

The biological and physiological effects of rainforest degradation on eight bird species in Equatorial Guinea

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Abstract

Rainforest degradation and destruction are major sources of extinction of tropical avifauna. Selective logging was established in many tropical nations as a viable compromise between timber demand and the need to preserve forest biodiversity, but recent studies have suggested that selective logging also reduces avian species richness and abundance. However, the literature on this topic is still scarce. In particular, the Afrotropical rainforests is the most understudied ecosystem when it comes to the effect of selective logging. The few studies in the Afrotropical region showed a reduction in species richness and abundance in some bird guilds, although no study looked at the drivers of reduction of these metrics. My study was designed to identify physiological and biological effects of selective logging on the avifauna in Equatorial Guinea's tropical forests. This study compared six life history and population traits that are shown to be good indicators of a bad quality habitat (breeding individuals, moulting birds, moult-breeding overlap, age and sex ratios, mass corrected for body size (MBS)). I used eight bird species from the ant-followers and insectivores guild as birds from these guilds are sensitive to disturbance. Furthermore, I also compared feather corticosterone (fCORT) concentration in five selected species in the two forest types, in order to complement the life history and population data. Four of the species showed a higher proportion of adult birds in secondary forests and one species had a higher proportion of adult birds in primary forest. In addition, three species showed a higher proportion of moulting birds in primary forests and one species had higher proportion of moulting birds in secondary forests. Moreover, the average MBS of birds from one of the studied species in secondary forests was higher than in primary forests. I found no difference in the fCORT concentration of birds in the two forest types. Finally, the overall proportion of adult insectivores was higher in secondary forest. The skewed age ratio in combination with the reduced moulting individuals and the high MBS suggest that secondary forests are a poor-quality habitat for at least some of the species. This study shows the importance of developing more sustainable logging practices to ensure the survival of the local avifauna.

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Introduction

In recent decades, many conservation efforts were established in the tropical regions of the world and in tropical forests specifically. The ecological value of the tropical rainforests was re-evaluated after the replacement of the tropical rainforests with urban settlements or agricultural land led to changes in the local biodiversity and other ecological systems (Malhi et al., 2013). Despite the understanding of their importance, there are predictions for further exploitation of the tropical rainforests (Newbold et al., 2013). The affected areas can be as big as 7 million ha/year (Achard et al., 2014). These ecosystems host important biodiversity, and some species depend on the many roles that the ecosystems play in the local, regional, and global scale (Malhi et al., 2013). If the rate of deforestation continues, some of these species will go extinct (Malhi and Grace, 2000). Some tropical forest nations introduced new laws and policies such as selective logging in an attempt to reduce deforestation and cover timber demand sustainably (Drigo et al., 2009). About 25% of the remaining tropical forests are selectively logged regularly (Blaser et al., 2011). In some cases, selective logging is done unsustainably due to a lack of regular inspections (Edwards et al., 2019).

The literature disagrees on whether selective logging is a sustainable logging practice. Some studies have shown a decrease in species richness and abundance in selectively logged forests (Barlow et al., 2006; Powell et al., 2013). Other studies have shown that species richness and abundance are not affected (Sodhi et al., 2010; Edwards et al., 2011). However, some forest specialists are being replaced by more generalised species because the specialists cannot withstand the effects of selective logging as well as other species (Gibson et al., 2011). Since these changes do not affect the species richness and abundance of the area, these criteria fail to show the direct effects of selective logging. Even if there is a decrease in species richness and abundance, that is only the after-effect of selective logging. When comparing selectively logged forests and intact forests, it is being shown that selectively logged forests differ in heterogeneity, density, and fragmentation (Hardwick et al., 2015; Putz et al., 2012). These changes in the forest's structure come with

secondary effects such as increased edge effects, and a hotter and drier microclimate (Haddad et al., 2015). Changes in the microclimate were induced by the increased light intensity and higher air flow resulting from less dense vegetation (Gray et al., 2007). Some of the biodiversity in these forests is affected directly as the trees that birds rely on for food or protection are being cut down, or indirectly by the disturbance of the invertebrate communities that provide food for birds (Ostrich, 2000). Jullien and Thiollay (1996) showed that the population of predatory raptors is significantly increased in selectively logged forests. Increasing the predator population is causing chronic stresses to understory birds (Lens et al., 1999).

The avian biodiversity of a forest could be used as a good conservation tool to determine if an area is affected by long term changes such as selective logging (De Heer et al., 2005). Many studies have shown that the avian biodiversity in selectively logged forests is reduced (Lambert, 1992; Johns, 1992; Waltert et al., 2004; Holbech, 2005; Latja et al., 2016). In contrast, some studies found no reductions (Gray et al., 2007; Burivalova et al., 2015), or even an increase in avian biodiversity in selectively logged forests (Lambert, 1992). This disagreement in the literature suggests that the effects on avian biodiversity differ in intensity in different forests because the geographic location, the logging intensity and the logging times are different. Further, not all groups of species that share ecological traits (guilds) have the same response to selective logging (Sekercioglu, 2011). Some guilds can adapt better than others to the potential effects of selective logging (Holbech, 2005). Ant-followers and insectivores are the first guilds to reduce in number after selective logging (Barlow et al., 2006). The insectivore guild is very sensitive to disturbance which is why it is the first to reduce, the ant-follower guild is also sensitive but less so than insectivores (Powell et al., 2013). In addition, both guilds take a long time to recover after the forest is allowed to regrow naturally (Barlow et al., 2006). Other guilds that are reduced after selective logging are frugivores and omnivores but not to the same extent as insectivores and ant-followers (Newbold et al. 2013).

The majority of the literature is based on using the avian species/guild richness and abundance as a tool to show the effects of selective logging. This technique is useful to test which species/guilds were driven away by the effects of selective logging or if they were driven to local extinctions (Ostrich, 2000). However, this only shows the results, not the potential problems that cause the reduction in the abundance of these birds. In addition, this method fails to address potential extinctions of specific species since in some cases the species in a study is not specified and only the abundance of the guild is shown. Fefferman and Romero (2013), suggested that looking at the physiological state of individual birds in selectively logged forests would give a better understanding of how these birds are affected. An early understanding of physiological effects on birds in a habitat will give the chance for improved conservation efforts.

Stress Hormones

A new ecological tool to examine whether an organism is under stress has been proposed which measures the organism's glucocorticoid (GCORT) hormone levels (Dickens and Romero, 2013). These steroid hormones and other metabolic pathways are regulated by the Hypothalamic-Pituitary-Adrenal (HPA) axis (Romero, 2004). When the energy demand exceeds the energy available, the HPA releases these hormones to promote energy-saving behaviour (Busch and Hayward, 2009). Vertebrates commonly have seasonal and life-history stage variation in their GCORT secretion (Romero, 2002). If GCORT levels stay elevated for an abnormally long time, it could result in negative effects on an individual's fitness (Romero, 2004). In addition, elevated GCORT levels weaken the immune system of a vertebrate, which can cause metabolic dysfunctions (Franchimont, 2004).

Avian studies measure feather corticosteroid (fCORT) levels in birds, which represent the HPA-axis activity over the time of the growth of the feather that was examined (Bortolotti et al., 2008). It is possible to use passive netting to measure fCORT as the CORT is stored

inside the feather in contrast to blood CORT which requires the bird to be sampled as soon as possible. The fCORT levels represent approximately 3 weeks of HPA-axis activity (depending on the species) during the time of feather growth, whereas blood CORT only represents a few hours prior to the bird's capturing (Romero and Fairhurst, 2016). A three-year study on ten different understory bird species found no differences in the fCORT levels in birds from primary and secondary forests (Messina et al., 2020). Although, they found that increased levels of fCORT were related to reduction in the abundance of the particular species the next year. High fCORT levels were also related to a negative impact on reproductive success and increased mortality the following year in common eiders (*Somateria mollissima borealis*).

