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Physiological stress as a mechanism underlying the effects of forest logging on tropical birds

Dissertation for the degree of Doctor in Science, Biology,

at the University of Antwerp, to be defended by

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Summary

Land-use changes are one main cause of biodiversity loss. Selective logging is the most common technique of timber extraction applied to tropical forests, driving species loss and population abundance changes. One main question to understand species’ responses to selective logging is which proximate mechanisms underlie species abundance changes. In this Ph.D. project I have used a cross-sectional approach to investigate the effects of selective logging on the stress physiology and body traits of understorey birds, and correlative analyses to investigate the effects of physiological changes on population abundance, across unlogged and selectively logged forest of Borneo.

The first goal of the project was to determine which physiological endpoints of vertebrates are affected by forest disturbance. To this end, I reviewed all available literature and used meta-analytical techniques to quantify the size of the effects of different forest disturbances, including selective logging, on physiological and immunological parameters.

I have then investigated the effect of selective logging on the activity of the hypothalamic-pituitary-adrenal (HPA) axis in 10 understorey bird species. I used as marker of HPA axis activity the concentrations of corticosterone, the avian glucocorticoid hormone, deposited in feathers.

Another important physiological mechanism for maintaining homeostasis is the regulation of cellular oxidative status. Thus, I measured eight different markers of oxidative status in 15 understorey bird species living either in unlogged and selectively logged forests. I also investigated differences in the oxidative status between feeding guilds (i.e. insectivores and omnivores) and how they are affected by selective logging.

Last, I tested for differences in body size and body condition index of more than 50 bird species across unlogged and selectively logged forests. Changes in body size and body condition can

be sub-lethal effects of habitat degradation that may act as early signals to predict future population responses. This hypothesis was tested correlating changes in body size and body condition with changes in population abundance between the two types of forest.

Results of this project show (i) small to moderate effects of forest logging on the physiological status of birds and (ii) larger effects on the body size of omnivorous and frugivores bird species. Importantly, I found that differences in feather corticosterone between forest types were linked to those in co-specific population abundance. This result also points to feather corticosterone as a promising tool for monitoring the impacts of sylvicultural practises on understorey birds and predicting the effects on population abundance.

Chapter I

General Introduction

White-crowned shama (*Copsychus stricklandii*)

Menelia VK Illustration

Forest ecosystems cover 31% of the global land area, harbour most of Earth's terrestrial biodiversity, and provide critical ecosystem services for the regulation of global climate cycles (Hairston et al. 2005, FAO and UNEP 2020). From an anthropogenic perspective, forests are important providers of food and timber, and sustain livings of many people. The challenge of balancing economic development and preservation of ecological value of forest ecosystems has emerged in the second half of the past century as an important task of forest management (Li et al. 2011). Nonetheless, deforestation and forest degradation have continued taking place at alarming rates, contributing significantly to the loss of biodiversity (Newbold et al. 2015) and climate changes (Lawrence and Vandecar 2015, Mitchard 2018). Tropical forests historically occupied about 12% of Earth's land area, but today they cover less than 5% (600 million ha.) of the Earth terrestrial surface (Corlett and Primack 2011). Since 1990, about 420 million hectares of forest have been converted to other land uses, typically logging estates, agricultural fields, pastures and urban lands (FAO and UNEP 2020). The increase in human population will further increase the demand for food and hardwood. Much of the projected growth in global populations will occur in developing tropical nations; thus, the fate of tropical forests and their biodiversity is particularly at risk (Laurance et al. 2014).

Tropical forests are primarily degraded by selective logging, which is the most common form of timber extraction for commercial exploitation in the tropics. Selective logging removes only commercially valuable trees above a specified diameter limit, with the intensity of timber removal depending on the density of marketable trees. The remaining forest will be less heterogeneous, with higher prevalence of younger, and smaller trees (BOX 1). Highest intensities of trees' removal typically occurred in South-east Asian rainforests, which are dominated by valuable timber species of the Family Dipterocarpaceae (Johns and Burley 1997). Currently, more than 400 million hectares of natural tropical forest are designated for timber extraction (Blaser et al. 2011), most of which is being done unsustainably (Edwards et al.

2019). Selectively logged tropical forests are now more prevalent than intact old-growth forests in most tropical countries (Lewis et al. 2015).

Selectively logged forests are particularly susceptible to clearing for land-use conversion (e.g. palm oil plantations) because they are perceived as highly degraded forests (Koh and Wilcove 2008). However, recent studies found that negative effects of selective logging on biodiversity are limited compared to other land-use changes, and selectively logged forests still retain high levels of biodiversity (Gibson et al. 2011, Putz et al. 2012). Given the limited extent of remaining undisturbed tropical forests, the preservation of selectively logged forests, along with remaining old-growth undisturbed forests, is increasingly being recognised as pivotal for reaching global goals of tropical biodiversity conservation (Edwards et al. 2014b, Putz et al. 2019). Nonetheless, the impact of selective logging differs significantly among species (Edwards et al. 2011, Ewers et al. 2015, Costantini et al. 2016b), with local abundances of vertebrate and invertebrate species increasing, remaining similar or declining after logging. One important unresolved question is which proximate mechanisms make species resilient or vulnerable to the environmental conditions of selectively logged forests. Understanding how organisms respond and adapt to environmental alterations in a changing world is an important challenge for ecologists to inform focused conservation plans on the short- and the long-term (Wingfield 2013a).

BOX 1 – Ecological impacts of selective logging on lowland rainforests

Tropical forests are typified by tall and heterogeneous canopies with even taller emergent trees, and dark humid forest interiors. Studies conducted in South-East Asian lowland dipterocarp forests found that selective harvesting of large-size trees reduced the canopy height and the crown projection area, leaving a monotonic (i.e. less variable) canopy cover with large forest gaps, for more than 50 years (Okuda et al. 2003, Okuda et al. 2019). The thinner canopies in selectively logged forests can be more easily and homogenously penetrated by sunlight, leading to longer sunfleck time (i.e. transient increase in solar irradiance that occurs in understorey) than in old-growth unlogged forests (Yamada et al. 2014, Hardwick et al. 2015). Despite this, selectively logged forests and unlogged forests of Borneo have similar potential for thermal buffering, and macroclimate and microclimate temperatures are comparable between the two forest types (Senior et al. 2018).

Figure 1 – The two pictures show the forest canopy of an intact old-growth forest (on the left), and a twice-selectively-logged forest (on the right) in Sabah. Photo credit: Rhett A. Butler / Mongabay.

Vegetation cover at canopy and understorey levels is reduced in naturally regenerating selectively logged forests, but vegetation at ground level is similar between the two forest types (Senior et al. 2018). Contrary to unlogged forests, the understorey vegetation in Bornean selectively logged forests is dominated by fast-growing pioneer species (especially *Macaranga* spp), with higher presence of large saplings and fewer large trees, and elevated abundance of lianas (Imai et al. 2019). The heavier liana loads may reduce survival and growth rates of slow-growing trees, but more lianas provide more fruits and nesting sites for understorey bird species, and locomotive support for monkeys and small vertebrates (Magrach et al. 2016). Different taxa and functional groups of invertebrates and vertebrates have changed their local abundance in selectively logged forests compared to old-growth undisturbed forests of Borneo (Edwards et al. 2011, Edwards et al. 2012, Ewers et al. 2015).

Proximate mechanisms underlying changes in population abundance

Understanding cause-and-effect mechanisms of variation in local abundance of animal populations is one major challenge for conservation biologists (Wikelski and Cooke 2006). To this aim, a promising approach is the comparison of physiological and morphological traits among co-specific individuals living in disturbed or undisturbed habitats, and to test how this variation is linked with metrics of fitness, such as reproduction or population abundance (Coristine et al. 2014). Unravelling proximate mechanisms linked to population decline may help conservationists developing new tools for monitoring the efficacy of management strategies, and predicting the long-term viability of animal populations (Fefferman and Romero 2013, Madliger and Love 2015).

Habitat changes can impose abiotic (physical and chemical factors) and biotic (direct and indirect effects of other organisms) stress on species. Coping with environmental changes can be energetically expensive for organisms, thus animals might need to physiologically adjust rapidly to these changes, for instance through physiological acclimatization (Wingfield 2013b, Vitousek et al. 2014). Mechanisms of stress physiology (glucocorticoid hormones and oxidative stress) have been proposed as important molecular mediators of species responses to novel environmental conditions because they may both affect fitness traits, such as survival and reproduction (Romero 2004, Beaulieu et al. 2013). In particular, glucocorticoid hormones (GCs; the most widely used biomarker of stress) may link environmental disturbance with changes in population abundance of wild vertebrates (Hammond et al. 2018, Lea et al. 2018, but see also Martin et al. 2018). Furthermore, habitat changes may also affect the oxidative status of organisms, for example, through reduced availability of dietary antioxidants, increased metabolic demands or higher GCs production (Costantini et al. 2011, Beaulieu and Costantini 2014). Thus, integration of GCs with oxidative stress might provide novel ecologically relevant insights to foster our understanding of the proximate mechanisms underlying population abundance variation in changing environments.

Glucocorticoid hormones

Glucocorticoids are steroid hormones produced by the hypothalamic-pituitary-adrenal (HPA) axis in birds and mammals (Hypothalamic-Pituitary-Interrenal axis in fish, amphibians, and reptiles) in response to internal and external stimuli (Sapolsky et al. 2000, Romero 2004). GCs coordinate organismal responses to predictable and unpredictable circumstances for the maintenance of body energy balance (Sapolsky et al. 2000). At baseline levels, GCs have main roles in the regulation of metabolism, increasing in response to energetic needs. For example, levels of baseline GCs increase in birds when food availability is lower or unpredictable (Kitaysky et al. 2007, Fokidis et al. 2012). In addition, several studies reported positive relationships between investment in reproduction and baseline GCs (e.g., Bonier et al. 2009a, Love et al. 2014), although such relationship may be affected by species life-history traits (Bókony et al. 2009, Apfelbeck et al. 2017, Schoenle et al. 2021). Differently from baseline levels, stress-induced GCs promote energy-saving behaviours that promote survival, which comes at a cost for expensive fitness-related activities, such as reproduction (Wingfield et al. 1998).

GC hormones can be measured in different biological matrices, including blood, faeces, hairs and feathers. For example, concentration of corticosterone (CORT), the main avian GC hormone, deposited in feathers (fCORT), is considered a long-term integrated measure of the HPA-axis activity over the time of growth of the feather (Bortolotti et al. 2008, Romero and Fairhurst 2016). fCORT is a less-invasive marker compared to blood CORT, which is particularly advantageous in studies correlating environmental conditions during feather growth with birds' physiology or fitness proxies. For example, several studies on birds during the pre-reproduction season found that birds with higher fCORT reduced their investment into the next breeding season or had reduced survival probability (Harms et al. 2015, Hansen et al. 2016). Thus, levels of fCORT are a valuable metric to investigate the links between environmental changes and fitness-related traits.

Oxidative stress

Another major physiological mechanism for maintaining homeostasis in changing environments is the regulation of cellular oxidative status (Beaulieu and Costantini 2014). Variation in oxidative status is due to different levels of reactive oxygen species (ROS) production, oxidative damages caused by ROS to biomolecules (e.g. lipids, proteins) and/or enzymatic and non-enzymatic (dietary and endogenous) antioxidant molecules (Costantini 2019). Changes in abiotic and biotic conditions of selectively logged forests may impair the oxidative status of organisms, with possible detrimental effects for fitness traits, such as growth, reproduction, or life span (reviewed in Costantini 2014). Negative effects on fitness traits may arise from increased levels of oxidative damage which compromise survival and reproduction (Costantini 2008, Monaghan et al. 2009), or from higher investment in certain antioxidant mechanisms (e.g. glutathione system) that might require a trade-off between self-maintenance and fitness traits. Experimental studies inducing oxidative imbalance in birds have reported negative effects on the expression of fitness-related traits (Costantini 2019). For example, the suppression of glutathione synthesis reduced clutch size in canaries *Serinus canaria* (Costantini et al. 2016a), and song rate in common starlings *Sturnus vulgaris* (Messina et al. 2017). To the best of my knowledge, very little attention has been paid to assess whether oxidative status varies across environments and is linked to differences in population abundance.

