044)</td>
<td>P=0.922</td>
<td></td>
</tr>
<tr>
<td>IF</td>
<td>0.457(0.015)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>MFI</td>
<td>0.556(0.100)</td>
<td>0.401</td>
<td>P=0.667</td>
<td></td>
</tr>
<tr>
<td>N</td>
<td>0.578(0.132)</td>
<td>0.509</td>
<td>P=1.000</td>
<td></td>
</tr>
<tr>
<td>SVLI</td>
<td>0.572(0.025)</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Table 4: Comparison of relative reproductive investment between similar families and feeding guilds in the tropical and temperate regions. Average value (with Standard Error) is shown. Mann-Whitney U test and Independent T-test show significance of difference between these regions. See Table 2 for abbreviations of feeding guilds.

<table>
<thead>
<tr>
<th>Family</th>
<th>Tropical</th>
<th>Temperate</th>
<th>T-test</th>
<th>Mann-Whitney U-test</th>
</tr>
</thead>
<tbody>
<tr>
<td>Alcedinidae</td>
<td>0.572(0.025)</td>
<td>1.435</td>
<td>P=1.000</td>
<td></td>
</tr>
<tr>
<td>Columbidae</td>
<td>0.297(0.062)</td>
<td>0.290(0.096)</td>
<td>P=0.950</td>
<td></td>
</tr>
<tr>
<td>Cuculidae</td>
<td>0.814</td>
<td>0.279</td>
<td>P=1.000</td>
<td></td>
</tr>
<tr>
<td>Emberizidae</td>
<td>0.666(0.071)</td>
<td>0.991(0.077)</td>
<td>P=0.017</td>
<td></td>
</tr>
<tr>
<td>Falconidae</td>
<td>0.304(0.037)</td>
<td>0.373</td>
<td>P=1.000</td>
<td></td>
</tr>
<tr>
<td>Picidae</td>
<td>0.270</td>
<td>0.407(0.073)</td>
<td>P=0.508</td>
<td></td>
</tr>
<tr>
<td>Troglodytidae</td>
<td>1.099(0.074)</td>
<td>2.030</td>
<td>P=1.000</td>
<td></td>
</tr>
<tr>
<td>Turdidae</td>
<td>0.585(0.059)</td>
<td>0.978(0.123)</td>
<td>P=0.012</td>
<td></td>
</tr>
<tr>
<td>Feeding guild</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>F</td>
<td>0.587(0.055)</td>
<td>0.491(0.103)</td>
<td>P=0.399</td>
<td></td>
</tr>
<tr>
<td>I</td>
<td>0.628(0.034)</td>
<td>0.810(0.070)</td>
<td>P=0.024</td>
<td></td>
</tr>
<tr>
<td>IF</td>
<td>0.550(0.061)</td>
<td>0.770(0.069)</td>
<td>P=0.023</td>
<td></td>
</tr>
<tr>
<td>MFI</td>
<td>0.675(0.099)</td>
<td>1.317(0.318)</td>
<td>P=0.051</td>
<td></td>
</tr>
<tr>
<td>MFIF</td>
<td>0.270</td>
<td>1.213(0.327)</td>
<td>P=0.305</td>
<td></td>
</tr>
<tr>
<td>SVLI</td>
<td>0.376(0.064)</td>
<td>0.412(0.041)</td>
<td>P=0.649</td>
<td></td>
</tr>
</tbody>
</table>

Life-history data in the tropical regions and in the temperate regions could be found only for the families presented in Table 4. For Emberizidae and Turdidae, a significant (P<0.05; independent t-test) difference between species in the tropics and temperate regions was found. In both families, species in the temperate regions have a higher RRI than related species in the tropics (Table 4).

Comparison of feeding guilds resulted in a significant difference between temperate and tropical regions for all insectivore-guilds: the RRI-value was higher in the temperate regions for insectivores, insectivore-frugivores, and mixed species flock insectivores. Other feeding guilds did not show a significant different RRI-value between these regions (Table 4). Army ant followers and nectarivores were not present in temperate regions.
The basic life-history traits in the significantly different RRIs for families and feeding guilds showed that in all situations temperate clutches were larger and number of clutches hardly differed in Emberizidae and Turdidae, but was lower in temperate insectivores and insectivore-frugivores and higher in mixed species flock insectivores. Egg mass was lower in the tropics in all insectivorous feeding guilds and Emberizidae, but not in Turdidae where female body masses were much higher (Table 5).