Life History and Population Traits

The effect of habitat quality on the overlap between breeding and moulting time

The vast majority of birds in a good quality habitat are able to breed and raise their offspring successfully. On the other hand, birds in poor quality habitats have reduced reproductive success and, in some cases, they are not able to breed at all due to the many stresses that they face. Birds in poor quality habitats can be exposed to long-term high GCORT levels. This long-term change in the endocrine system inhibits the breeding success of these birds (Ellenberg et al., 2006). Furthermore, this long-term increase of GCORT levels also inhibits the reproductive status of individuals, reducing the number of breeding individuals in a poor-quality habitat (Buttemer et al., 2015). Some birds have their peak level of GCORT during their reproductive period (Salvantes and Williams, 2003). A study on song sparrows (*Melospiza melodia*) showed that increased stress before the reproductive period, which increased the plasma corticoid levels, led to the first egg laying day being delayed by a week (Wingfield, 1985a). Longer term stress during the breeding season could lead to breeding failure for that population since they have a set breeding season. Failed breeding

years are shown to happen in tropical birds with no set breeding season. Tropical stonechats (*Saxicola torquata axillaris*) that shared a habitat with predatory fiscal shrikes (*Lanius collaris*), had long term elevated CORT levels which led to delayed reproductive attempts and failed second reproductive attempts (Scheuerlein et al., 2001). It could also be the case that bad quality habitats have juvenile or bad-quality individuals which are not able to breed (Hannon and Martin, 2006).

Moulting is another costly life stage which also affects GCORT levels in birds. However, most bird species, instead of having high GCORT levels during moulting, exhibit the lowest GCORT levels at this stage (Romero, 2002). This occurs because moulting is a process that requires critical amino acids which are otherwise used to synthesise GCORT hormones (Romero et al., 2015). Stressful events during the moulting cycle, or other nutritional stresses result in poor quality feather replacement, concluding in poor thermoregulatory and flight functions of the feathers (Dawson et al., 2000; DesRochers et al., 2009). Some passerine species in North America have developed a strategy to avoid having to migrate with poor quality post-moulting feathers. If the spring breeding sites are of poor quality, they postpone their autumn moulting until after they migrate (Reudink et al., 2020).

In some cases, tropical birds have moult-breeding overlap since they do not have set periods for these life stages (Webster and Handley, 1986). The literature reaches no consensus as to why some birds choose to have this overlap since both life stages are costly and important. Some species are able to cope with having this overlap if they are in habitats with favourable conditions or if they stretch one or both life stages over a longer period of time (Foster, 1975). In contrast, in some cases birds that have the moult-breeding overlap replace their feathers with worse-quality feathers which, in some cases, results in reduced escape flight speed as well as reduced reproductive success (Echeverry-Galvis and Hau 2013). Furthermore, Johnson et al. (2012), suggested that the two life stages are meant to be separated since the overlap occurred at the start or the end of the moult cycle. Different

species might evolve different strategies to cope with stresses in their habitat. It is possible that they were forced to have the moult-breeding overlap because moulting was extended due to a poor-quality habitat.

The effect of habitat quality on age structure and sex ratio

Stressful habitats tend to have higher densities of younger birds as the better-quality habitats are already occupied by adult birds which force the younger birds out, driving them to disperse to any available habitats which might be of poor quality (Hannon and Martin, 2006). For example, small forest fragments in Costa Rica had a higher juvenile population because adult birds were avoiding these habitats (Şekercioglu et al., 2015). Further evidence for this assumption comes from Amazonian primary forests which were hosting significantly higher counts of adult birds than secondary forests (Wolfe, 2003). A possible explanation as to why older birds would avoid poorer quality habitats is that they would have to go through difficult life stages such as moulting and breeding while supporting themselves. Younger individuals, on the other hand, would only need enough resources to support their own dietary requirements, but not necessarily the effort of breeding.

The social dominance hypothesis predicts that the sex ratio and age in poor habitats are skewed (Catry et al., 2006). An example comes from American Redstarts (*Setophaga ruticilla*), where the more territorial males push females out of good-quality habitats (Marra and Holmes, 2001). This is further suggested in a study of common frugivores in Costa Rica; deforested forests had higher female counts than male. It is possible that the sex ratio in stressful habitats is skewed due to differences in the HPA-axis in male and female birds. This is shown to happen in northern spotted owls (*Strix occidentalis caurina*), where males with habitats close to logging roads had significantly higher GCORT levels than females living far from logging roads (Wasser et al., 1997). Different species differ as to which sex is more vulnerable to stress. In the case of American kestrels (*Falco sparverius*), females that lived in disturbed habitats had higher GCORT levels than males in the same habitats

(Strasser and Heath, 2013). In the tropics, subordinate females may be more susceptible to stress than dominant males (Catry et al., 2006; Marra and Holmes, 2001).

Mass corrected for body size (MBS)

Another ecological tool used to understand if birds in a habitat are under stress is to study the mass corrected for body size (MBS) which represents a regression of the bird's body mass against a linear morphometric measure (Jakob et al., 1996). Kraft et al. (2019) conducted a study where nestling common kestrels (*Falco tinnunculus*) were artificially introduced to stress via CORT administration, which resulted in tarsus size restriction. Another example comes from a study on little greenbuls (*Eurillas virens*), where individuals from primary forests had greater wing and tarsus length as well as bigger bill size than individuals in secondary forests (Smith et al., 2007). This ecological tool has been widely used to identify vertebrates under stress and identify poor-quality habitats (Stevenson and Woods, 2006). This tool also indicates how "healthy" a bird is because it compares muscle and fat content with the size of the bird (Wikelski and Cooke, 2006). MBS is a far more useful metric than species richness and abundance. For example, in the study on little greenbuls in Cameroon, the abundance of greenbuls in secondary forests was higher than in primary forests but the MBS of the population in the secondary forests was lower, which indicated that the population was under stress (Smith et al., 2007).

The Afrotropics

Rainforests in the Afrotropics have been under-studied when it comes to forest degradation, compared to other tropical regions (Cazzolla et al., 2015), even though these forests are decreasing at faster rates than in any other region (FAO, 2015). The small number of studies done in the Afrotropics showed that species richness and abundance was decreased drastically in disturbed and degraded forests (Beier et al., 2002; Dale et al., 2000; Watson et al., 2004). Equatorial Guinea is among the most interesting Afrotropical countries in which to examine the effects of forest degradation on avifauna, since it hosts many

species that are vulnerable to anthropogenic disturbance (Borrow and Demey, 2001).

Furthermore, Equatorial Guinea has accessible lowland primary forests where these species have not been disturbed, which allows for physiological comparisons.

The previous studies in the disturbed Equatorial forests were focused on species richness and abundance and showed that bird guilds such as ant-followers, forest specialists and insectivores were declining (Peters et al., 2008; Waltert et al., 2004; Jarret et al., 2021). However, these findings failed to highlight specific species that were declining as well as the mechanisms behind these declines. A more species-specific, individual-level comparison between birds in untouched primary forests and selectively logged forests using life history and population traits (breeding individuals, moulting individuals, sex ratio, age ratio, and MBS) as well as GCORT levels can show if bird populations in secondary forests have altered biological and physiological characteristics, which would indicate they live in a poor-quality habitat. Furthermore, sensitive species in the vulnerable guilds will be identified as this study will investigate at the individual level as well as the guild level.