Body size and body condition index

Changes in body size and body condition may signal unfavourable environmental conditions, and can potentially be used to predict future population decline in vertebrates (Janin et al. 2011, Irwin et al. 2019). Environmental stressors during early-life stages have permanent impacts on individuals' phenotype, possibly mediated by GCs hormones and oxidative stress (Groothuis et al. 2005, Monaghan et al. 2009). Studies on birds found smaller body size in individuals living in secondary tropical forests (Smith et al. 2008) or in cities (Liker et al. 2008, Caizergues et al. 2021), compared to the undisturbed habitat. On the one hand, reduced body size can indicate unfavourable environmental conditions, for example, due to low availability of food during the critical stages of growth. On the other hand, morphological changes in new environments may be the result of successful coping strategies. For example, to reduce the probabilities of nest location discovery from predators, parents may reduce food provisioning rate constraining nestlings' development, with limited or no effects on nestlings' survival (Martin 1995, Remeš and Martin 2002). Changes in adult body condition index (BCI) reflect variations of energy stores (mainly fat mass) accumulated in the body, available to support energetically demanding life processes, such as reproduction (Peig and Green 2009). Higher foraging activity and lower diet quality can reduce BCI, respectively, via increased metabolic rate and reduced intake of nutrients (Köhler et al. 2012). A recent experimental study on common bulbuls (*Pycnonotus barbatus*), a tropical omnivorous bird, showed that adult birds fed on fruits were in better condition than individuals fed on invertebrates, indicating important causal effects of diet composition on birds' body condition (Nwaogu et al. 2019).

Mechanisms of phenotypic variation

Genotype and environment interact through development to determine biochemical, physiological, and morphological traits (Fig. 1). Comparative analyses of mean trait values across populations can provide insights into the mechanisms of phenotypic adaptation to new environmental conditions, but such analyses cannot differentiate between evolved differences and environmentally driven plasticity in trait expression (Bonier and Martin 2016; BOX 2). Rapid evolutionary responses of wild vertebrates may occur within decades from the onset of anthropogenic environmental changes (Reznick and Ghalambor 2001, Hairston et al. 2005, Ellner et al. 2011), but Hendry et al. (2008) found evidence for a major contribution of phenotypic plasticity over genetic variation in driving rates of phenotypic changes in anthropogenically modified habitats. Assessing the relative role of genetic variation and phenotypic plasticity goes beyond the aims of this project, but possible mechanisms driving phenotypic variation in the study species are integrative parts of the discussion of my results.

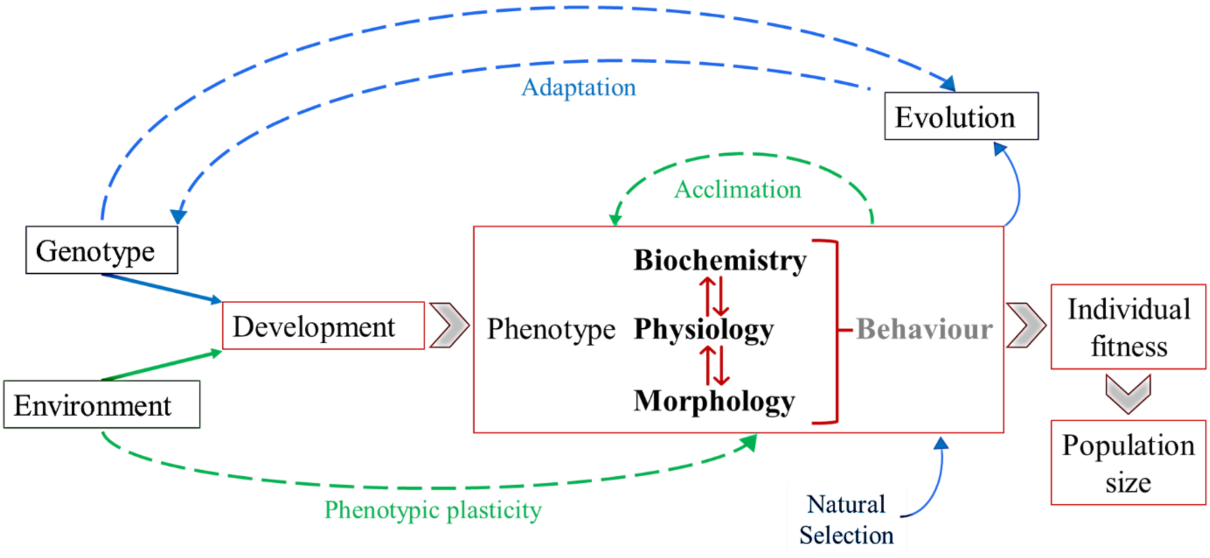

Fig. 1 – The genotype and environment interact through developmental processes to give a particular phenotype a suite of biochemical, physiological and morphological traits. The phenotype also includes behaviour, which is limited by all the other phenotypic characters. Phenotypic traits and plasticity influence individual fitness that govern population performance. Modified from (Willmer et al. 2017).

BOX 2 – Glossary

Adaptation involves the **selection** for particular **genotypes** that improve reproductive fitness or survival over multiple generations, with consequent change of genetic variation in the population. Studies of natural populations show that ecologically important evolutionary changes can happen rapidly, within few decades (Thompson 1998, Hairston et al. 2005).

Acclimatization (component of **phenotypic plasticity)** is a reversible process by which an individual adjusts physiologically to a change in its environment in order to maintain performance and fitness (Fox et al. 2019). The capacity for acclimatization can be affected by **epigenetic** modifications or **maternal effects** (Kappeler and Meaney 2010).

Epigenetic modifications are heritable molecular changes of the genome (e.g. methylation) that occur without changes in the nucleotide sequence (Riggs and Xiong 2004).

Maternal effects are the causal influence of maternal phenotype on the phenotypes of her offspring (Bernardo 1996).

The study area

The island of Borneo was covered with evergreen rainforests until the 1950s, but deforestation has decreased total forest cover to around 50% of its original area (Langner et al. 2007, Gaveau et al. 2014, Gaveau et al. 2019). For the Malaysian state of Sabah (North Borneo), logging played an important role in raising the economy through the 1970s, 1980s and well into the 1990s (Reynolds et al. 2011). After decades of commercial timber exploitation and subsequent conversion of the land cover to palm oil plantations in Sabah, pristine forests are reduced to less than 20% of the actual forested areas (Bryan et al. 2013).

The Yayasan Sabah (YS) logging concession (Fig. 2) is one of the largest (~1 million hectare) and biologically most important areas of lowland dry dipterocarp forest in Sabah (Lambert and Collar 2002). Within the YS logging concession, I conducted fieldwork in the 45,200 ha of unlogged old-growth forest within the Danum Valley Conservation Area (DVCA) and adjacent Palum Tambun Watershed Reserve, and in the contiguous 238,000 ha of selectively logged forest within the Ulu Segama-Malua Forest Reserve (US-MFR). These dipterocarp forests are dominated by the presence of trees of the Family Dipterocarpaceae,

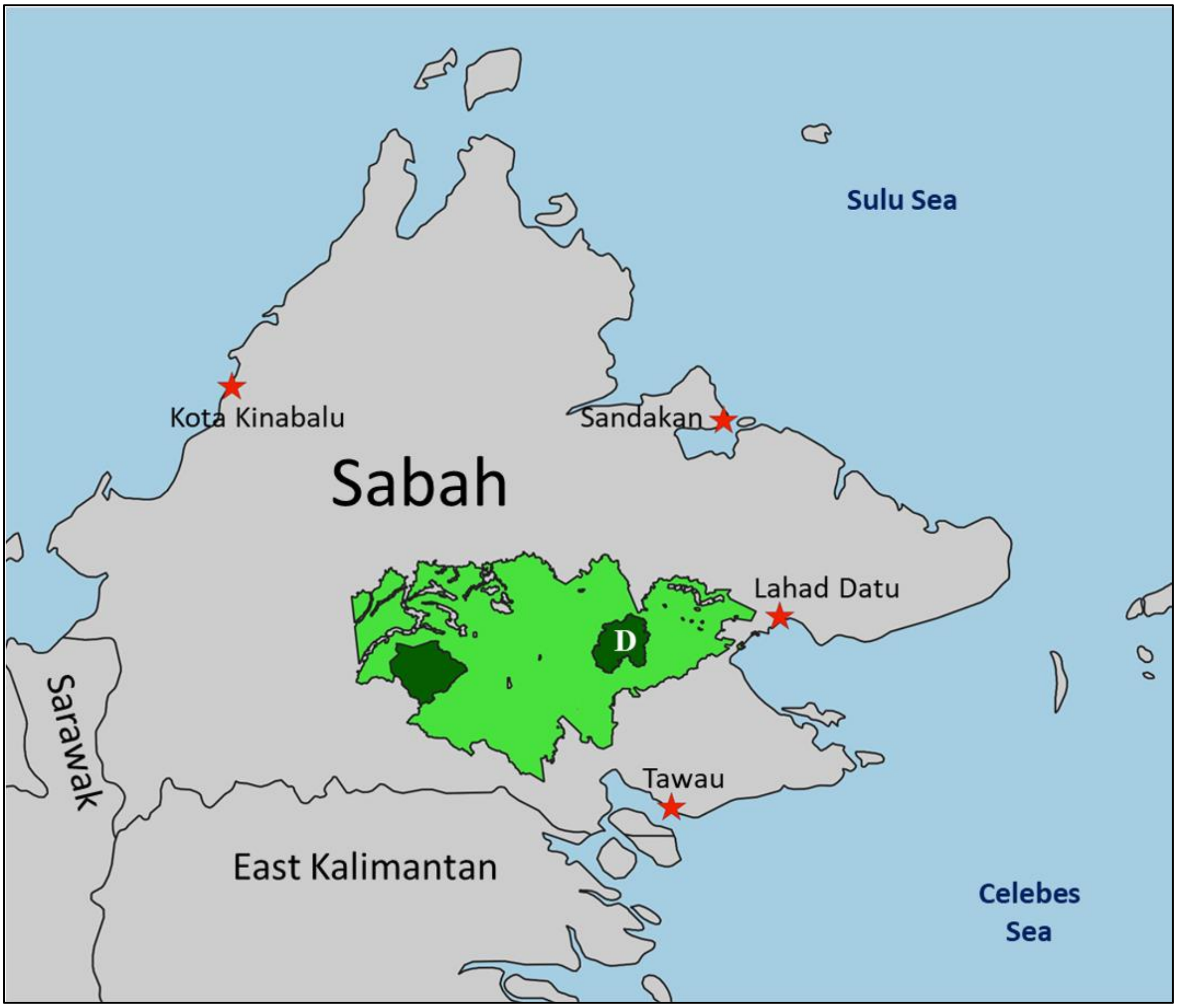

Fig. 2 –In light green, the Yayasan Sabah logging concession (YS), within the Malaysian state of Sabah in Borneo. In dark green, protected areas of old-growth undisturbed forests within the YS; the Danum Valley Conservation Area is marked with a D letter. Red stars correspond to main cities of Sabah.

which are valuable timber species. Selective logging in the US-MFR occurred in the late 80's and early 90's at high rates of timber removal (~115 m^3 ha^{-1}), cutting-down all commercially valuable trees of more than 0.6 m diameter. A second rotation of timber removal occurred between 2000 and 2007, with the minimum tree diameter for extraction reduced to more than or equal to 0.4 m, which left a heavily disturbed forest (~31 m3 ha-1 of additional wood extracted; Fisher et al. 2011). After the last logging rotation, the forest was left to recover naturally.

Aims of the study

The aims of my project are to identify possible proximate mechanisms linking forest disturbance and status of vertebrates. First, I used a meta-analytical approach to identify which physiological and immunological metrics are mostly affected by forest disturbance, then I used cross-sectional studies to investigate physiological and morphological responses of a number of understorey bird species, belonging to different families and feeding guilds (BOX 3; Table 1), to forest selective logging in Borneo. Further, to investigate links between phenotypic changes and population abundance variation, I tested for correlations between the effect sizes of species' physiological or morphological differences between forest types and shifts in population abundance, between unlogged and selectively logged forests.

In **Chapter II**, I reviewed the literature on the effects of different types of forest disturbance (e.g., logging, fragmentation) on a number of physiological, immunological, and hematological traits of vertebrates and I used meta-analytical technique to estimate the size of effects and to synthesize relevant literature.

In **Chapter III**, I tested for differences of fCORT levels in 10 understorey bird species, between unlogged and selectively logged forests, because I expected to find higher levels of fCORT in the type of forest where a population is less abundant. Furthermore, I tested whether the differences in fCORT levels were associated with within-year or next-year variation in local abundances of birds between forests. I expected to find significant within-year association between fCORT and the relative population abundance if CORT production reflects current conditions in the forest; and significant association between fCORT and the relative population abundance of the subsequent year if any carry-over effects would have occurred.

In **Chapter IV**, I measured eight blood-based markers of oxidative damage and antioxidants, in 15 understorey bird species, to test for the effects of forest logging on oxidative status. I expected to find: (a) higher oxidative damage in birds living in selectively logged forest if the new environmental conditions are metabolically stressful; and (b) similar antioxidant levels between birds of logged and unlogged forests if they are physiologically adapted (or acclimatised) to the new environment. I also tested whether higher abundance of birds in a given type of forest will be negatively associated with (a) oxidative damage levels owing to its detrimental effects on reproduction or survival, and (b) antioxidant levels if the need to upregulate them is costly for the individual.

Species included in **Chapters III** and **IV** were selected based on their capture rates and local changes in abundance during the years previous to my fieldwork, and they are representative of the understorey avifauna of the forest (Ansell et al. 2011, Edwards et al. 2011). I did not collect tail feathers and blood samples at same time from any individuals, to reduce the impact on their energetic balance which could have affected recapture rates. For this reason, some species were different between studies in **Chapters III** and **IV**.