**Discussion**

The variation in distribution of all tropical bird species in the Madre de Dios region might be due to specific abiotic factors within the floodplain and terra-firme forest. Although no significant difference was found in species richness and diversity, a trend suggested that these estimators were higher in terra-firme forest. This is in line with the idea that there is more stratification in terra-firme forest, as trees are taller, and more diversity and density of trees create more available niches for various bird species [13]. On the other hand, for most feeding guilds numbers are higher in the floodplain forest, so productivity may be higher there than in terra-firme forest (Fig. 3). Habitat associations were found for a large number of species that preferred either floodplain or Terra-firme forest. Frugivore-insectivores and mixed species flock insectivores had more habitat specialists in floodplain forest, whereas insectivores had more in terra-firme forest. Comparison of total avian populations where division was based on feeding guilds showed a higher abundance of frugivores and insectivore-frugivores in floodplain forests, possibly because there is more flowering and fruiting of plants in floodplain forests [17], although for nectarivores no difference was found. Solitary insectivores, on the contrary, preferred terra-firme forests where the high diversity of trees is a source for a wide variety of insects [13].

Abundance of specific bird populations in habitats indicates an important role for different food availability in terra-firme and floodplain forest. Munn and Terborgh [17] and Henrieques et al. [16] already suggested that insectivores were likely to be more abundant in terra-firme forest and frugivores more abundant in floodplain forest. This study supports those suggestions, with these specific feeding guilds being more abundant in their respective habitats. These habitats are threatened by deforestation, which increases fragmentation of areas and is detrimental to various bird species [27]. According to Gray et al. [10] insectivores and frugivores are the feeding guilds most prone to forest disturbance. As terra-firme and floodplain forests are severely reduced by deforestation in the Amazon, abundance of these feeding guilds is likely to decrease, affecting both trophic organization and ecological functioning of these areas. This ecological study was a pilot, as for certain species only trends

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**Table 5: Average value (with SE) of life-history traits used in calculation for RRI. Average clutch size (c), Number of broods per season (Nc) Egg mass in grams (megg) and Female body mass in grams (mfemale). See Table 2 for abbreviations of feeding guilds.**

<table>
<thead>
<tr>
<th>Feeding Guild</th>
<th>c</th>
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have become visible a larger scale study might more precisely determine species composition within these habitats. Such future research could also include monitoring of food availability within these habitats to define habitat-feeding guild relationships with more power.

Comparison of the values for life-history traits, especially the RRI, among the various feeding guilds within the tropics showed differences, as frugivores had a relatively low relative reproductive investment compared to insectivores. Significant differences in RRI were found not only among feeding guilds but also among families, resulting in different tactics of reproduction and survival of these avian populations.

Floodplain forests are fast-changing habitats for tropical birds due to flooding, biomass deposition from rivers, and secondary growth of the forest. These conditions seemed to lead to a higher RRI-value, as has been reported for frugivores, than for similar species in terra-firme forest. Other feeding guilds showed a similar trend, but due to lack of values of life-history traits for a number of species, numbers were quite low to base a conclusion on. The increased RRI in floodplain forest compared to terra-firme forest indicates a shift in the balance of reproduction and survival towards higher reproduction, made possible by the more nutrient-rich conditions in the floodplains, probably compensating for a higher risk of loss of either broods or higher juvenile and/or adult mortality due to flooding, for instance. Neotropical families of birds, especially those with low RRI, are more prone to deforestation and other environmental changes as these species do not easily compensate for increased adult mortality. Species composition of avian populations in terra-firme forests consists of birds with a relatively low relative reproductive investment, which are more susceptible to these anthropogenic impacts from, for example, deforestation.

It has been long recognized that tropical birds differ fundamentally from temperate zone birds in their life-history traits. Tropical birds have high nest predation, high adult survival, and small clutch sizes [28,29]. Various other studies have questioned the validity of these differences [30,31]. This study showed that the RRI for comparable groups of behaviourally similar species is in most cases higher for species in the temperate regions than in the tropical regions. Significant differences were found between Emberizidae and Turdidae and insectivorous feeding guilds, in all of which the RRI was higher in the temperate species. As nest predation is high in tropical birds, these species invest less in offspring, resulting in a lower RRI; they may therefore have lower adult mortality and can spread the risks of failed broods over a longer time. In other words one may state that spring in the temperate regions gives the possibility of an increased investment in reproduction, due to its increased biomass production. The downside being the increased risk of either surviving winter or facing the costs and risks of migration.

Tropical birds have smaller clutches than temperate zone birds, which is in line with other studies [32,33]. Larger clutch sizes have reduced food delivery, higher predation risk, and lower juvenile recruitment. In temperate regions, the food limitation hypothesis suggests that daylength in temperate regions allows these birds to gather more food to sustain larger clutches [34]. Growth rate in the tropics is slower [35] and food delivery rates are low [36]. Most tropical birds will renest after a first brood failure or have multiple broods per season, especially as in the tropics a relatively high nest predation is present as about 80% of the nests are lost to predators [29,36]. This number is so high because there is a large number and
diversity of nest predators in the tropics [32,37]. Tropical birds seem to invest less in their offspring, as the egg mass of tropical species is lower compared to temperate species. Female body mass as such varies extremely, without clear patterns. Because tropical birds have a lower RRI and invest less in their offspring due to higher predation risk, food limitation, and spreading the risk over the years, their naturally higher adult survival renders them extra vulnerable to increased adult mortality from anthropogenic influences.