Aims and Hypotheses

The overall aim of the project was to investigate whether secondary selectively logged forests are poor-quality habitats, using life history and population traits that are good ecological tools for detecting if birds are under chronic stress. In addition, an fCORT analysis in some species could provide further evidence for any patterns that are found using the life history and population traits. The data that was used in this study was from bird species from guilds (insectivores and ant-followers) that were shown to have a lower abundance in secondary forests in the area (Barrie, 2020).

If secondary forests are indeed a suboptimal habitat relative to primary forests, I predict that:

1. There are fewer breeding individuals in secondary forests compared to primary forests.
2. The number of birds moulting in secondary forests is fewer than in primary forests.

3. There is a higher proportion of individuals that go through a moult-breeding overlap in secondary forests.
4. There are more adults in primary forests than in secondary forests.
5. There are fewer female birds in primary than in secondary forests.
6. The mean MBS of birds in secondary forests is lower than in primary forests.
7. There is, on average, a higher concentration of fCORT in birds in secondary forests than in birds in primary forests.
8. There is a positive correlation between fCORT concentration and MBS.

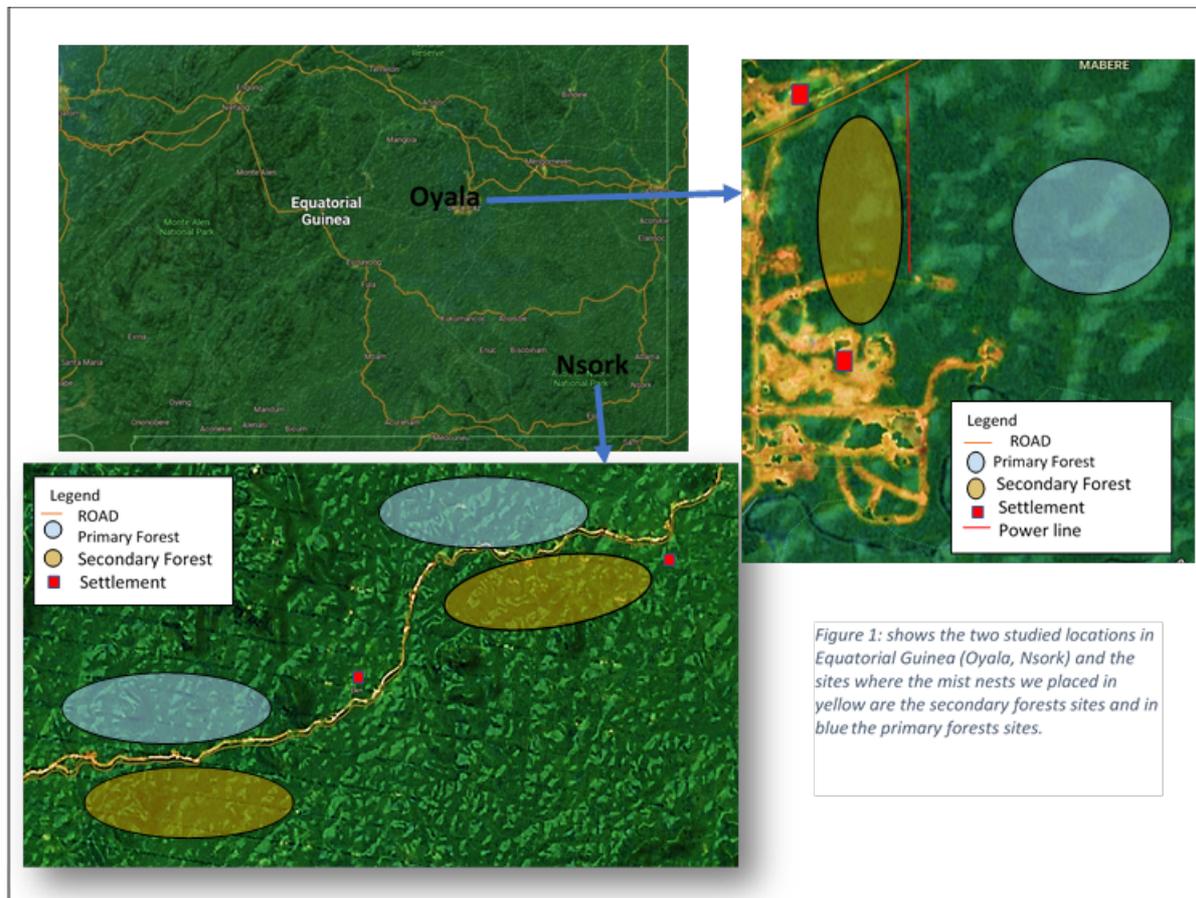
Methodology

This study aimed to investigate if tropical birds were affected by selective logging and its effects on their habitat. Tropical birds of primary and secondary (selectively logged) forests were compared to find differences in their physiological and biological characteristics. Data were collected by Biodiversity Initiative (an international nature conservation NGO) in two locations in Equatorial Guinea: Oyala every winter from 2016 to 2020, and Altos de Nsork National Park in 2014. Only species that had at least 10 captures in each forest type were used to ensure the analysis yielded significant results (Abolins-Abols et al. 2016).

Study area

The two studied areas in Equatorial Guinea and the location of the primary and secondary forests are shown in Figure 1. The primary forest in Oyala is only accessible by walking through forest and is about 500 m from the nearest road and 1.5 km from the closest settlement. It was also only selectively logged in the 1980s but has remained intact since then. The secondary forest in Oyala is located next to the city with a road running through its southern part and a power line through its eastern part. The secondary forest has been commercially logged in the past century and regularly selectively logged since the commercial logging stopped. Its proximity to the city and the regular selective logging suggests that it is a poor-quality habitat for primary forest-dependent birds. The primary

forests in Nsork were located away from the main road and further away from the settlements and were only selectively logged in the 1980s. In contrast, the secondary forests in Nsork were located very close to the main road, their eastern part was next to settlements, and they were selectively logged for years.



Data collection

Mist nets were set up by members of Biodiversity Initiative in both forest types, forming net lanes covering different forest sites. Each mist net was 12 m long and 2.5 m high, and they were set inside a clear path 1 m wide. Approximately 40 nets were set up simultaneously at two sites in each forest type and left for 2 days. The nets were opened each day at about 6:30AM and closed after 6 hours. The nets were checked every half an hour starting at the furthest end of the net and all the captures were placed inside cloth bird bags and taken to the ringing station, which was located in the middle of the two sites. Each bird was identified, sexed, and weighed, and had its wingspan and tail measured. Feathers

were collected for fCORT analysis. In the data, females were set to 1 and males were set to 0. Furthermore, each bird was assigned a code which categorised it according to its breeding status, moulting stage and fat content. Each bird was assigned a category depending on the size of its brood patch (for females) or its cloacal size (for males). Then, these categories were used to determine whether the bird was breeding or not. Likewise, each bird was assigned into one of five categories depending on the stage of its moult and the category it was assigned to was used to determine if the bird was moulting. Finally, each bird was assigned a three-letter code using the WRP system and then grouped into juveniles (0) and adults (1) depending on its code. This is summarised in Table 1 (Johnson and Wolfe, 2017).

Table 1: The three-letter code from the WRP system that was used to define if a bird was an adult or young. Each letter from the three-letter code is summarised in Table 2.

Adult	Young
DCB	FCF
DPB	FCJ
DSB	FPB
SCB	FPF
SPB	FPJ
DPB	FMJ
DMB	FMS
FAF	FMF
FAJ	

Table 2: A summary of what each letter of the three-letter code in table 1 represents.