In **Chapter V**, I tested for differences in body condition index and body size of 51 and 54 bird species respectively, across unlogged and selectively logged forests, to investigate impacts of the new environmental conditions on species' current energetic balance and post-natal development. I also tested if changes in body size and body condition were associated with that in population abundance, to investigate patterns of causality at community level. If environmental conditions in selectively logged forest were detrimental for birds, I expected to find reduced body size and/or BCI, along with lower population abundance.

Finally, in **Chapter VI** I summarize and discuss all the obtained results, and suggest future research directions to further understand proximate mechanisms of adaptation to forest logging.

Box 3 – Common Families of birds in lowland forests of Sabah (Billerman et al. 2020)

Pellorneidae: ground babblers are long-legged, short tailed birds which spend most of the time on the ground or in lower vegetation. Pellorneids feed almost entirely on insects and spiders, worms, and snails, mostly by probing the soil, and picking through leaf litter. Others glean insects from leaves and branches, most often in lower strata.

Photo credit: Suntoro Tjoe

Timaliidae: tree babblers occupy all strata of Asian forests, but only a few spend much time on the ground. Many species are quite social, but a few appear to be monogamous, defending simple all-purpose territories. Timaliids feed primarily on insects and other invertebrates, mostly gleaning them from leaves and branches.

Photo credit: Richard Chong

Muscicapidae: Old World flycatchers are upright-postured birds, most of which catch their prey by gleaning or pouncing on insects on the ground, as well as sallying into mid-air. Muscicapids feed mostly on insects and other invertebrates, but in a few species berries and seeds are a significant part of the diet.

Photo credit: Alex Bernard

Pycnonotidae: bulbuls are mid-sized passerines with an irresistible fondness for fruit. Their diet includes also seeds, leaves, nectar, and invertebrates. Pycnonotids mostly feed by gleaning from branches, but insect prey may also be caught during sallying flights. Their name “bulbul” derives from the Persian word for nightingale (an unrelated species).

Photo credit: James HP Neoh

Nectariniidae: sunbirds and spiderhunters are primarily insectivorous, but most also rely heavily on nectar, using their long, pointed bills to reach deep into flowers. The tongues of nectarinids are brush-tipped and have a tubular shape much like those of hummingbirds. Most sunbirds are territorial in the breeding season, while spiderhunter are often trapliners.

Photo credit: Ganesh R. Mandavkar

Table 1 – Common species of understorey birds used in this project. Feed. Str. = feeding strata; Br. Sea. = breeding season; Cl. Siz. = clutch size; ab. gr. = above ground (Billerman et al. 2020).

		Species name	Diet & Feed. Str.	Nesting	Br. Sea.	Cl. Siz.
Pellorneidae		Black-capped babbler *Pellorneum capistratum*	-Insects, worms, snail, spiders. -On ground.	-Cup -Ground/bushes - ~0.5 m ab. gr.	Apr-Jun	2
		Ferruginous babbler *Pellorneum bicolor*	-Insects -Understorey	-Cup -On plants -up to 2 m ab. gr.	Feb-Sep	2
		Short-tailed babbler *Pellorneum malaccense*	-Insects -On ground	-Cup -ground/small saplings	Feb-Sep Nov	2-3
		Horsfield's babbler *Turdinus sepiarius*	-Insects -Mostly on gr.	-Cup -On saplings -Up to 1 m ab. gr.	Feb-Sep Nov	2
		Scaly-crowned babbler *Malacopteron cinereum*	-Arthropods -Understorey, middle-storey	-Cup -On saplings or bushes -Up to 1.2 m ab.	May-Jul	2
Timaliidae		Gray-headed babbler *Stachyris poliocephala*	-Insects -Understorey	-Dome -On ground	Apr-Sep	2
		Chestnut-winged babbler *Stachyris erythropterum*	-Insects -Understorey	-Dome -On creepers, saplings or bushes -0.4 to 5 m ab. gr.	Dec-Sep	2-3
Leiotric.		Brown fulvetta *Alcippe brunneicauda*	-Insects -Understorey, lower mid-storey	Unknown	May-Jul	Unk.
Muscica.		White-crowned shama *Copsychus stricklandii*	-Insects; fruits (occasional) -Understorey	-Cavity -trees and bamboos -2 to 5 m ab. gr.	Sep-Oct Jan-May	2-3
Pycnonotidae		Hairy-backed bulbul *Tricholestes criniger*	-Fruits, arthropods -Understorey, middle-storey	Unknown	Feb-Aug	Unk.
		Yellow-bellied bulbul *Alophoixus phaeocephalus*	-Fruits, arthropods -Understorey, middle-storey	Unknown	Apr-Aug	2
Nectarin.		Little spiderhunter *Arachnothera longirostra*	-Nectar, insects, spiders -Understorey	-Cup with entrance hole -Underside leaf -Understorey	Mar-Apr Sep-Jan	2-3

Chapter II

Physiological and immunological responses of birds and mammals to forest degradation: A meta-analysis

Simone Messina, David P. Edwards, Marcel Eens, David Costantini

Biological Conservation 224: 223-229 (2018)

Abstract

Dramatic changes in species composition have been found following selective logging and forest fragmentation. The different responses of bird species to these disturbances suggest that some species are more sensitive to environmental changes than others. Recent studies have suggested that the chances of species to adapt to new environments may be mediated by their stress physiology and immunity. We reviewed and performed a meta-analysis of studies that compared physiological and immunological endpoints of bird and mammal species between degraded (logged and fragmented) forests and undisturbed forests. We found that stress hormones and immunity markers show consistent changes in response to habitat degradation in birds and mammals. Higher physiological and immunological responses were found in those animals living in forests that were subjected to clear-cutting. Furthermore, we found that birds and species belonging to IUCN ‘Threatened’ categories exhibited significantly larger effect size estimates than mammals and ‘Least Concern’ species, respectively. Our meta-analysis revealed that changes in the production of stress hormones and in some immune traits are a significant consequence of forest disturbance. Physiology and immunity might be two important mediators of the adaptiveness of a given species to changing forests.

Introduction

Land-use change is a key driver of the global extinction crisis, driving losses in biodiversity and functional diversity (Newbold et al. 2015, Tilman et al. 2017). Selective logging and conversion to agricultural lands or pastures, fragmenting natural habitat and increasing edge effects, are the main processes by which humans are modifying natural landscapes worldwide (Fletcher et al. 2007, Lewis et al. 2015). Such habitat changes alter abiotic conditions and biotic interactions, leading to changes in species' population and community structure (Fahrig 2002, Ries and Sisk 2004, Bogdziewicz and Zwolak 2013, Perry and Thill 2013).

Although primary forests and strictly protected areas are vital to achieve global biodiversity goals (Laurance et al. 2012, Chaudhary et al. 2016), their relatively small areal extent means that logged and secondary forests are increasingly recognised to be essential to preserve global biodiversity (Edwards et al. 2014b). In particular, mature logged forests retain a similar species richness to that of primary forests and far higher than that of agricultural and agroforestry systems (Gibson et al. 2011, Putz et al. 2012, Newbold et al. 2015). Protecting logged forests from land-use change thus provides a valuable contribution to slowing biodiversity loss (Edwards et al. 2011, Lewis et al. 2015).

Species adaptiveness to environmental changes may be determined by a number of factors, including ecological, functional or morphological traits. For example, Hamer et al. (2015) found that bird species from a single-source feeding guild (i.e., dietary specialists) are more prone to decline in selectively logged forests than species that use two or more groups of food. Other studies observed that different forest dependent bird and mammal species, such as cavity-nesting (e.g., pine marten: *Martes martes*; white-backed woodpecker *Dendrocopos leucotos*) and larger-bodied (e.g., northern spotted owl *Stryx occidentalis*; baird's tapir *Tapirus bairdii*) species, are particularly sensitive to clear-cutting and fragmentation (Wasser et al. 1997, Fisher and Wilkinson 2005, Czeszczewik and Walankiewic 2006, Jordan et al. 2016).

By contrast, a recent study investigating edge sensitivity of endotherms found lower edge-sensitivity in large compared to small-to-medium-sized forest mammals, and minimal evidence supporting a positive relationship between edge-sensitivity and body size in birds (Pfeifer et al. 2017).

Although we now have a better understanding of the functional and morphological traits that determine whether a species is going to decline or succeed in degraded environments (Gray et al. 2007, Edwards et al. 2013b, Pryde et al. 2016), there remains a need to understand the physiological mechanisms that determine how organisms respond and adapt to environmental alterations (Wingfield 2013a). A recent meta-analysis of the impact of selective logging on tropical birds and mammals concluded that there are unidentified explanatory variables that determine a species' response to logging and pointed to the importance of physiology as a mediator of the consequences of land-use change (Costantini et al. 2016b).

The study of physiological responses of vertebrates to habitat changes has an extraordinary potential to recognize environmental stressors and to quantify their potential impact on individual reproductive fitness (Wikelski and Cooke 2006, Coristine et al. 2014). The stress response of vertebrates to environmental stimuli is mediated by glucocorticoid hormones, which are the end products of a hormonal cascade modulated by the hypothalamic-pituitary-adrenal (HPA) axis in response to stress exposure (Romero 2004). Quantification of glucocorticoids in biological matrices (e.g., plasma, feces, feathers) is one of the most widely used approaches to assess the physiological stress state of organisms (Johnstone et al. 2012b). For instance, Suorsa et al. (2003) showed that Eurasian treecreeper (*Certhia familiaris*) chicks from young regrowth forests exhibit higher plasma corticosterone (CORT) than chicks from sparse, old forests.

Habitat alterations can also affect the immune system, hematological parameters and parasite load. Immunosuppression resulting from habitat changes may represent an adaptive form of energy savings or a direct effect of allostatic overload (McEwen and Wingfield 2003, Martin 2009). Irwin et al. (2010) found that diademed sifakas (*Propithecus diadema*) inhabiting fragments of selectively logged forest exhibit lower levels of white blood cell (WBC) and packed cell volume (PCV) compared to individuals living in undisturbed forests. Renner et al. (2016) found that blackcaps (*Sylvia atricapilla*) and chaffinches (*Fringilla coelebs*) were more likely to acquire an infection in less structured forests, even if they exhibited different immune responses.

In this article we have reviewed, for the first time, studies that compared physiological and immunological endpoints of bird and mammal species between degraded (logged and fragmented) forests and undisturbed forests. We conducted a meta-analysis to estimate the size of the effects of logging and fragmentation and we assessed whether the effect size differs between birds and mammals and between species with different International Union for Conservation Nature (IUCN) Red List status.

Materials and Methods

Data collection

We focused on studies that compared glucocorticoids, immune endpoints and hematology (Table A1, Appendix B) of mammals and birds between disturbed and undisturbed (control) forests. As types of forest disturbance we considered clear-cutting, selective logging, fragmentation and edge effects. We considered only studies where selective logging occurred within 10 years of data collection. Forest fragments frequently visited for ecotourism were not taken into account because tourism can affect species' stress responses (Müllner et al. 2004, Shutt et al. 2014). Reptiles and amphibians have been excluded due to the scarcity of results found in the literature (1 and 3 studies respectively matched our search criteria). We performed a review of the literature on the Web of Knowledge using combinations of the keywords "forest log*", "clear cutting", "forest disturb*", "forest fragm*", "forest edge", with "glucocort*", “corticostero*”, “cortisol”, “parasit*”, “stress physiol*” and “health parameter*”. The last search was conducted on 18 September 2017. This search resulted in the screening of approximately 2,100 articles.

From each article that matched our search criteria, we collected sample sizes and statistical outcomes (mean, standard error or standard deviation or 95% confidence interval) of the response parameters considered, in undisturbed and disturbed forests. If data were not reported in the text or tables, we extracted them from graphs using the software GetData Graph Digitizer (Fedorov 2014). When extraction of data was not possible, the authors were contacted. Twelve out of 16 authors responded (Appendix B) and eight of them provided data which were used to calculate the effect size.

Effect size calculation

We calculated effect size Hedges’ *g* from test statistics collected from selected papers using the *compute.es* package (Del Re 2013) in R (R Core Team 2013). Hedges’ *g* is the result of the multiplication of Hedge’s *d* (i.e., standardized mean difference) with a correction factor calculated from the degrees of freedom. This conversion is necessary due to the small within-study sample sizes (Cooper et al. 2009, Smith et al. 2016). Our work included 170 effect size estimates from 28 studies (Table A1, Appendix B) (Wasser et al. 1997, Mazerolle and Hobson 2002, Chapman et al. 2006, Lucas et al. 2006, Martínez-Mota et al. 2007, Trejo-Macías et al. 2007, Wells et al. 2007, Arriero et al. 2008, Gillespie and Chapman 2008, Cottontail et al. 2009, Mbora et al. 2009, Irwin et al. 2010, Johnstone et al. 2011, Jaimez et al. 2012, Johnstone et al. 2012a, Leshyk et al. 2012, Butler et al. 2013, Grava et al. 2013, Leshyk et al. 2013, Rivers et al. 2013, Balestri et al. 2014, Mastromonaco et al. 2014, Rangel-Negrin et al. 2014, Aronsen et al. 2015, Santicchia et al. 2015, Carlitz et al. 2016, Rakotoniaina et al. 2016, Cantarelli et al. 2017). For the statistical analyses, all estimates of effect size were made positive because we were interested in the magnitude of the effect rather than in the direction. Effect sizes were considered to be small (Hedges g=0.2, explaining 1% of the variance), intermediate (g=0.5, explaining 9% of the variance) or large (g=0.8, explaining 25% of the variance) as suggested by Cohen (1988).