Fig. 4: Some bird species from the Amazon Basin within the Tambopata National Reserve and Bahuaja Sonene National Park. A. Band-tailed Manakin (Pipra fasciicauda) B. American Pygmy-kingfisher (Chloroceryle aenea) C. Plumbeous antbird (Myrmeciza hyperythra) D. Green-and-gold Tanager (Tangara schrankii) (All photos by Alexis Diaz Campo).

Implications for conservation
Understanding distribution differences of behaviourally similar species among tropical forest types is important for identifying bird species prone to anthropogenic factors, as these forests are currently subjected to deforestation and fragmentation. The results in this study show specific foraging groups to be more abundantly present in either terra-firme or floodplain forests (Fig. 4). The species-specific life-history traits of these birds show that the relative reproductive effort is lower in terra-firme forest species. Which means that birds here invest less in reproduction and more in adult survival, these birds cannot compensate for the high adult mortality caused by deforestation, whereas floodplain forest species invest more in reproduction and can better cope with such anthropogenic factors. These values for
distribution and relative reproductive investment are important in understanding the differences in the ability of birds to cope with environmental changes and is therefore advised to be used in conservation activities.

Acknowledgements
Special thanks to A. Diaz Campo and L. Cueto for their field assistance and critically reviewing this study, and thanks to all the interns and staff at Fauna Forever and the Department of Animal Ecology and Ecophysiology for their help in our research.

References


## Appendix 1

Classification of sites with terra-firme forest or floodplain forest (X indicates presence of forest type at location).

<table>
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<th>Site</th>
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Appendix 2

Guild classification of captured bird species in Madre de Dios region, Peru based on Henriques et al. [16], Wunderle et al. [14] and Schulenberg et al. [23]. Life-history traits (average clutch size, number of broods per season, egg mass and female body mass) for estimation of the relative reproductive investment (RRI) based on Jetzt et al. [38], Del Hoyo et al. [39], Schönwetter and Meise [40] and field-data.

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<th>Egg mass (g)</th>
<th>Female body mass (g)</th>
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Species and English names based on Schulenberg et al. [23] and Del Hoyo et al. [39]. Feeding guild: AA= army ant follower, F= solitary frugivore, FI= solitary frugivore-insectivore, I= solitary insectivore, IF= solitary insectivore-frugivore, MFI= mixed species insectivore flocks, MFIF= mixed species insectivore-frugivore flocks, N= nectarivore, SVLI= small vertebrates and large insects.
Appendix 3

Guild classification and life-history traits (average clutch size, number of broods per season, egg mass and female body mass) of West-European birds for estimation of the relative reproductive investment (RRI) based on Del Hoyo et al. [39] and field-data.

<table>
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<th>Species[a]</th>
<th>English name[a]</th>
<th>Average clutch size</th>
<th>Number of broods per season</th>
<th>Egg mass (g)</th>
<th>Female body mass (g)</th>
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**Cuculidae**

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**Emberizidae**

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**Falconidae**

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**Fringillidae**

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\[1\] Species and English names based on Del Hoyo et al. [39]. \[a\] Feeding guild: F= solitary frugivore, FI= solitary frugivore-insectivore, I= solitary insectivore, IF= solitary insectivore-frugivore, MFIF= mixed species insectivore-frugivore flocks, SVLI= small vertebrates and large insects.
### Appendix 4

Species of birds captured more frequently in floodplain (FP) or terra-firme forest (TF). Test statistics and P-values are provided for Chi-square tests. Abundance data corrected per sampling effort.

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<td><em>Amazilia lactea</em></td>
<td>Sapphire-spangled Emerald</td>
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<td><em>Automolus infuscatus</em></td>
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<td><em>Habia rubica</em></td>
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[1] Bold indicates species captured more frequently in FP than TF.