1 st Position	1 st Position Definition	2 nd Position	2 nd Position Definition	3 rd Position	3 rd Position Definition
F	First moult cycle	A	After a given plumage	S or X	Supplemental or auxiliary-formative plumage
S	Second moult cycle			F	Formative plumage
T	Third moult cycle			B	Basic plumage
4	Fourth moult cycle			A	Alternate plumage
U	Unknown moult cycle	C	Not moulting	U	Unknown plumage
D	Definitive moult cycle	P	Moulting	J	Juvenile plumage

Due to local COVID-19 restrictions, the fCORT concentrations were measured in Ohio State University by Dr Chris Torna. For each species (*Alethe castanea*, *Bleda notatus*, *Bleda syndactylus*, *Chamaetylas poliocephala*, and *Illadopsis spp.*), 20 feathers were used (10 from each forest type). Although only some of the feathers were used for this study as only adult birds were examined to ensure more accurate analysis. The sample size for the fCORT analysis for each species is summarised in Table 2. fCORT was extracted using the protocol described by Bortolotti et al. (2008) and by using ELISA kits (Corticosterone ELISA kit; Neogen Corporation, Ayr, UK) as validated by Carbajal et al. (2014). Each feather was measured from the quill to the tip using a ruler. Next, the vanes were minced inside a borosilicate glass scintillation tube, methanol shanking bath was added, and the buffer was incubated overnight. Vacuum filtration was used to separate the extract from solid mass by evaporating it under nitrogen gas. The extract was then reconstituted in Neogen extraction buffer, and an ELISA kit was run using the extract. fCORT levels were measured by adding 20µL of tritium-labelled CORT to each sample and using a scintillation counter with a recovery rate of 0.93.

Focal species

This study focused on eight species of birds from two guilds (ant-followers and insectivores), as they were the only species from these guilds with at least 10 captures in each forest type. These are summarised in Table 2. Five of the studied species were ant-followers (*Alethe castanea*, *Bleda notatus*, *Bleda syndactylus*, *Chamaetylas poliocephala*, *Neocossyphus poensis*). These birds live on or near the forest floor and follow army ants feeding on arthropods flushed from the vegetation by driver ants (*Hymenoptera: Formicidae*) (Roberts et al., 2000). This ant species serves many ecological functions in this ecosystem, and it has been used as an indicator of the processing and functioning of the ecosystem (Folgarait 1998; Andersen and Majer 2004). Peters et al., (2008) showed a reduction in the species richness and abundance of the ants in selectively logged forests. Ant-followers were the first organism to decrease after disturbance in neotropical rainforests (Lovejoy et al., 1986; Sieving and Karr, 1997). Although afrotropical and neotropical species of ant-followers are unrelated, they are ecologically similar. This makes it possible for them to have related responses to disturbance in the afrotropics. According to the above, it is very important to look at the response of afrotropical ant follower species. The other three studied species are non-ant-following insectivores (*Illadopsis spp*, *Hylia prasina*, and *Sheppardia cyornithopsis*) that live near the ground of the forest and forage mainly for insects. This guild is very broad and some of the species have different foraging strategies, one of them being part of mixed-species flocks. In the Afrotropics, non-ant-following insectivores was the first guild to decrease after disturbance as they are very sensitive to any changes in their habitat (Powell et al., 2015).

Table 3: The studied species with the guild that they belong to according to their trophic status as well as the capture number in the two forest types. Also, the sample size for the fCORT analysis in each forest type. *Illadopsis spp.* represents the family and not an individual *Illadopsis* species.

Species	Guild	Captures		fCORT Sample Size	
		Primary	Secondary	Primary	Secondary
<i>Alethe castanea</i>	ant-follower	268	109	10	10
<i>Bleda notatus</i>	ant-follower	131	112	10	10
<i>Bleda syndactylus</i>	ant-follower	58	61	10	7
<i>Chamaetylas poliocephala</i>	ant-follower	135	54	10	10
<i>Illadopsis spp.</i>	insectivore	126	40	6	9
<i>Hylia prasina</i>	insectivore	18	24		
<i>Neocossyphus poensis</i>	ant-follower	20	29		
<i>Sheppardia cyornithopsis</i>	insectivore	71	10		

Statistical analysis

The data were analysed by fitting general linear models (GLMMs), with both fixed and random effects in R version 3.6.3 via RStudio. The data were formatted so that each row/observation belonged to an individual capture, with the measurements and other information next to it. Each model had, as response variable, one of my focal life history and population traits (breeding status, moulting stage, age ratio, sex ratio, and body mass/wing length ratio). The explanatory variables for each model were the forest type, the species, and the interaction between forest type and species. Finally, the random effects were the ring number of the birds, to account for repeated measurements of the same individual, and the year, to account for possible year-dependent differences. Best-fit models were selected through a likelihood ratio test, beginning from the most complex model, followed by subsequent reverse step-wise deletion of non-significant terms. In addition, a model was made for each life history or population trait, with the guild and the forest type as fixed effects and the species, forest type and year as random effects. This was done to check for effects at the guild level. The models that were run on the data are summarised in Table 3. Each model was used to predict a value for each forest type, which was then used for plotting. The plots included error bars with the confidence intervals from the model and where the error bars did not overlap, this was interpreted as a significant difference.

Table 4: Summary of the response and explanatory variables with the random effects, if any, that were fitted to the dataset.

Response Variable Group	Response Variable	Fixed Effects	Random Effects
Life History and Population Traits	Breeding Status, Moulting Birds, Moulting-Breeding overlap, Age, Sex, MBS	Forest Type, Species, Forest Type * Species	Year, Ring Number
	Breeding Status, Moulting, Moulting-Breeding overlap, Birds, Age, Sex, MBS	Forest Type, Guild, Forest type * Guild	Year, Ring Number, Species
fCORT	CORT	Forest Type, Species	
	CORT	Forest Type + MBS + Forest Type * MBS	Species

Results

This study included 1262 bird captures of 8 different species from 2 different guilds (977 ant-followers and 285 insectivores) in two forest types (secondary and primary). Models were applied to determine the probability that a bird was breeding, moulting, undergoing a moulting-breeding overlap, was an adult, was a male or was a female. Three species had a higher proportion of moulting individuals in the primary forests, and one species had a higher proportion of moulting individuals in the secondary forests. Four of the species showed a higher proportion of adult birds in secondary forests, and only one species showed a higher proportion of adult birds in primary forests. The overall adult population of insectivores was higher in secondary forests. Furthermore, models comparing the predicted average MBS, fCORT levels, and the relationship between MBS and fCORT levels of birds in the two-forest types were applied to the data. Here the only finding was that one species had a higher MBS in the secondary forests.

Effects of forest type and species guild on life history and population traits

I only applied the best-fit models for breeding to adult birds, both at the species and guild level. This included only 1039 captures and none of them included any fixed effects, as is shown in Table 5. Due to insufficient data, I could only include ring number and not year as a random effect in the model at the species level. In contrast, I could fit all three random effects (year, ring number, and species) at the guild level. The fact that the best-fit models did not include forest type as a fixed effect leads to the conclusion that there were no significant differences between the proportion of breeding individuals in the two forest types.

Because the models for sex and moult-breeding overlap at neither the species nor the guild level did not include any fixed effects, I did not find any significant differences in the proportion of female birds between the two forest types, or any significant differences in the proportion of birds that had moult-breeding overlap between the two forest types (Table 5). Due to insufficient data, I could only include ring number as a random effect for the sex and the moult-breeding overlap at the species level and the guild level.

When I modelled the probability that a bird was moulting, I found that the best-fit models included forest type, species, and the interaction between forest type and species as fixed effects (Table 5). Three of the species (*Alethe castanea*, *Chamaetylas poliocephala*, and *Sheppardia cyornithopsis*) had a significantly higher proportion of moulting individuals in the primary forest, and one species (*Neocossyphus poensis*) had a significantly higher proportion of moulting birds in the secondary forest (Figure 3A). I found no significant differences in the proportion of moulting insectivores and ant-followers in the two forest types since the best-fit model for moulting birds at the guild level included no fixed effects (Table 4).