Meta-Analysis

The effect of logging on physiological and immunological parameters can be influenced by various factors. For this reason we included in the analysis some explanatory variables (termed moderators in meta-analysis). An important moderator is the ‘Disturbance’ occurring in the forests and this moderator included ‘Clear Cutting’, ‘Selective Logging’, ‘Fragmentation’ and ‘Edge Effect’. Selective logging and clear-cutting occurred in tropical and temperate biome, respectively (only two studies reported selective logging in temperate forests, none reported clear cutting in the tropics), and thus to avoid redundancy we did not include biome as moderator in the meta-analysis (MA).

To assess whether the effect of disturbance varies among physiological endpoints, we also included in the analyses the moderator ‘Parameter’ categorized as follows: (1) ‘Hormonal Response’ (e.g., corticosterone and cortisol measured in scats, integument or blood); (2) ‘Immunity’, which included white blood cell counts (WBC) and relative presence of different WBC types; (3) ‘Parasite-load’ measured in blood, feces or ectoparasites; and (4) ‘Hematology’ including a range of reference blood values (e.g., electrolytes, enzymes, vitamins).

Stress hormones measured in different substrates or following a capture-restraint protocol may change in their intensity of response to disturbance. Thus, we tested whether there were differences in effect size among the subcategories of ‘Hormonal Response’: ‘Baseline’ (corticosterone or cortisol measured in plasma collected within 3 minutes from the capture), ‘Stress Induced’ (corticosterone or cortisol measured in plasma collected after a restraint protocol), ‘Short-term’ and ‘Long-term’ (corticosterone and cortisol measured in scats and integument (fur or feathers), respectively).

We finally tested for the moderator ‘Class’ (‘Birds’ vs. ‘Mammals’ or ‘Birds’ vs. ‘Primates’ vs. ‘Other Mammals’, because primates were the most representative taxa within mammals) and the moderator ‘IUCN’, which indicates the conservation status of the study species. We considered ‘Least Concern’ category versus ‘Threatened’ category (near threatened, vulnerable, endangered and critically endangered pooled together).

Meta-analytic technique

The rma.mv function of the *metafor* package of R (R Core Team 2013) was used to implement our meta-analytic multilevel mixed-effects models. To test the absence of publication bias we performed funnel plot analysis of ‘unsigned g’, and to quantify the bias we calculated the fail-safe N using Rosenthal approach (Rosenthal 1979). The fail-safe N represents the minimum number of additional studies that would be needed to overturn the results of the meta-analysis. We used the Hedges’ *g* values weighted for their variances (calculated using compute.es) as response variables in our statistical models. Estimates of effect size derived from the same article or from the same species are not independent, thus to control for pseudoreplication we included as random factors the article ‘ID’ and the ‘Species’. The factors ‘Class’ and ‘Parameter’ were also included as random factors in the models; they were retained in the models whether they improved the fitting of the model tested by Akaike Information Criterion with correction for small sample sizes. The QE-test for residual heterogeneity was performed to test whether there is significant unexplained variance not accounted for by the moderators included in the model. The QM-test of model coefficients was performed to test the effects of moderators and predictions of mean and 95% confidence interval of single moderators were calculated.

Results

The symmetrical shape of our funnel plot indicates the absence of publication bias in our dataset (Fig. A1, Appendix A). Moreover, the fail-safe number was very large (N = 23,725).

Unsigned effect size estimates were generally small to intermediate according to Cohen (1988). The effect of forest disturbance on species' physiology and immunology was significantly larger for 'Birds' compared to 'Mammals' (Q_M = 5.64, df = 1, *P* = 0.0176) and for 'Threatened' species compared to 'Least Concern' species (Q_M = 10.39, df = 1, *P* = 0.0013). To reduce differences in sample size between 'Birds' and 'Mammals' categories (see Table A1, Appendix B), we split the latter in 'Primates' and 'Other Mammals', respectively. The effect of category was still significant (Q_M = 8.3287, df = 2, *P* = 0.0155; Figs. 1 and 3) with both mammal categories exhibiting lower effect size estimates than birds ('Primates': mean = 0.36, CI = 0.26-0.47; 'Other Mammals': mean = 0.25, CI = 0.12-0.38; 'Birds': mean = 0.52, CI = 0.37-0.66).

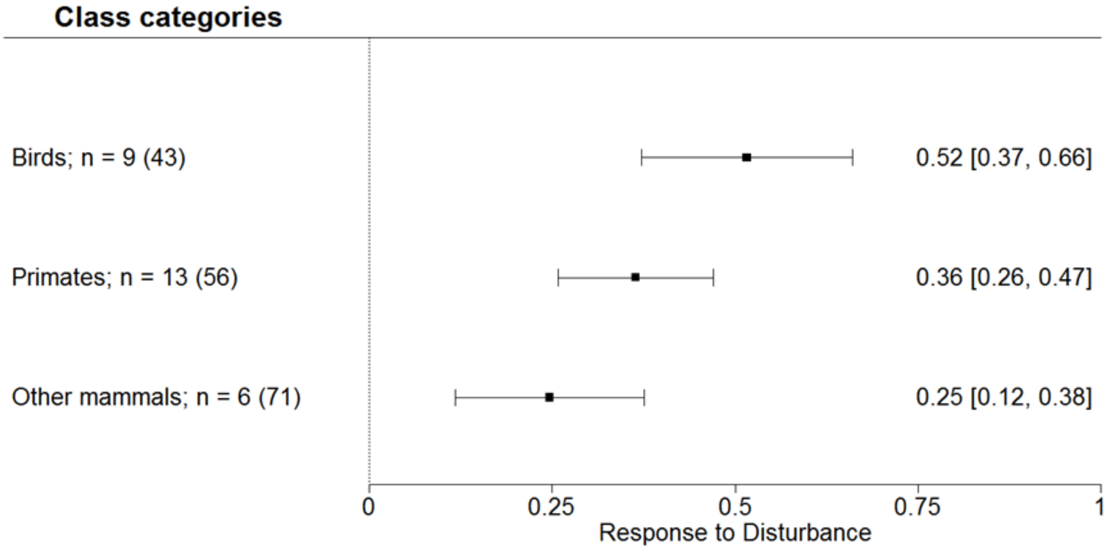

Figure 1. Predicted unsigned effect sizes (mean and 95% confidence interval) for Class categories. 'n' is number of studies (number of effect sizes).

The effect size of forest disturbance significantly differed among parameters (Q_M = 9.41, df = 3, *P* = 0.0243). The size of effect (i.e., response to disturbance) was larger for immunity (mean = 0.42, CI = 0.29-0.56) and stress hormones (mean = 0.44, CI = 0.32-0.55) than for hematology (mean = 0.31, CI = 0.18-0.45) and parasites load (mean = 0.31, CI = 0.21-0.42; Fig. 2). A pairwise comparison, however, highlighted significant differences between immunity and hematology only (Table 1). The subcategories of 'Hormonal responses' did not significantly differ in effect size (Q_M = 3.25, df = 3, *P* = 0.3546).

Table 1. Pairwise comparison between effect sizes for (A) 'Disturbance' and (B) 'Parameter' categories.

Pairwise comparison	Estimate	Standard Error	*P* value
A. Disturbance			
Clear Cutting – Selective Logging	-0.142	0.098	0.1504
Clear Cutting – Fragmentation	-0.200	0.092	0.0328*
Clear Cutting – Edge Effect	-0.274	0.117	0.0193*
Selective Logging - Fragmentation	-0.054	0.075	0.4742
Selective Logging - Edge Effect	-0.132	0.106	0.2146
Fragmentation - Edge Effect	-0.08	0.099	0.431
B. Parameter			
Hematology – Hormones	0.14	0.09	0.1213
Hematology – Immunity	0.112	0.044	0.011
Hematology – Parasites	-0.002	0.07	0.98
Hormones - Immunity	0.028	0.09	0.7595
Hormones - Parasites	-0.138	0.08	0.0869
Immunity - Parasites	-0.1103	0.07	0.1157

Non-significant differences were found for overall forest disturbances (Q_M = 6.54, df = 3, *P* = 0.0881). However, clear-cutting (mean = 0.52, CI = 0.36-0.69) showed a larger effect size compared to other disturbances (Fig. 2). Significant differences emerged between clear-cutting and fragmentation (mean = 0.33, CI = 0.22-0.44) or edge-effect (mean = 0.25, CI = 0.07-0.43; Table 1), respectively.

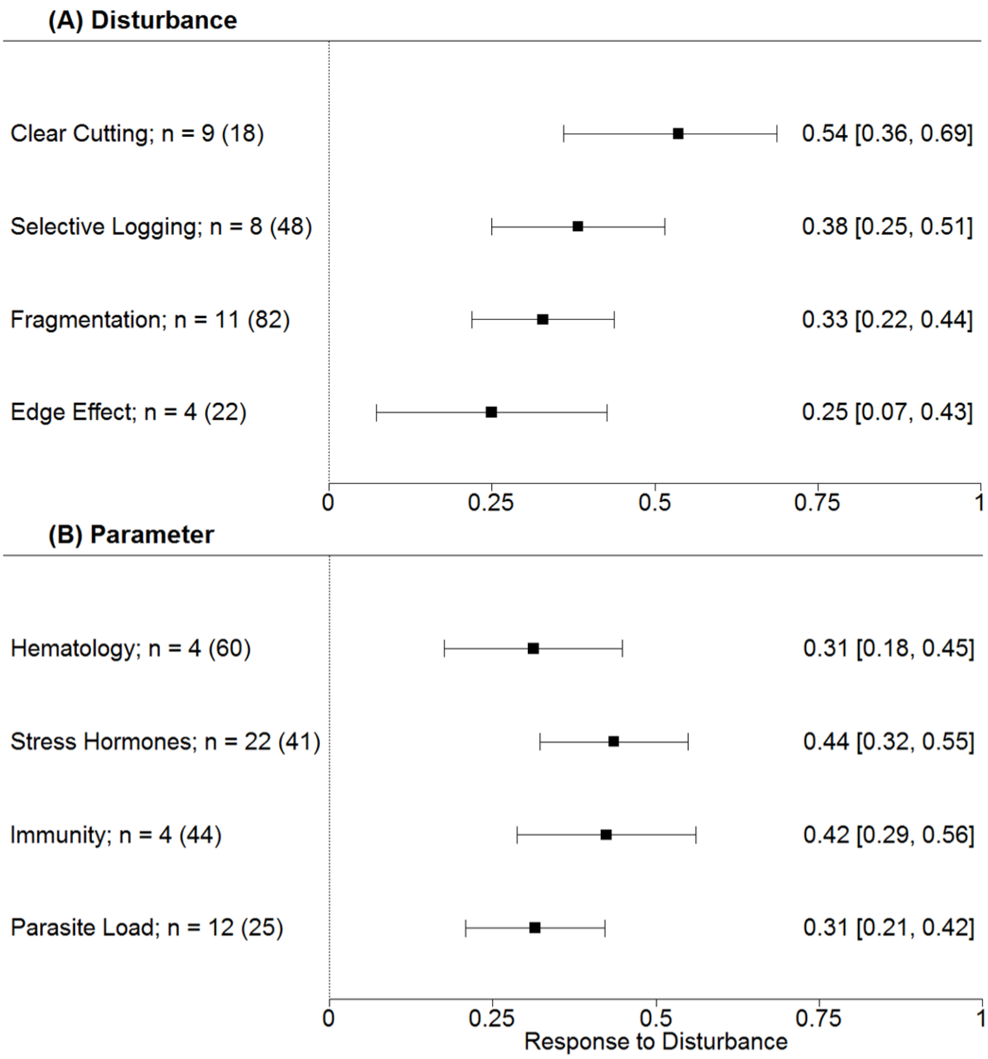

Figure 2. Predicted unsigned effect sizes (mean and 95% confidence interval) for Disturbs and Parameters categories. ‘n’ is number of studies (number of effect sizes).

The significant levels of residual heterogeneity revealed by Q_E-test (Table 2) indicated that moderators used in this meta-analysis were not sufficient to explain all the variance.

Table 2. Q_E-test for residual heterogeneity.