Notes:
- FEEDING GUILD:
  - **F**: frugivore
  - **I**: insectivore
  - **AA**: omnivore
  - **MFI**: mixed fruit invertebrate
  - **SVLI**: small vertebrate invertebrate
  - **N**: nectarivore

- **RRI**: Relative Richness Index
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<th>Dominance</th>
<th>Relative Abundance</th>
<th>Significance</th>
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<th>AA Mean</th>
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<td>&lt;0.001</td>
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<td>72</td>
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<td>66</td>
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<td>0.005</td>
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<td>77</td>
<td>23.96</td>
<td>0.001</td>
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<td>Stripe-chested Antwren</td>
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<td>11.00</td>
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<td>Pipra chloromeros</td>
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<td>50</td>
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<td>0.046</td>
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<td>0.033</td>
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<td>Feeding Guild</td>
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<td></td>
<td></td>
<td></td>
<td></td>
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<td>------------------</td>
<td>-------------------</td>
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<tr>
<td><em>Xiphorhynchus elegans</em></td>
<td>Elegant Woodcreeper</td>
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</table>

Species and English names based on Schulenberg et al. [23] and Del Hoyo et al. [39]. Feeding guild based on classification in Henriques et al. [16]. AA = army ant follower, F = solitary frugivore, FI = solitary frugivore-insectivore, I = solitary insectivore, IF = solitary insectivore-frugivore, MFI = mixed species insectivore flocks, N = nectarivore, SVLI = small vertebrates and large insects.
Appendix 5

Relative reproductive investments of tropical region birds per family and per feeding guild. Value of RRI with Standard Error and number of species used is shown.

### Tropical regions

<table>
<thead>
<tr>
<th>Family</th>
<th>RRI(SE)</th>
<th>n</th>
<th>Family</th>
<th>RRI(SE)</th>
<th>n</th>
</tr>
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<tbody>
<tr>
<td>Alcedinidae</td>
<td>0.572(0.025)</td>
<td>2</td>
<td>Picidae</td>
<td>0.270</td>
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</tr>
<tr>
<td>Bucconidae</td>
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<td>Pipridae</td>
<td>0.561(0.033)</td>
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<td>0.468</td>
<td>1</td>
<td>Psittacida</td>
<td>0.266</td>
<td>1</td>
</tr>
<tr>
<td>Columbidae</td>
<td>0.297(0.062)</td>
<td>4</td>
<td>Rhampastida</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Conopophagida</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cotingidae</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cuculidae</td>
<td>0.814</td>
<td>1</td>
<td>Thamnophilida</td>
<td>0.601(0.034)</td>
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<td>Thraupidae</td>
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<td>Tinamidae</td>
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<tr>
<td>Formicariidae</td>
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<td>Trochilidae</td>
<td>0.526(0.038)</td>
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</tr>
<tr>
<td>Furnariidae</td>
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<td>14</td>
<td>Troglodytida</td>
<td>0.587(0.074)</td>
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<td></td>
<td>Trogonidae</td>
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<tr>
<td>Icteridae</td>
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<td>Turdidae</td>
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<td>Tyrannidae</td>
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### Feeding guild

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</tr>
<tr>
<td>F</td>
<td>0.588(0.056)</td>
<td>20</td>
</tr>
<tr>
<td>FI</td>
<td>0.474(0.064)</td>
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</tr>
<tr>
<td>I</td>
<td>0.629(0.034)</td>
<td>38</td>
</tr>
<tr>
<td>IF</td>
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</tr>
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<tr>
<td>MFIF</td>
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</tr>
<tr>
<td>N</td>
<td>0.526(0.038)</td>
<td>12</td>
</tr>
<tr>
<td>SVLI</td>
<td>0.376(0.064)</td>
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</tr>
</tbody>
</table>

Feeding guilds based on classification in Henriques et al. [16]. AA= army ant followers, F= solitary frugivores, FI= solitary frugivore-insectivores, I= solitary insectivores, IF= solitary insectivore-frugivores, MFI= mixed species insectivore flocks, MFIF= mixed species insectivore-frugivore flocks, N= nectarivores, SVLI= small vertebrates and large insects.
### Appendix 6

Relative reproductive investments of temperate region birds per family and per feeding guild. Value of RRI with Standard Error and number of species used is shown.

**Temperate regions**

<table>
<thead>
<tr>
<th>Family</th>
<th>RRI(SE)</th>
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<th>Family</th>
<th>RRI(SE)</th>
<th>n</th>
</tr>
</thead>
<tbody>
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<td>Accipitridae</td>
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<td>Muscicapidae</td>
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<td>Paridae</td>
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<td>Phalacrocoracidae</td>
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**Feeding guild**

<table>
<thead>
<tr>
<th>RRI(SE)</th>
<th>n</th>
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</thead>
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<td>AA</td>
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<td>0.491(0.103)</td>
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<tr>
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</tbody>
</table>

Feeding guilds based on classification in Henriques et al. [16]. AA= army ant followers, F= solitary frugivores, FI= solitary frugivore-insectivores, I= solitary insectivores, IF= solitary insectivore-frugivores, MFI= mixed species insectivore flocks, MFIF= mixed species insectivore-frugivore flocks, N= nectarivores, SVLI= small vertebrates and large insects.