Modelling the age ratio of the birds, I found that the best-fit model included forest type and the interaction between forest type and species as fixed effects (Table 5). I found that four of the species (*Sheppardia cyornithopsis*, *Neocossyphus poensis*, *Illadopsis spp.*, and *Chamaetylas poliocephala*) showed a significantly higher proportion of adult birds in

secondary forests compared to primary forests. Only *Bleda syndactylus* showed a significantly higher proportion of adult birds in primary compared to secondary forests (Figure 3C). In addition, I found that the best-fit model for the age ratio at the guild level included forest type, guild and the interaction between forest type and guild as fixed effects (Table 3). The results of the model suggest that there is a significantly higher proportion of adult insectivores in secondary forests than in primary forests, but no significant difference in adult ant-followers in the two-forest types (Figure 4A).

Finally, I found that the best-fit model for MBS at the species level included forest type, species, and the interaction of forest type with species as fixed effects (Table 4). Only the *Illadopsis* genus showed a significantly higher average MBS in secondary forests (Figure 3B). I also found that the best-fit model of MBS at the guild level included forest type, guild and the interaction of forest type and guild as fixed effects. There were no significant differences between the average MBS in the two forest types for either of the guilds (Figure 4B).

Table 5: The best fit models for each life history or population trait at the species and guild level. The fixed and random effects for each model are shown, if the best-fit model included any. Model selection was carried out by starting with the most complex model and carrying out reverse stepwise deletion, so the chi-square and p-value refer to the final model which was selected as the best model. The sample size for each model is also shown, representing the number of captures that were included in each model as some models were applied to only some of the data to account for possible recaptures of the same bird. The p-values show whether each model was significant (yellow) or not significant (red) depending on if the last model comparison resulted in the more complex model being kept or a simpler model being adopted. The level of the significance from the p-value is shown by the asterisks next to each p-value (= <0.05, ** = <0.01, *** = < 0.0001).*

Life History or Population Traits	Fixed Effects Included in the Best Fit Model	Random Effect	Chi-squared Value	P-value	Sample Size
Species Level					
Breeding Status	Null Model: No fixed effects	Ring Number	0.1071	0.7434	1039
Moulting Birds	Forest Type + Species + Forest Type * Species	Ring Number + Year	16.683	0.0336*	1262
Moult-Breeding overlap	Null Model: No fixed effects	Ring Number	6.554	0.5854	1039
Age	Forest Type + Forest Type * Species	Ring Number + Year	26.299	0.00093 ***	1262
Sex	Null Model: No fixed effects	NA	3.2638	0.9167	1262

MBS	Forest Type + Species + Forest Type * Species	Ring Number	36.634	1.344e-05 ***	1262
Guild Level					
Breeding Status	Null Model: No fixed effects	Ring Number + Year + Species	0.5925	0.7436	1262
Moulting Birds	Null Model: No fixed effects	Ring Number + Year + Species	1.7589	0.415	1262
Moult-Breeding overlap	Null Model: No fixed effects	Ring Number	0.485	0.9222	1262
Age	Forest Type + Guild + Forest Type * Guild	Year + Ring Number	6.6919	0.03523 **	1262
Sex	Null Model: No fixed effects	Ring Number	0.0383	0.981	1262
MBS	Forest Type + Guild + Forest Type * Guild	Ring Number + Species	8.1872	0.01668 *	1262

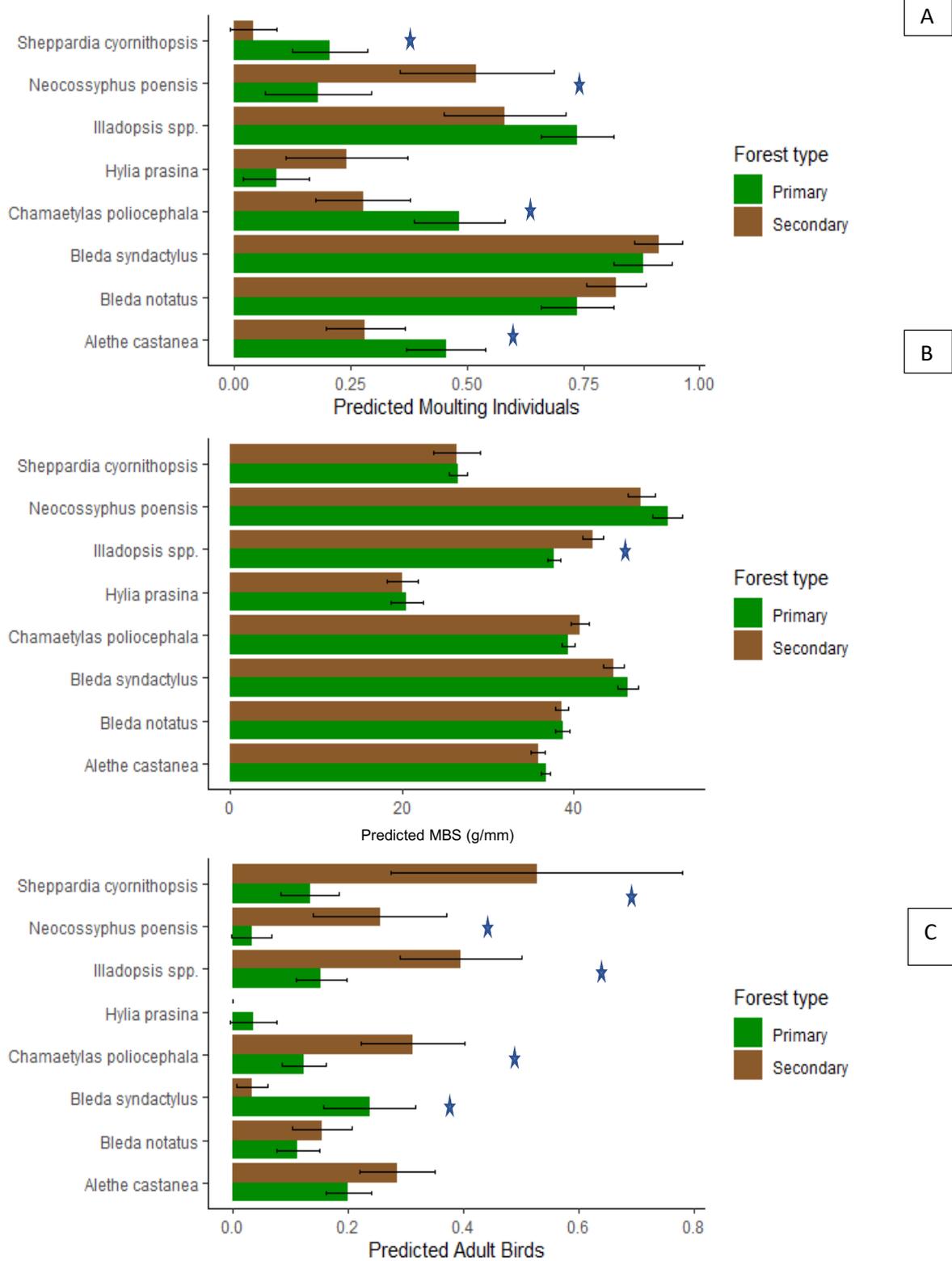


Figure 2 : The plots of the predicted values from the best fit models of life history and population traits (A = Moulting birds, B = mass corrected for body size (MBS), C = age) for primary (green) and secondary (brown) forests, at the species level. The error bars represent the 0.95 confidence intervals and where the error bars are not overlapping a significant difference is shown. Asterisks indicate the significant levels in the plot. Sample sizes for each species in each forest type are summarised in Table 3