Model	Q_E	d.f.	P value
Disturb	212.949	166	0.0081*
Class (Birds vs Mammals)	220.818	168	0.0039*
Class (Birds vs Primates vs Other Mammals)	213.609	167	0.0086*
Parameter	232.804	166	0.0005*
IUCN	226.148	168	0.0019*

Discussion

Fragmented and selectively logged forests now dominate globally and can harbour high levels of biodiversity compared to agricultural fields, but how individual species respond physiologically to disturbance remains an open question. Stress physiology (e.g., glucocorticoid hormones) mediates a rapid organismal response to environmental changes before genetic adaptations occur and such responses may have an important role in determining the chances of a species to adapt to new environments. Using a meta-analytical approach, we found that stress hormones and immunity markers show consistent changes in response to habitat degradation in birds and mammals (Fig. 1). Furthermore, stronger physiological and immunological responses were found (i) in animals living in forests that were subjected to clear-cutting (Fig. 2), which is the most destructive method of logging, and (ii) in those species that are currently classified as threatened by IUCN. Finally, we also found that in birds the effect size of physiological and immunological responses to habitat degradation was higher than that of mammals, even if the among species variation in effect size estimates was high (Fig. 3).

Mean effect size estimates in our MA were generally small to intermediate, in line with findings in ecological and physiological research (e.g., Møller and Jennions 2002, Dantzer et al. 2014). This result might be due to the fact that all studies included in our MA were conducted in the wild, where many sources of variation could not be taken into account. However, small to intermediate effect size are thought to be biologically meaningful when showing consistent patterns of variation (Garamszegi 2006), as shown by most of the 95% confidence intervals of the predicted variables included in this MA.

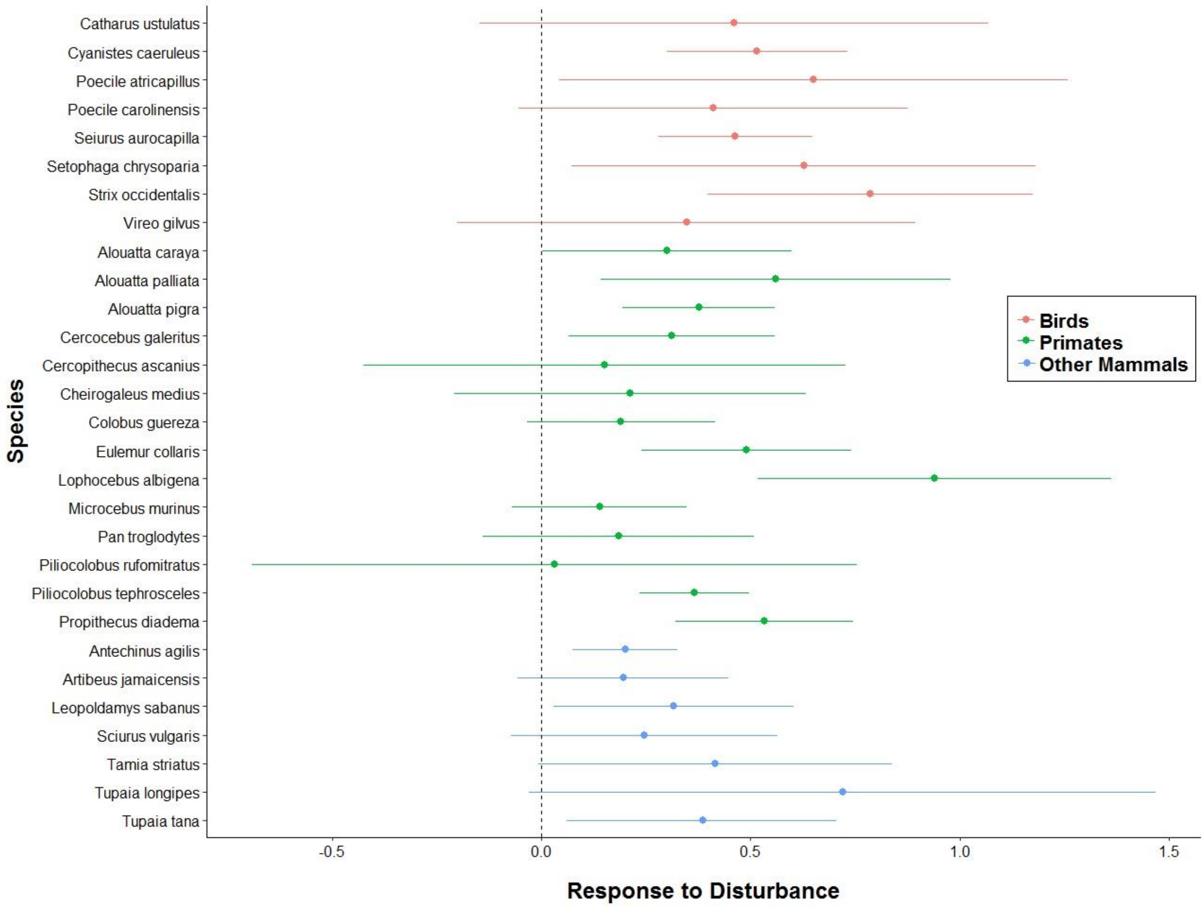

Figure 3. Bird, Primate and Other Mammal species response (unsigned mean ES and 95% confidence interval) to forest disturbance.

The use of unsigned effect size in our MA allowed us to find a general marked response of stress hormones in those animals living in disturbed forests. The high responsiveness of stress hormones indicates the implication of the HPA axis in the mechanisms of adaptation of bird and mammal populations to habitat changes (consequent to the regulation of glucocorticoids level). We chose to not investigate the direction of the physiological response (i.e., increase or decrease) for three main reasons: 1) habitat degradation may also induce chronic stress that could lead to HPA axis hypo-activity with a consequent reduction in baseline concentration of stress hormones (Dickens and Romero 2013); 2) different species perceive new environments differently and some species may benefit from new conditions created by habitat changes. For example, Aronsen et al. (2015) found significantly higher cortisol concentrations in two species of monkeys (*Cercopithecus ascanius* and *Piliocolobus rufomitratus*) living in undisturbed forests compared to disturbed sites; and 3) the lack of data on fitness traits complicates interpretation of the direction of the change, e.g. if this is indicating a detrimental effect on reproduction.

Glucocorticoids can induce a number of cascade effects on metabolism, such as the mobilization of stored nutrients to be used to fuel other physiological functions, including immunity or resistance to molecular oxidative damage (Costantini et al. 2011, Marasco et al. 2017). Although our MA supports a significant impact of forest disturbance on immunity, we did not find any studies that looked at the impact of land-use changes on oxidative damage resistance. As previously suggested by other authors (Davis et al. 2008, Müller et al. 2011, Beaulieu and Costantini 2014), we recommend that future studies would complement analyses of stress hormones with those of immunity and oxidative stress status in order to have a clearer picture of how land-use changes are affecting a given species and how this species is responding.

Our results also show that clear cutting has a stronger impact than selective logging, fragmentation or edge effect. Clear-cutting and selective logging differ markedly in their impact on the vegetation and the amount of timber that is being removed from the forest (Woodcock et al. 2015). Several studies found a limited effect of selective logging on vertebrate species richness (Edwards et al. 2011, Gibson et al. 2011, Putz et al. 2012, Chaudhary et al. 2016), while major changes in bird and mammal communities were observed in post clear-cutting environments (Fisher and Wilkinson 2005, Fraixedas et al. 2015). We could not include important variables in our MA, such as the intensity of logging (Burivalova et al. 2014), the size of forest fragments (Arroyo-Rodríguez et al. 2013) and the distance to forest edge (Ewers and Didham 2006), which might have a strong impact on the species' physiology and immunology. Thus, we highlight the importance of testing the effects of logging intensity, fragment size and distance to forest edge on the physiological and immunological status of vertebrates in future studies.

We found a larger effect of forest disturbance on birds than on primates or other mammals. This result might be affected by the high number of studies on birds inhabiting clear-cut forests included in the MA. It is well known that forest stand homogeneity in structure and composition limits the availability of nest sites and canopy cover (e.g., Müller et al. 2007, Rosenvald et al. 2011) and reduces sources of food for many bird species (Paillet et al. 2010), with potential negative effects on individual fitness and survival. In contrast, results of studies investigating physiological responses to habitat changes in group-living primates may be influenced by inter- and intra-group social dynamics (Chapman et al. 2006, Aronsen et al. 2015), which can have a strong influence on individual health (Sapolsky 2005).

Recent studies found that logging or fragmentation may differentially affect species with different conservation statuses (IUCN category; Boyle 2016, Costantini et al. 2016b). For example, a study conducted on the two sympatric species, the ‘least concern’ red howler monkey (*Alouatta seniculus*) and the ‘critically endangered’ variegated spider monkey (*Ateles hybridus*) found that only the latter had higher levels of stress hormones due to anthropogenic disturbance (Rimbach et al. 2013). In agreement with this study, we also found that species Red listed by the IUCN as threatened or near threatened are more affected by forest disturbance than species classified as of least conservation concern.

Variation in effect sizes in our MA might be affected by a number of factors that we could not take into account because of lack of data. Some limiting factors of our results are pointed out and discussed in the paragraphs above, but sources of variation might be many and different. For example, sex and age were excluded from our MA because in most studies they were mixed or unknown. Similarly, different diet specialization and body size may affect the species sensitivity to forest disturbance (Keinath et al. 2017). Moreover, given the broad array of physiological and immunological parameters and samples analysed, it has not been possible to estimate the effect size of each parameter separately. We could only test the effect size of subcategories of Hormonal Response (Baseline vs. Stress Induced vs. Long-term vs. Short-term), and we did not find any significant differences between them.

In conclusion, our MA revealed that changes in the production of stress hormones and in some immune traits are significant consequences of forest disturbance, particularly of clear-cutting. The significant association between threatened IUCN category and higher physiological response suggests that physiology and immunity might be two important mediators of the (mal)adaptiveness of a given species to the changing forests. Our work has also identified many gaps in current literature and stresses the importance of experimental approaches aimed to better clarifying the role of physiology and immunity in determining the chances of species to survive or disappear in human-impacted environments.

Supporting information

Table A1 and all supplementary information cited in this chapter can be found online at https://doi.org/10.1016/j.biocon.2018.06.002.

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Chapter III

Glucocorticoids link forest type to local abundance in tropical birds

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Abstract

1. Selective logging is a major driver of environmental changes in the tropics. Recently, there has been increasing interest in understanding which traits make bird species resilient or vulnerable to such changes. Physiological stress mediated by the steroid hormone corticosterone (CORT) might underlie changes in local abundance of species because it regulates a range of body functions and behaviours to maintain homeostasis in changing environments.

2. We conducted a three-year study to assess: (i) the variation in CORT levels in feathers (where CORT is deposited during the moult) of ten understorey bird species across both unlogged old-growth forest and selectively logged forest in Borneo, (ii) how this variation is associated with within-year variation in population abundance between forest types, and (iii) whether the difference in feather CORT (fCORT) between co-specific populations living in unlogged and logged forests in one year is related with their difference in population abundance the following year.

3. We used effect size estimates to measure standardized magnitude and direction of fCORT changes between unlogged and selectively logged forest. We found small to large effect sizes, indicating large among species variation in physiological acclimatization to changes in forest conditions. In 2016 and 2018, species with relatively higher fCORT in unlogged forest were relatively more abundant in logged forest in the same year; in 2017, species with relatively higher fCORT in logged forest were relatively more abundant in logged forest. Importantly, we found that for a given species, the difference in fCORT at year (*x*) between unlogged and logged forests was negatively related with a difference in its local abundance between the two forest types in the following year (*x+1*).

4. Our results point to glucocorticoid hormones as potential mediators of carry-over effects on population abundance due to direct and indirect effects of silvicultural practices in tropical forests of Borneo, suggesting fCORT as a potential marker of population changes.

Introduction

Forest degradation and land-use change are major threats to biodiversity worldwide (Tilman et al. 2017). Growing demand for hardwood products and conversion of forests to agricultural areas are the main reasons for the habitat transformation and loss in tropical regions (FAO 2016). In the tropics logging is selective, with commercially valuable tree species harvested above a minimum diameter, opening the closed-canopy and driving a change in forest structure (Woodcock et al. 2015). More than 400 million hectares of natural tropical forests are designated for selective timber extraction (Blaser et al. 2011) and selectively logged forests are more prevalent than intact old-growth forests in most of the tropics (Lewis et al. 2015).

Although selective logging can result in a loss of biodiversity, naturally regenerating logged forests still have high species richness of plants, invertebrates, birds and mammals (i.e., Sodhi et al. 2010, Edwards et al. 2011, Putz et al. 2012). Nonetheless, the local abundance of species may change following selective logging and different species of vertebrates have been found to flourish or to decline in logged tropical forests (Koh 2007, Costantini et al. 2016b). For example, in a recent meta-analysis, Costantini et al. (2016b) found that selective logging negatively impacted the local abundance of larger Bornean birds and mammals, but did not alter dramatically the abundance between closely related species. An important question is which proximate and ultimate factors drive species to persist or decline after selective logging.