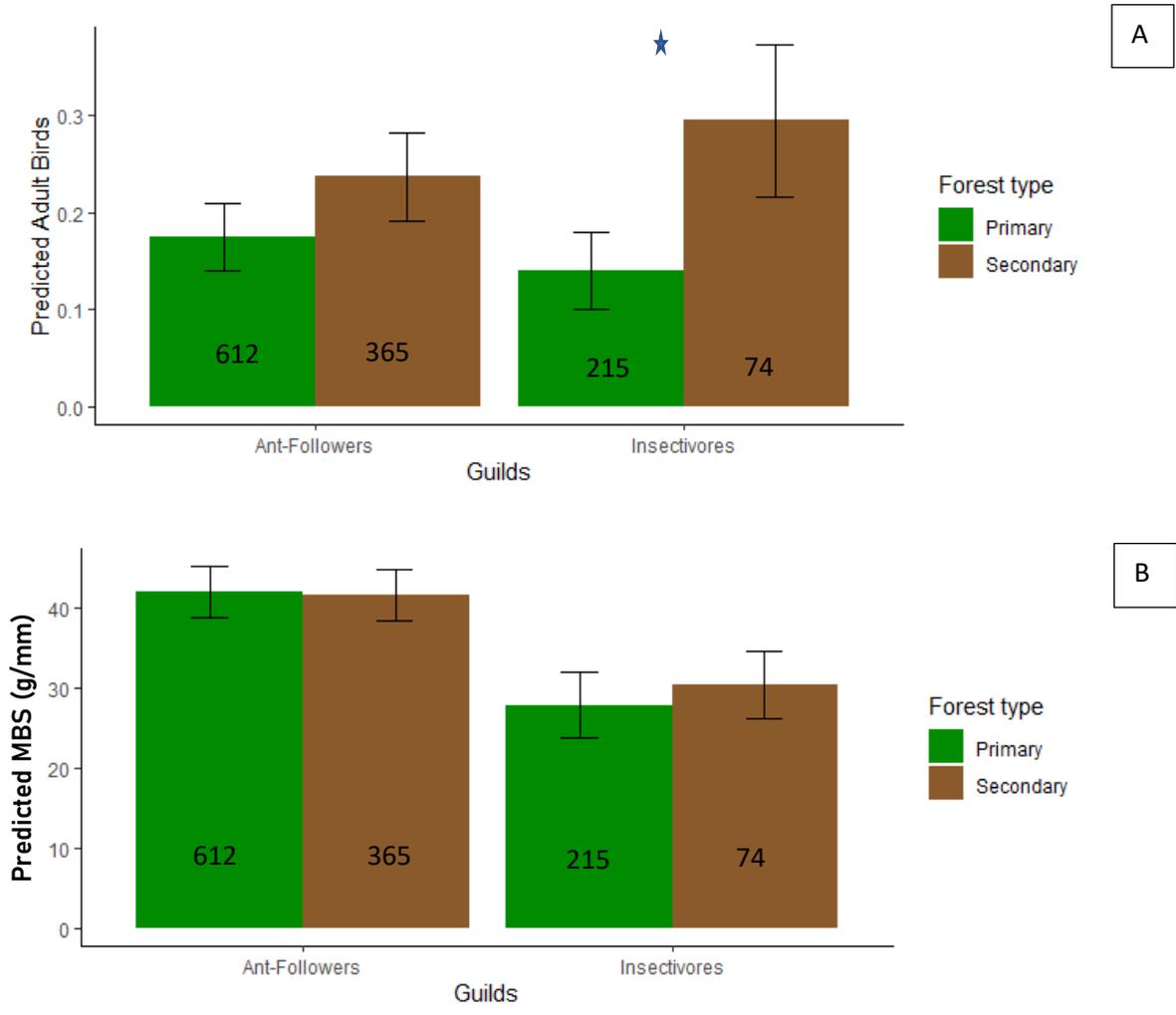


Figure 3: The plots of the predicted values from the best fit models of the life history and population traits (A = Age, B = mass corrected for body size (MBS)) for primary (green) and secondary (brown) forests, at the guild level. The error bars represent the 0.95 confidence intervals and where the error bars are not overlapping a significant difference is shown. Asterisks indicate the significant levels in the plot. Sample size of each guild in each forest type is shown on each bar.

Effects of forest type and species guild on feather corticosterone concentrations

I found that the average fCORT levels in the two forest types was not significantly different for any of the five species. I also found that the average fCORT levels of neither ant-followers nor insectivores was significantly different between the two forest types. This conclusion was drawn because the best-fit models for fCORT levels at the species and guild

level did not have any fixed effects (Table 6). To determine if there was a relationship between the birds with high MBS and high fCORT levels in any of the forest types, I ran a model with fCORT as a response variable and the interaction between forest type and MBS as a fixed effect (Table 6). This model showed that there was no significant relationship between the fCORT levels and the MBS of birds in either of the forest types.

Table 6: The best fit models of feather corticoid (fCORT) levels at the species and guild level. The fixed and random effects for each model are shown if the best-fit model included any. Model selection was carried out by starting with the most complex model and carrying out reverse stepwise deletion, so the chi-square and p-value refer to the final model which was selected as the best model. The p-values show whether each model was significant (yellow) or not significant (red) depending on if the last model comparison resulted in the more complex model being kept or a simpler model being adopted. The level of the significance from the p-value is shown by the asterisks next to each p-value (= <0.05, ** = <0.01, *** = < 0.0001).*

Response variable	Fixed Effects Included in the Best Fit Model	Random Effect	Chi-squared Value	P-value	Sample size
Species Level					
fCORT	Null Model: No Fixed Effects	NA	0.8771	0.9719	90
fCORT * MBS	Null Model: No Fixed Effects	Species	2.9817	0.0842	90
Guild Level					
fCORT	Null Model: No fixed effects	NA	0.6879	0.709	90

Discussion

This study examined the effects of selective logging on the biology and physiology of birds from eight different bird species from two guilds. This was done by comparing life history and population traits, and fCORT concentrations of the same bird species and guild in primary and secondary forests.

Effects of forest type and species on life history and population traits

Summary of main findings

I found no significant difference between the proportion of birds breeding in Equatorial Guinea's primary and secondary forests, for any of the studied species. Three of the studied species (*Alethe castanea*, *Chamaetylas poliocephala*, *Sheppardia cyornithopsis*)

had a significantly higher proportion of moulting individuals in the primary forests compared to secondary forests. In contrast, one species (*Neocossyphus poensis*) had a significantly higher proportion of moulting birds in the secondary compared to primary forests. I found no difference in the proportion of birds that undergo a moult-breeding overlap between the two forest types.

One of the studied species (*Bleda syndactylus*) had a significantly higher proportion of adult individuals in primary compared to secondary forests. Although, surprisingly, four of the studied species (*Sheppardia cyornithopsis*, *Neocossyphus poensis*, *Illadopsis spp.*, and *Chamaetylas poliocephala*) showed a significantly higher proportion of adult birds in secondary forests compared to primary forests, the remaining three species did not have any significant differences between the adult bird proportions in the two forest types.

Additionally, only birds from the *Illadopsis* genus showed a significantly higher average MBS in secondary forests compared to primary forests. Moreover, no significant differences were found in the sex ratio between the two forest types for any of the study species. Table 7 summarises the main findings for the analysis of the life history and population traits between the two forest types for each species.

Table 7: Summary of the significant differences in Life History and Population Traits between the two forest types for each studied species (Orange = the proportion of birds in primary forest is greater, Green = the proportion of birds in secondary forest is greater).

Species	Breeding Status	Moulting Birds	Moult-Breeding overlap	Age	Sex	MBS
<i>Alethe castanea</i>	NA	Primary > Secondary	NA	NA	NA	NA
<i>Bleda notatus</i>	NA	NA	NA	NA	NA	NA
<i>Bleda syndactylus</i>	NA	NA	NA	Primary > Secondary	NA	NA
<i>Chamaetylas poliocephala</i>	NA	Primary > Secondary	NA	Primary < Secondary	NA	NA
<i>Illadopsis spp.</i>	NA	NA	NA	Primary < Secondary	NA	Primary < Secondary
<i>Hylia prasina</i>	NA	NA	NA	NA	NA	NA
<i>Neocossyphus poensis</i>	NA	Primary < Secondary	NA	Primary < Secondary	NA	NA
<i>Sheppardia cyornithopsis</i>	NA	Primary > Secondary	NA	Primary < Secondary	NA	NA

Interpretation of results of forest type and species on life history and population traits

The lack of a significant difference in the proportion of breeding birds in the two forest types, suggests that the studied species are not affected by selective logging and showed signs that their bodies enable them to breed. The data was collected over the same time period every year, during the dry season. Also, that not all of the studied species have the same breeding period and some of the species have multiple breeding attempts during the year (Birdsoftheworld, 2020) . This study looked at the probability that a bird was breeding by analysing morphological characteristics that suggested it was breeding. Even if there were no differences in the number of breeding individuals in the two forest types, it is possible that birds in secondary forests had reduced reproductive success. Ellenberg et al., (2006) suggested that this might happen if birds are in a bad-quality habitat. For example, it is possible that there is a higher rate of predation and brood parasitism in nest of birds in secondary forests, as this was the case in degraded and fragmented forests (Hoover et al., 1995; Robinson *et al.*, 1995). In addition, it is possible that there is a lower fledgling survival in secondary forests for some of the species, as their food sources are reduced in secondary forests. The reduce species richness and abundance in ant species in secondary forests mean that obligate ant-follower species would have reduce food which could lead to high fledgling mortality (Peters *et al.*, 2008). However, this could not be assessed in this study directly. Further studies could focus on monitoring nest performance of this species perhaps by cameras to look at the predation rates, food provided by parents in the two forest types, and juvenile fledging. Also, a more frequent netting and ringing of birds would give an idea of the survival rate of fledgling in the two forest types.

One way to indirectly compare the reproductive success of birds in the two forest types is to examine the age ratio of the birds in the two forest types. It is possible that multiple failed reproductive attempts over the years have skewed the age ratio in favour of adult birds. This could explain why four of the studied species (*Sheppardia cyornithopsis*,

Neocossyphus poensis, *Illadopsis* spp., and *Chamaetylas poliocephala*) had a significantly higher proportion of adult birds in secondary compared to primary forests. This has been shown to happen in black-throated blue warblers (*Dendroica caerulescens*). Birds in denser shrub habitats had higher reproductive success than those in less dense habitats, and the overall population in the less dense habitats consisted of fewer juvenile birds as a result (Holmes et al., 1996). A reason for this variation in the age ratio between species could be different dispersal strategies. It is possible that in the species with higher adult proportions in the secondary forests, most of the juvenile birds dispersed out of the secondary forests in search of a better-quality habitat. In the other species the juvenile birds may not have dispersed out of the secondary forests, either because they were not affected by the disturbances therein, or because their dispersal range was lower, or they could not cross the habitat barrier to exit the secondary forest, which was essentially a 200-ha fragment (Woltmann et al., 2012; Stacey and Ligon, 1987). However, the opposite of this trend is seen in *Bleda syndactylus*, which had a higher proportion of adult birds in primary forests. It is possible that adult *Bleda syndactylus* avoided secondary forests because of their poor quality and migrated to other nearby forests, which has been shown to happen in neotropical birds (Wolfe, 2003). In addition, it is possible that some of the species benefit from selective logging, and they prefer secondary forests over the continuous primary forests, which would explain why there was a higher proportion of adult birds in secondary forests. A more accurate interpretation of these results could have been made if enough behavioural characteristics of these bird species were known, however, this is not the case, so we can only speculate. To test these speculations a more species-specific study that would include a more intensive netting and bird ringing should take place at the months just after their breeding attempts. Another study that would give a better understanding of the dispersal ranges of these species would look at the molecular genetic parentage, which would show how far the juveniles dispersed from their home range (Woltmann et al., 2012).

Three of the studied species (*Alethe castanea*, *Chamaetylas poliocephala*, *Sheppardia cyornithopsis*) showed a higher proportion of moulting birds in primary compared to secondary forests. Perhaps birds from these species residing in the secondary forests avoided moulting as a mechanism to avoid a moult-breeding overlap and potential negative effects on their plumage or their reproductive success (Moreno, 2004). This could explain why no difference was found in the proportion of birds that undergo a moult-breeding overlap between the two forest types. Additionally, *Chamaetylas poliocephala* and *Sheppardia cyornithopsis* had a higher proportion of adult birds as well as a significantly lower proportion of moulting individuals in secondary forests. It is possible that there were fewer moulting birds from these species because there more juvenile birds in the primary forests. Juvenile birds are more likely to be moulting as they change their plumage multiple times in a year whereas adults only change their plumage once (Johnson and Wolfe, 2017). However, this interpretation fails to explain the significantly higher proportion of adult and moulting *Neocossyphus poensis* in secondary forests. It should be noted that the studied bird species do not have a strict set moulting season, and if they have it varies among the studied species (Birdsoftheworld, 2020). The analysis represents the probability that a bird was undergoing moulting at the set time that the data collection took place. These speculations could be further analysed with a study in which the netting time is done over the months that each species is more likely to moulting and compare the proportion of moulting birds in the two forest types, and if there is enough data the age should be an explanatory variable to account for potential differences between the proportion of moulting adult and juvenile birds.

Finally, the most sensitive focal species seemed to be the species from the *Illadopsis* genus. Birds from the *Illadopsis* genus had both a significantly higher proportion of adult birds and a significantly higher MBS on average in secondary compared to primary forests. The fact that the populations of these species in secondary forests was more adult based suggests either that the reproductive success of individuals in this forest type was reduced (Holmes et al., 1996) or that the juvenile birds of these species dispersed out of secondary

forests because they are poor quality habitats (Van Houtan et al., 2007). Furthermore, the remaining elder populations in the secondary forests seemed to have body development issues as the average MBS was significantly higher than in primary forests. MBS represents a comparison of the muscle and fat of a bird against their wingspan, so a high MBS indicates that a bird has a higher body weight per mm of wingspan which suggests that they may have had stunted wing growth (Wikelski and Cooke, 2006). This is seen to happen in American Redstarts where a food reduction (poor quality habitat) led to increased furcular fat and a decrease in pectoral muscle (Cooper et al., 2015). It could also mean that the birds from the *Illadopsis* genus in primary forests were lighter than secondary forest birds. It should be noted that the three *Illadopsis* species are combined together, and each had a different count of captures in the two forest types, which might have skewed the MBS in the primary forest as the species have naturally different weights. A way to understand which interpretation is more accurate is to compare the condition index of the species in the two forest types, which is a better indicator of the relative size of energy reserves than the MBS (Paig and Green, 2009). The condition index represents a standardized body mass at a fixed value of a linear body measurement which comes from a scaling relationship between mass and length, whereas the MBS represent the absolute measurements of mass and wingspan.