Predicting which species will suffer a decline in population after land-use change is an important but difficult challenge for ecological and conservation scientists. One way to overcome such issues is to quantify the physiological state of individuals under the assumption that individuals' physiological response to changing environmental conditions underlies population viability (Wikelski and Cooke 2006, Fefferman and Romero 2013, Madliger and Love 2015). The disciplines of macrophysiology and of landscape physiology focus on the variation of physiological traits over time and space with the aim to unravel the causal link between physiological changes and population ecology across different habitats or the same habitats with different degrees of human disturbance (Chown and Gaston 2008, Ellis et al. 2012, Chown and Gaston 2016). Estimates of local abundance inform us that a given population is at risk only after it has already declined. In contrast, markers of physiological state might (i) have a higher predictive power about the effects of environmental changes on wildlife and (ii) provide a cause-effect relationship between environmental change and fitness outcomes (Cooke et al. 2013, Madliger et al. 2018).

Glucocorticoid hormones have been widely used as biomarkers of physiological stress and population health because they are linked to anthropogenic disturbance and population declines (e.g., Boonstra and Singleton 1993, Dickens and Romero 2013, Messina et al. 2018). Glucocorticoids are steroid hormones regulated by the Hypothalamic–Pituitary–Adrenal (HPA) axis, which control many metabolic pathways (Sapolsky et al. 2000, Romero 2004). For example, glucocorticoids influence feeding behaviour to maintain allostatic balance between required and available energy (Rabasa and Dickson 2016). When energy demands exceed available energy, circulating levels of glucocorticoids rise to fulfil metabolic requirements and to promote adaptive energy-saving behaviours (Wingfield et al. 1998, Wingfield and Sapolsky 2003, Busch and Hayward 2009). High baseline glucocorticoid levels over a longer time scale may, however, induce negative consequences for individual fitness (McEwen and Wingfield 2003, Romero 2004), although this might depend on stressor type and magnitude, as well as the individual's age in which stressful conditions are experienced (Canoine et al. 2002, Marasco et al. 2018).

Coping with environmental changes can be energetically expensive for organisms and requires physiological acclimatisation (Vitousek et al. 2014, Wingfield et al. 2017, Messina et al. 2018). Corticosterone (CORT) is the main glucocorticoid stress hormone in birds and can be measured in different biological matrices, including blood, faeces, and feathers. Prior work has shown that CORT may be higher in individuals living in logged forests as compared to co-specific individuals living in undisturbed forests (Wasser et al. 1997, Leshyk et al. 2012, Grava et al. 2013, Leshyk et al. 2013). However, the strength and the directional change (i.e., increase or decrease) of stress responses to habitat transformation is affected by a number of ecological variables, such as life-history stage (Bonier et al. 2009b), the species' habitat suitability (Lodjak et al. 2015), and weather conditions (Henderson et al. 2017).

Plasma concentration of CORT provides a short-term indication of how an organism is physiologically adjusting to the concomitant environmental conditions. Conversely, CORT concentration in avian feathers (fCORT) is considered a long-term, integrated measure of an individual's HPA-axis activity over the time of growth of the feather (Bortolotti et al. 2008, Romero and Fairhurst 2016). fCORT is a less-invasive marker compared to blood CORT, which is particularly advantageous in studies correlating environmental conditions during feather growth with birds' physiology or fitness proxies. For example, studies on migratory birds successfully used fCORT to measure carry-over effects of habitat quality on reproductive output (Harms et al. 2015, Hansen et al. 2016). Carry-over effects are events occurring in one season that influence individual fitness and population abundance the subsequent breeding season, for example, through differential survival of individuals having different CORT levels or dispersion of "stressed" individuals towards new environments (Norris 2005, Norris and Marra 2007). Carry-over effects often emerge as consequence of limited food availability due to harsher environmental conditions (Harrison et al. 2011).

Key unexplored questions are whether variation in fCORT levels is associated with forest type and/or with differences in local abundance of birds between unlogged old-growth forests and logged forests. New environmental conditions created by selective logging can be favourable for some species while deleterious for others even many years after the logging has taken place as is reported for forests in Borneo (e.g., Costantini et al. 2016b). We conducted a three-year study on 10 understorey bird species in intensively logged and neighbouring unlogged forests in Sabah, Malaysian Borneo, to assess whether: (i) fCORT differs between unlogged and selectively logged forests; (ii) the difference in fCORT reflects within-year variation in relative local abundances of birds between forests and (iii) the difference in fCORT in one year (year *x*) between co-specific populations living in unlogged and logged forests, respectively, is related with a difference in their local abundance between the two forest types in the following year (year *x*+1). We expected to find (i) higher levels of fCORT in the type of forest where a population is less abundant, (ii) significant within-year association between fCORT and the relative population abundance if CORT production reflects current conditions in the forests and (iii) a negative correlation between fCORT and the relative population abundance of the subsequent year if any carry-over effects would have occurred.

Material and Methods

Study area

The study was carried out in the Yayasan Sabah logging concession in Sabah, Malaysian Borneo. The Yayasan Sabah logging concession is a contiguous and extensive lowland dipterocarp forest containing 45,200 ha of unlogged old-growth forest within the Danum Valley Conservation Area (DVCA) and Palum Tambun Watershed Reserve, and selectively logged forest within the 238,000 ha Ulu Segama-Malua Forest Reserve (US-MFR). These dipterocarp forests are dominated by the presence of large trees of the Family Dipterocarpaceae, which are valuable timber species.

The fieldwork was carried out in three unlogged old-growth forest plots, located within the DVCA (4°57045.2″N, 117°48010.4″E), and in three forest plots that have been logged

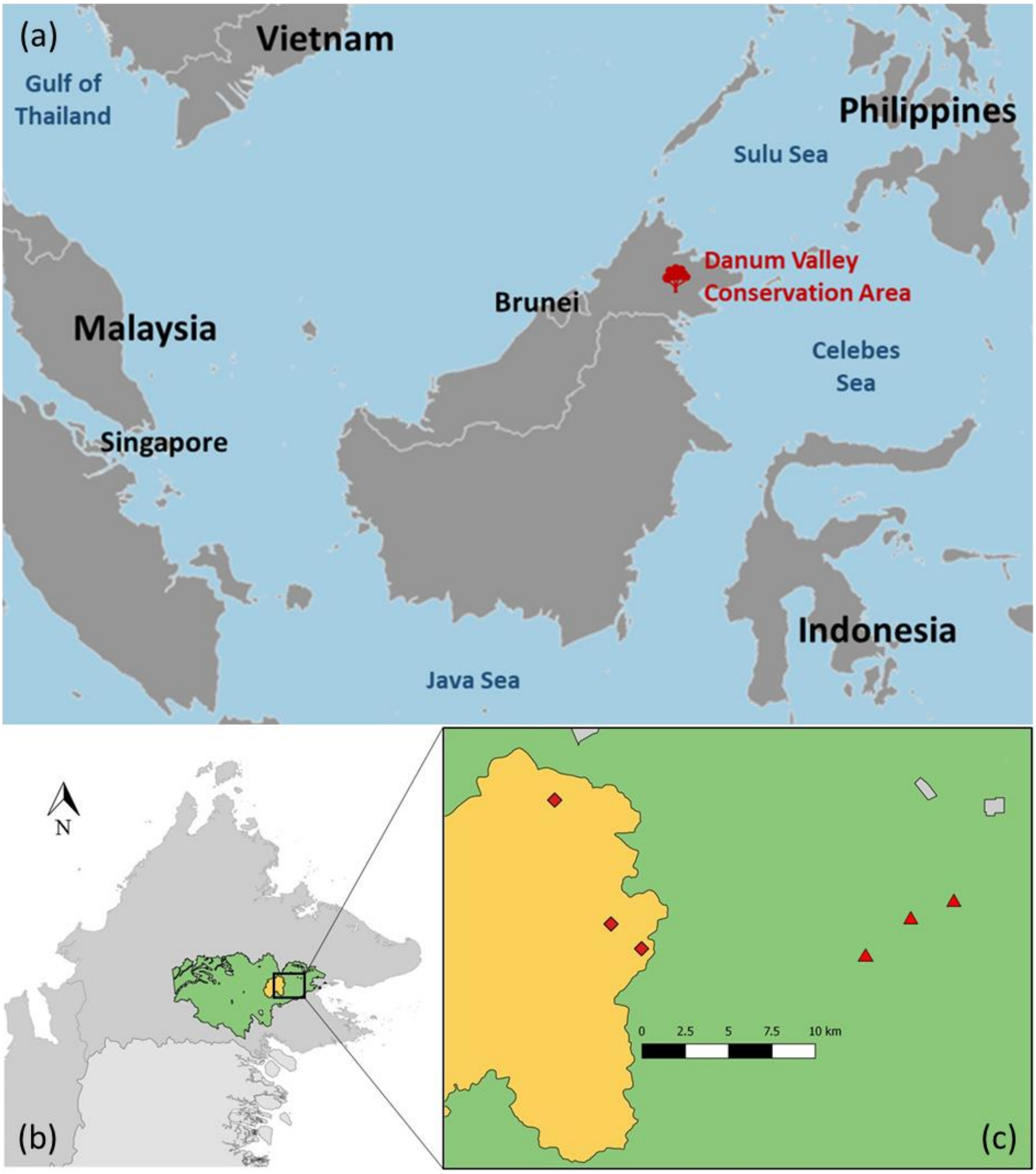

Figure 2 – (a) Danum Valley Conservation Area in the Malaysian state of Sabah, Borneo (b) The green area corresponds to the Yayasan Sabah logging concession, and the yellow area corresponds to the Danum Valley Conservation Area and Palum Tambun watershed reserve. (c) Distribution of study plots between unlogged forest (square symbols) and selectively logged forest (triangular symbols); grey areas are plantations.

twice (1987-1991 and 2001-2007) within the US-MFR (4°57042.8″N, 117°56051.7″E; Fig. 1). Logging occurred at high rates of timber removal ($145m^3$/ha, Fisher et al. 2011), and the last logging rotation occurred about 10 years prior to the study, leaving a heavily disturbed recovering forest.

Data collection and study species

Mist-netting for birds took place from early June to late August in the years 2016-2018, during the drier season (climatic summary data in Supplementary Table S5-S6). Our experimental design involved three plots in unlogged forest and three plots in selectively logged, forest with plots located at least 500 m away from the nearest road to avoid edge effects. Plots were located at least 1.8 km apart (mean unlogged forest = 6.64 km; mean logged forest = 4.04 km). Each plot was visited on two consecutive days and, within each plot, three parallel transects spaced at 250 m intervals (sufficient to ensure independence; Hill and Hamer 2004) and each containing fifteen nets (12 x 2.7 m; 25-mm mesh size) erected end-to-end were run simultaneously from 06:00 to 12:00 h. Nets were hourly checked during each working session. Mist-netting was rotated among plots to minimise potential temporal effects, with each plot visited three times per field-season (overall: six days of mist-netting per plot, 1,944 mist-net hours in total, see details in Supplementary Table S3). The entire sequence of plots was visited for three consecutive rounds, corresponding approximately to the month of June (round one), July (round two) and August (round three). The sequence of plots was adjusted to avoid unfavourable working conditions, such as tree falling on transects or ranging elephants in the plots. Mist-netting and bird processing were performed following the same methods between unlogged and logged forests.

Ten understorey bird species belonging to five different passerine families were included in this study because capture rates enabled us to obtain a sample size suitable for statistical analyses (Supplementary Table S1), and they show different responses to forest logging in terms of abundance between unlogged and logged forest within the Yayasan Sabah concession (Edwards et al. 2011). The study species were: little spiderhunter (*Arachnothera* *longirostra*); hairy-backed bulbul (*Tricholestes criniger*); brown fulvetta (*Alcippe brunneicauda*); chestnut-winged babbler (*Stachyris erythroptera*); fluffy-backed tit-babbler (*Macronus ptilosus*); rufous-crowned babbler (*Malacopteron magnum*); ferruginous babbler (*Trichastoma bicolor*); black-capped babbler (*Pellorneum capistratum*); Horsfield’s babbler (*Malacocincla sepiaria*), and short-tailed babbler (*Malacocincla malaccensis*).

Understorey birds are highly sedentary residents and forage predominantly in the lower stratum of the forest. All study species are either fully or partially insectivorous (Wilman et al. 2014; Supplementary Table S2, Billerman et al. 2020). The timing of the moult in the differing study species remains to be clarified, but likely occurs throughout the year (Mulyani et al. 2017). Reproduction occurs opportunistically throughout wide reproductive windows (Billerman et al. 2020; more information about seasonal reproductive windows in Supplementary Table S2).

Two tail feathers (outer rectrices) were plucked from each study bird that had completed the moult of juvenile plumage (hereafter adults). Following an aging system for tropical birds based on moult cycles (Wolfe et al. 2010, Johnson et al. 2011), we considered as ‘juvenile’ birds in active pre-formative moult or in formative (pre-basic) plumage. We did not encounter any birds with known or distinguishable alternate plumage. Feathers were stored in individual paper envelopes at room temperature. Each bird was marked with a unique numbered metal ring to enable individual recognition. Data on body moult were collected at the time of capture; individual birds were assigned scores from 0 to 4 on the base of the moult of contour feathers, following the protocol of DeSante et al. (2015) (i.e., 0 = none: no body moult, 4 = heavy: > than 2/3 of all contour feathers are moulting).

All experimental procedures were approved by the Sabah Biodiversity Council (access licence number: JKM/MBS.1000-2/2 JLD.6(39) and JKM/MBS.1000-2/2 JLD.7(57)).

Samples were exported under the export licences JKM/MBS.1000-2/2 JLD.3(45) and JKM/MBS.1000-2/2 JLD.3(64).

Feather corticosterone measurements

A total of 559 feathers from 516 individuals were analysed for fCORT. We extracted fCORT using the protocol described in Bortolotti et al. (2008), with minor modifications. The protocol has been validated for several avian species (see below, i.e., Lattin et al. 2011, Jenni-Eiermann et al. 2015, Freeman and Newman 2018). First, each feather was measured with a ruler from the quill to the top, and then vanes were minced in borosilicate glass scintillation tubes in pieces smaller than 5 mm and weighed on a precision balance (Sartorius, Entris). After adding 7 ml of methanol (Carl Roth, HPLC-grade), glass tubes were placed in a sonicating bath at room temperature for 30 minutes and then incubated overnight (ca. 15 hr) in water bath at 50ºC. The methanol was then separated from feather samples by filtration, pipetting twice the syringe through a filter unit (Chromafil, Carl Roth) into a new tube. The second wash out was done adding 2.5 ml of methanol to the feather remains in original sample tubes. Methanol extracts were dried down under nitrogen flow at 50ºC and then re-suspended in 250 µl of saline buffer. To estimate extraction recovery, a tracer (~ 2600 cpm) of [1, 2, 6, 7-3M] corticosterone label (NET 399, PerkinElmer) was added to 15 samples with a pool of chicken feathers. Extraction efficiency was on average 85.9% +/- 5.8% (mean +/- SD), similar to other published work on avian feathers (e.g., Lattin et al. 2011, Lodjak et al. 2015).

After extraction, fCORT levels were quantified using an enzyme-immunoassay (EIA) (Assay Designs Corticosterone kit 901-097, ENZO Life Sciences). Given that fCORT depends on feather growth rate (Bortolotti et al. 2009), we expressed fCORT concentration per feather length as in previous studies (Romero and Fairhurst 2016). We found a strong positive correlation between values expressed per feather length (pg/mm) and per vanes mass (pg/g) (Pearson = 0.849, $P < 0.001$). To validate the assay, parallelism against the standard curve was ascertained by performing three different serial dilutions of pooled feathers from three different species (chicken, little spiderhunter, hairy-backed bulbul; five series of dilution for each pool). All study samples were measured across sixteen plates; two different feather chicken pools were included as internal quality control in each plate. Samples were standardized across plates to include most of the study species in equal numbers between unlogged and logged forest in each plate. The average inter- and intra-assay coefficients of variation were 10.75% and 2.34%, respectively. Analysis of fCORT was conducted in two batches, one including samples of 2017 and the other including samples of 2016 and 2018.

Statistical analysis

To assess relationships between fCORT, forest type and year of sampling, we ran linear mixed models (LMMs) for each species (Table 1), separately, using SPSS Statistics 23. We chose to run LMMs separately by species because it is still unclear the extent to which fCORT levels are comparable among different species (Romero and Fairhurst 2016). Models included Forest type (2 levels) and Year (3 levels) as fixed factors. Plot was included as a random factor to control for possible variability due to local topographic/environmental differences within each forest type. Transect nested within Plot was removed from the models due to overfitting. The factor individual was not included in the models because we only had seven or fewer birds with more than one measurement between years per species. The inclusion of individual identity as random factor in preliminary tests did not change the outcomes because it had a residual variance ranging from 1.09±0.22 (estimate±SE) to close to zero. For these recaptured individuals, the coefficient of variation of fCORT across years was actually large (46.45% on average), showing low individual consistency across seasons (Supplementary Table S7). Significance threshold of LMMs was set at $P < 0.05$ (results in Table 1). For each model, Shapiro-Wilk test of residuals were performed to check normality; heteroscedasticity was assessed by plotting residuals vs. fitted values (Zuur et al. 2010). Data were log-transformed

($\log_{10} + 1$) when model residuals did not meet the normal distribution, then normality was tested again. We also tested for potential differences in body moult state between unlogged and logged forest through Mann-Whitney Test and we found no differences (Supplementary Table S8).

Then, two different linear mixed models were performed to test whether the differences in fCORT between co-specific populations were related to their difference in abundance between unlogged and logged forests. To do so, first, we used means, standard deviations and sample sizes to calculate annual Hedges' *g* effect sizes for each comparison of fCORT between co-specific populations living in unlogged and logged forests. Standardized effect sizes are analytical tools helpful to compare magnitude and direction of biological patterns and to assess the relevance of weak, but biologically important effects (Garamszegi 2006). Effect sizes were calculated using the *compute.es* package (Del Re 2013) in R (R Core Team 2013). The Hedges' *g* effect size measures how much one group differs from another, accounting for small sample sizes (Cooper et al. 2009). Following Cohen (1988), effect sizes can be considered small (Hedges $g = 0.2$, explaining 1% of the variance), intermediate (Hedges $g = 0.5$, explaining 9% of the variance) or large (Hedges $g = 0.8$, explaining 25% of the variance). In our case, positive effect size estimates indicate that fCORT in a given species is higher in logged than in unlogged forest. Second, annual species' capture numbers for each type of forest were combined to estimate the Relative Population Abundance (RPA) Index as follows: [(abundance in logged forest – abundance in unlogged forest) / (abundance in logged forest + abundance in unlogged forest)] (Supplementary Table S4). The RPA Index is positive for species with higher abundance in logged forest and negative for species with higher abundances in unlogged forest. Abundance data were corrected for sampling effort [Number of captures / (Expected Effort (nets*hours)]. Recaptured individuals were included in the abundance counts because recapture rates were low (mean recapture rate across species: 0.16 individuals) and similar between unlogged and logged forests (mean frequencies difference: 0.01). Moreover, preliminary models showed that outcomes were unchanged if recaptured individuals were included or not.

After we calculated effect size estimates and RPA indices, we ran the two linear mixed models, including species' RPA Index as the dependent variable and fCORT effect sizes as independent factor. Given that species were sampled in all study years, we also included species as random factor. A first mixed model tested for a within-year relationship between fCORT and RPA Index (Fig. 3), including also the independent factors year and its interaction with fCORT (results of the interaction term in Table 2). The second mixed model tested for the relationship between fCORT at year (x) and the RPA Index of the next year (Fig. 4). To this end, we included in the model the species' fCORT effect sizes calculated for the years 2016 and 2017 and the species' RPA Index calculated for the years 2017 and 2018, respectively. The independent factor year was not included in this model because the data from two years were merged together. In support to this choice, a preliminary model showed that there were similar covariations between fCORT and RPA index in both years (2016-17: $r = -0.87$; 2017-18: $r = -0.37$; fCORT × year interaction: estimate±SE = 0.10±0.15, $P = 0.52$).

Given that interspecies data analysis may require accounting for phenotypic similarities due to common ancestry (Hansen and Martins 1996), we tested for a phylogenetic signal of the species-specific RPA Index to assess whether a phylogenetically based statistical method was needed for our linear mixed models (Supplementary Material; Revell et al. 2008). The phylogenetic signals of the RPA Index measured as overall between years, and separately for each year were low and not statistically different from 0 (Supplementary Table S9). Thus, in accordance with previous studies (Blomberg and Garland 2003, Rheindt et al. 2004), we did not include phylogeny in our multispecies model.

Results

fCORT levels were similar between forest types for all the investigated species (Table 1). Significant differences in mean fCORT levels among years (pooled values between forest types) were found in all species with the exception of the black-capped babbler, fluffy-backed tit-babbler and hairy-backed bulbul (Table 1). Post-hoc analyses showed that rufous-crowned babbler had significantly higher fCORT in 2017 compared to 2018, while brown fulvetta, little spiderhunter, Horsfield's babbler, short-tailed babbler, chestnut-winged babbler and ferruginous babbler had significantly higher fCORT in 2018 compared to 2016 and 2017 (Fig. 2).

Table 1 – Outcomes of linear mixed models implemented per species. Significant P-values are shown in bold.

	Best Models			
Species	**Factor**	**d.f.**	***F*-value**	***P*-value**
Black-capped babbler	FOREST	3.200	5.032	0.105
	YEAR	46.667	0.528	0.593
Brown fulvetta	FOREST	48	0.170	0.682
	YEAR	48	10.660	**<0.001**
Chestnut-winged babbler	FOREST	3.756	0.578	0.492
	YEAR	50.488	25.943	**<0.001**
Ferruginous babbler	FOREST	3.828	0.476	0.530
	YEAR	61.588	20.356	**<0.001**
Fluffy-backed tit-babbler	FOREST	3.305	0.188	0.691
	YEAR	37.386	0.209	0.812
Horsfield's babbler	FOREST	3.810	0.166	0.706
	YEAR	48.883	43.180	**<0.001**
Hairy-backed bulbul	FOREST	44	0.626	0.433
	YEAR	44	0.977	0.384
Little spiderhunter	FOREST	1.864	0.150	0.738
	YEAR	72.752	69.289	**<0.001**
Rufous-crowned babbler	FOREST	39	0.016	0.902
	YEAR	39	3.293	**0.048**
Short-tailed babbler	FOREST	3.368	0.739	0.447
	YEAR	56.616	16.078	**<0.001**

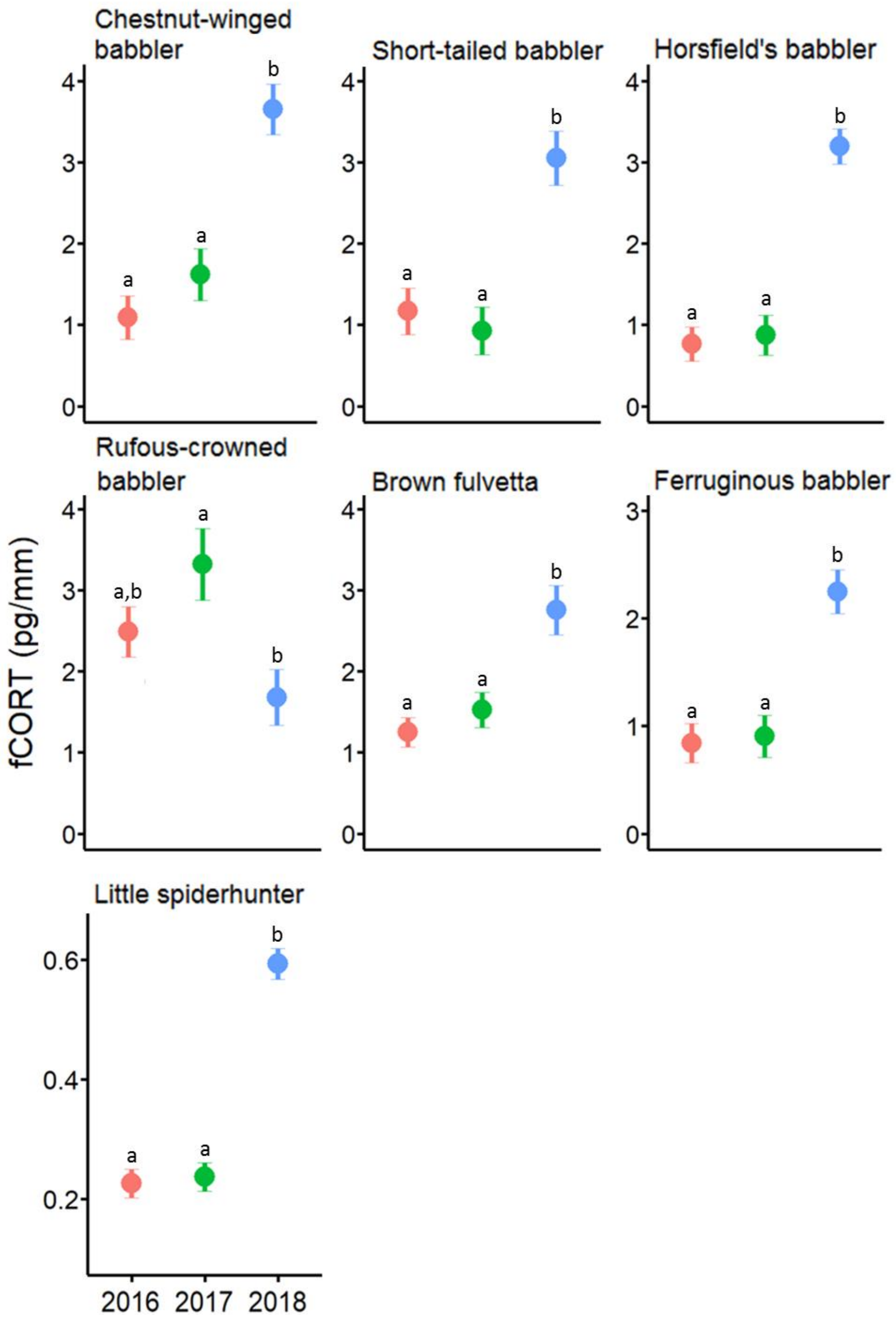

Figure 3 – Seven out of 10 understorey bird species showed significant among year variation in fCORT. Least square means +/- standard error of the mean fCORT levels of each sampling year are shown. Different superscripts (a and b) represent significant differences (P < .05). Note that only those cases where post-hoc tests were run are shown.