Effects of forest type and guild on life history and population traits

Summary of main findings

Both ant-follower and insectivores showed no significant differences in the proportion of breeding individuals in primary and secondary forests. I found no significant differences in the proportion of breeding birds at the species or guild levels. The results from both grouping levels contradict the hypothesis that there are more breeding individuals in the primary than in the secondary forests. Also, no significant differences were found between the proportion of moulting birds in the two forest types and the sex ratio of ant-followers and insectivores in the two forest types was not significantly different. Although because differences were found on the proportion of moulting birds at the species level, I cannot exclude the possibility that

there are more moulting birds in primary forest. In contrast, the sex ratio in both the species and the guild level contradict the hypothesis that they will be more female birds in primary forests.

When looking at the proportion of birds that undergo a moult-breeding overlap, no differences were found between the two forest types for either ant-followers or insectivores. Since no differences were found in the proportion of birds that undergo a moult-breeding overlap within the studied species or guilds, I cannot exclude the possibility that there are more moult-breeding overlap birds in the secondary forests compared to primary forests should be dropped. No significant differences were detected in the average MBS between the two forest types for either ant-followers or insectivores. The most surprising result was that there is a significantly higher proportion of adult insectivores in secondary forests compared to primary forests but no significant differences in the proportion of adult ant-followers between the two forest types.

Interpretation of results of forest type and guild on life history and population traits

The comparison between the proportion of breeding ant-followers and insectivores in the two forest types suggests that both guilds have approximately the same proportion of breeding individuals in secondary and primary forests. When comparing the proportion of moulting ant-followers and insectivores between the two forest types, no differences were detected at the guild level, even though some species within the guilds showed differences in the proportion of moulting individuals between the two forest types. This highlights why it is important to conduct more species-specific studies to determine if the biodiversity is affected by disturbances in its habitat.

When comparing the age ratio of ant-followers and insectivores in the two forest types, insectivores showed a significantly higher proportion of adult birds in secondary compared to primary forests, but no significant differences were found for ant-followers. Two of the three species of insectivores (*Sheppardia cyornithopsis* and *Illadopsis spp*) showed a significantly higher proportion of adult birds in secondary forests compare to primary, which

likely explains the significant difference at the guild level. Two of the ant-following species (*Neocossyphus poensis* and *Chamaetylas poliocephala*) also showed a significantly higher proportion of adult birds in secondary forests compared to primary forests. However, one of the ant-following species (*Bleda syndactylus*) had a significantly higher proportion of adult birds in primary forests. Some ant-follower species such as *Alethe castanea* are shown to have big home ranges and to live in big groups to up to 50 individuals, which would suggest that the offspring do not disperse as much as insectivores (Willis, 1986). Combining the age ratios from the ant-follower species could have evened out the age ratio and this might be the reason that no differences were shown at the guild level.

The average MBS of ant-followers and insectivores in the two forest types was also not significantly different, which does not agree with prediction that birds in secondary forests would have a higher MBS. Although, if the analysis for MBS was run only at the guild level, the significantly higher average MBS in secondary forests compared to primary forests within the *Illadopsis* genus would not have been identified. Conducting more species-specific studies is important as some species withstand the effects of disturbances better than others and grouping them all together can lead to misleading results.

Effects of forest type and species/guild on feather corticosterone concentrations

Summary of main findings

No significant differences were detected in the fCORT concentration between the two forest types for any of the studied species that were included in the fCORT analysis. In addition, no significant differences were found in the fCORT concentration between the two forest types for either ant-followers or insectivores. Since the fCORT in the two forest types was not different for any of the studied species nor for any of the guilds, the prediction that the concentration of fCORT in birds in secondary forests would be higher than birds in primary forests was not true. Finally, no significant relationships were found between the fCORT concentration and the MBS of birds overall or in the two forest types. Since no

significant relationships between fCORT concentration and MBS were found, the prediction that there is a positive correlation between fCORT concentration and MBS is not true. It should be noted that feathers from approximately 10 random adult birds from each species in each forest type were used for the fCORT analysis, to make sure that the comparison between the two forest types for each species was accurate. Also, four of the species were from the ant-follower guild and only a combination of the *Illadopsis* species were included from the insectivore guild. Since the *Illadopsis* species were combined together for the fCORT analysis the comparison between the insectivore guild is not accurate and it should not be taken into account as the species have different fCORT concentrations and also not the same number of individuals from each species was used.

Interpretation of results of forest type and species/guild on feather corticosterone

The result from the analysis of the fCORT concentrations between the two forest types suggests that none of the focal species or guilds, had elevated fCORT concentrations in the secondary forests. This does not necessarily mean that these birds were not under stress since fCORT, and GCORT in general, is a single component of a complex group of responses to stress (MacDougall-Shackleton et al., 2019). Furthermore, fCORT only represents stress the bird experienced during the time it was making the specific feather from which the fCORT was extracted. This analysis was performed to examine if there was a clear, significant difference in the fCORT levels of birds in secondary forests and primary forests. Any significant difference between the fCORT concentration would indicate that secondary forests are poorer quality than primary forests and support the analysis of life history and population traits. A study looking at the GCORT concentrations of blue tits (*Cyanistes caeruleus*) in urban and rural habitats is an example where birds were under stress and it affected their reproductive success but did not affect their GCORT concentration (Dominoni et al., 2021). Further studies should use more feathers to compare the fCORT concentrations between the two forest types and maybe include the age as an explanatory variable, as the HPA axis of birds with different ages response differently to

stress (Sapolsky et al., 1986). In addition, studies using other biological responses to stress should be used, for example look at how the DNA methylation of birds in secondary forests is impacted when compared to birds in primary forests. DNA methylation is seen to make it easier for birds to adapt to many environmental stressors. Comparing the levels of DNA methylation between birds from the two forest types would show if secondary forests were a more stressful habitat (Baerwald et al. 2016).

Conclusion

The main findings were that four of the studied species had an older population in the secondary forests than in the primary forests. This skewed age ratio could be due to failed reproductive attempts by those species in the secondary forests or high juvenile dispersal out of the secondary forest. Either scenario will indicate that secondary forests are poor quality habitats for those species compared to primary forests (Holmes et al., 1996; Van Houtan et al., 2007). In addition, one species showed a higher proportion of adult birds in primary forests which could also be interpreted as a sign that secondary forests are bad quality habitats. It is possible that adults from this species dispersed out of the secondary forests due to their poor quality, which can occur in certain Amazonian species (Wolfe, 2003). Three of the studied species had fewer moulting individuals in the secondary forests. This could indicate that birds in secondary forests avoided or delayed moulting to make sure that they did not undergo a moult-breeding overlap, which would potentially leave them with poor quality feathers and reduced reproductive success (Echeverry-Galvis and Hau 2013). However, one species showed a significantly higher proportion of moulting birds in secondary compared to primary forests, which complicates the interpretation of the results. Finally, birds from the *Illadopsis* genus had a higher MBS in the secondary forests, which suggests that birds from this genus had development issues as a result of living in secondary forests. This further suggests that secondary forests are bad quality habitats.

Insectivore species seem to be more sensitive to selective logging than ant-following species. Their populations appear to be more adult based and one of the species also had a higher MBS. Insectivores are often the first guild to reduce in abundance as a response to selective logging in the Afrotropics (Powell et al., 2015; Waltert et al., 2004). The mechanism behind this reduction in their abundance is unknown, but perhaps this is due to low nest, juvenile survival, or habitat-biased juvenile dispersal. This leads to an elder population which, as can be seen from the high average MBS, might have a reduced wingspan (Wikelski and Cooke, 2006).

The results from this study combined with the reduced species richness and abundance of bird species in the area shows the importance of primary forests and the potentially negative effects of selective logging on the local bird populations. Further species-specific studies should be conducted to determine if the patterns that were found in this study are caused by the effects of selective logging and if more species that were not included in this study are being affected.

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