The linear mixed model performed to explore the within-year relationship between fCORT and RPA Index showed a significant increase of negative RPA Index in 2018 compared to 2016 (LMM: estimate±SE = -0.32±0.11, $P < 0.01$), indicating that certain species switched their relatively higher population abundance from selectively logged forest (positive RPA

Index) to unlogged forest (negative RPA Index). The interaction between fCORT and year was also significant (Table 2); in 2016 and 2018, species with relatively higher fCORT in unlogged forest (negative effect size) were relatively more abundant in logged forest (positive RPA Index) in the same year; in 2017, species with relatively higher fCORT in logged forest (positive effect size) were also relatively more abundant in logged forest (positive RPA Index; Fig. 3).

Table 2 – Outcomes of the interaction between fCORT and year of the within-year linear mixed model testing for an effect of fCORT on the species relative population abundance index. Significant P-values are shown in bold.

Effect	Pairwise	Estimate	Standard Error	*t*	*P*
CORT*YEAR	2016-17	0.32	0.15	2.16	**0.04**
	2016-18	-0.16	0.17	-0.89	0.38
	2017-18	-0.48	0.17	-2.73	**0.01**

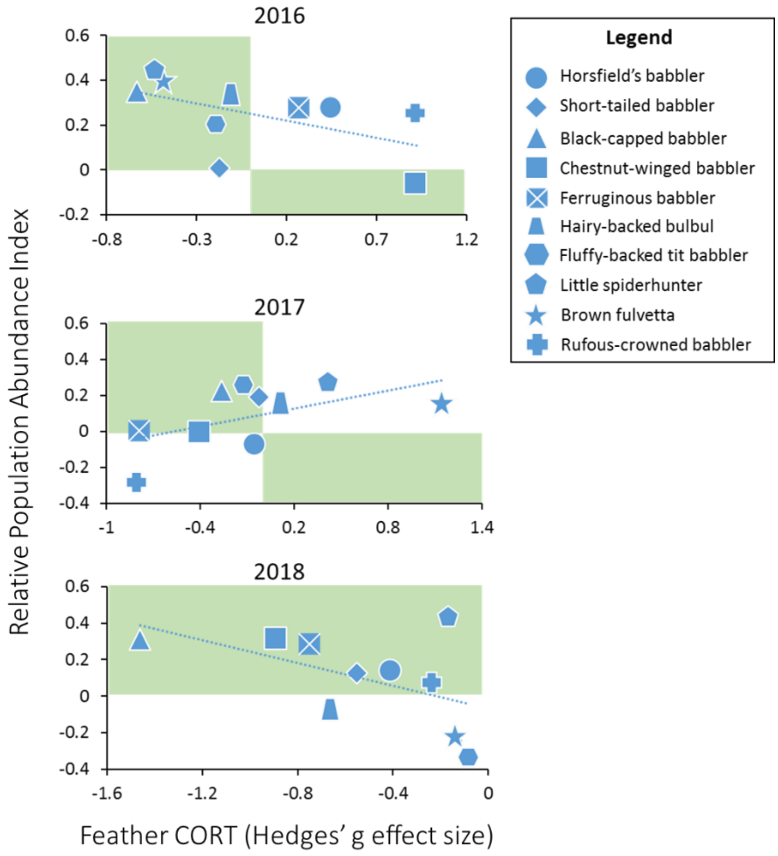

Figure 3 – Within-year relationship between changes in fCORT levels, measured as effect size (positive values mean higher fCORT of a given species in logged than in unlogged forest), and the relative population abundance index of each species (positive values indicate higher abundance of a given species in logged than in unlogged forest), between unlogged and selectively logged forest. Data relate fCORT effect size estimates of ten understorey bird species for the years 2016, 2017 and 2018, with relative population abundance indices of the same year. Green areas indicate that relative population abundances of species and effect sizes are higher in selectively logged forest than unlogged forest.

Finally, in the linear mixed model performed to explore if fCORT at year (*x*) predicted RPA Index of the following year (*x+1*), we found a significant negative relationship between fCORT and RPA Index (LMM: estimate±SE = -0.21±0.07, *P* = 0.01; random factor species: variance±SE = 0.002±0.05; Fig. 4). Specifically, higher concentrations of fCORT for the species within a given forest type, as compared to the other type of forest, at year (*x*), were associated with lower population abundance of that same species the following year (*x+1*), within the same forest type. The opposite trend was found for relatively lower concentrations of fCORT.

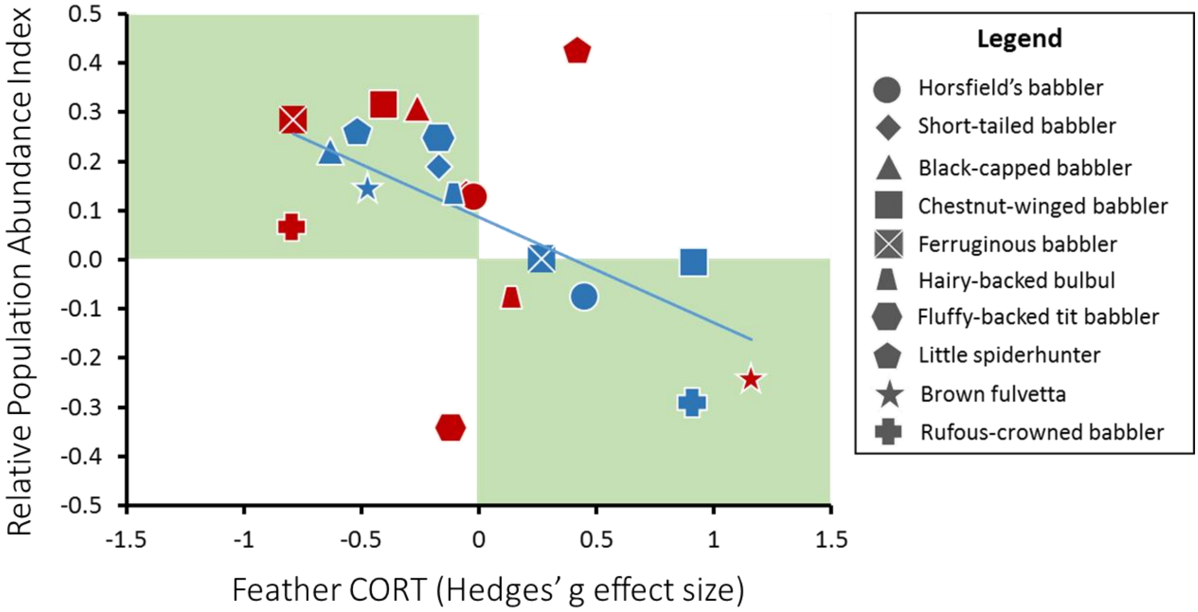

Figure 4 – Between-years relationship between changes in fCORT levels, measured as effect size (positive values mean higher fCORT of a given species in logged than in unlogged forest), and the relative population abundance (RPA) index of each species (positive values indicate higher abundance of a given species in logged than in unlogged forest), between unlogged and selectively logged forest. Data relate fCORT effect size estimates of ten understorey bird species for the years 2016 and 2017 and the relative population abundances of the following years (i.e. 2017 and 2018, respectively). Blue symbols indicate the relationship between fCORT levels for the year 2016 and RPA index for the year 2017. Red symbols indicate the relationship between fCORT levels for the year 2017 and RPA index for the year 2018. Trends were similar across years (see text). Green areas indicate that relative population abundances and effect sizes are higher in selectively logged forest than unlogged forest.

Discussion

This is the first study that compared concentrations of the hormone corticosterone in the feathers (fCORT) of understorey bird populations living in unlogged and logged tropical forests and tested the relationship between fCORT and local abundance using a macrophysiological approach. We found annual variation of fCORT levels and relative population abundances (RPA Index) in our study species. In 2016 and 2018, species with relatively higher fCORT in unlogged forest were relatively more abundant in logged forest in the same year; in 2017, species with relatively higher fCORT in logged forest were also relatively more abundant in logged forest. Importantly, we found that relatively high fCORT level in one year was related to a relatively lower abundance the next year within the same forest type. Overall, these results suggest that (i) physiological responses mediated by glucocorticoid hormones to unknown changes in the forest might be implicated in the reduced performance of the population and (ii) fCORT could be a valuable candidate biomarker to assess and predict the population responses of tropical non-migratory understorey birds to environmental changes.

We found that all species had similar fCORT levels between unlogged and logged forests, suggesting that such species could be physiologically acclimatised to the new environmental conditions created by logging. However, these classic statistical approaches based on significance levels treat the biological questions as all-or-nothing effect, ignoring that even small changes in physiological traits may be biologically important for the organisms (Møller and Jennions 2002, Garamszegi 2006). The use of effect size estimates allowed us to measure standardized magnitude and direction of fCORT changes between unlogged and logged forests.

We found small to large fCORT effect sizes in our study species (Cohen 1988), indicating wide plasticity in the physiological responsiveness. Small to intermediate effect sizes are common in ecological studies on free-living organisms, where it is difficult to take into account all sources of variation (Møller and Jennions 2002). However, we found large effect size estimates for four species in different years: black-capped babbler (year 2018, g = -1.46), brown fulvetta (year 2017, g = 1.16), chestnut-winged babbler (year 2016, g = 0.92, year 2018, g = -0.89), rufous-crowned babbler (year 2016, g = 0.93). Negative effect size estimates correspond to higher levels of fCORT in old-growth forest compared to selectively logged forest. Most of the study species showed changes in the direction of the effect size between years, suggesting the presence of other factors, rather than forest type, that could affect CORT levels. This was not the case for the black-capped babbler, fluffy-backed tit babbler and short-tailed babbler, which showed higher levels of fCORT in primary forest compared to selectively logged forest each year (i.e., negative effect size), suggesting that those species might be taking advantages from the environmental conditions present in logged forest.

Relying on a comparison of effect size estimates between unlogged and selectively logged forests, we found that species with relatively higher fCORT in unlogged forest were relatively more abundant in logged forest in two out of the three study years. Importantly, we also found that relatively higher concentrations of fCORT in a given forest type at year (x), were associated with lower abundances of the study species in the same type of forest the following year ($x+1$), and vice versa. Such result suggests that carry-over effects mediated by fCORT could have impacted on some processes of population dynamics. Prior work on reptiles and mammals found significant links between stress hormones and fitness. For example, poor body condition in snowshoe hare (*Lepus americanus)* (Boonstra and Singleton 1993) and marine iguanas (*Amblyrhynchus cristatus*) (Romero and Wikelski 2001) was associated with higher stress levels and with poorer survival perspectives. Similarly, Lea et al. (2018) found that cape mountain zebras (*Equus zebra zebra*) living in relatively lower quality habitat had highest faecal glucocorticoid concentrations, which were negatively correlated with long-term population growth and female fecundity. One possible explanation of the association between glucocorticoids and relative population abundance might lie with energy budget as survival probability decreases in individuals whose stress levels cause long-term energy needs that exceed energy intake (McEwen and Wingfield 2003).

Population dynamics can be affected by changes in survival, reproductive success and immigration/emigration. Carry-over effects of higher fCORT concentrations are negatively correlated with survival and reproduction. For example, harlequin ducks (*Histrionicus histrionicus*) show negative correlation between CORT levels in back feathers moulted pre-breeding and reproductive decision (Hansen et al. 2016). Similarly, in northern common eiders (*Somateria mollissima borealis*) an increase in fCORT following a disease outbreak had indirect negative effects on reproduction and survival the following breeding season, which occurred approximately nine months later (Harms et al. 2015). Although we did not find any study investigating the link between CORT, dispersion and habitat quality, it is probable that particularly stressed individuals are more prone to emigrate in search of better conditions (Massot and Aragon 2013). In our study, bird species are resident and opportunistic breeders (Mulyani et al. 2017, Billerman et al. 2020). Thus, a reduced local abundance might indicate lower survival or reproductive success of low-quality individuals (possibly having higher fCORT) rather than dispersion toward habitats of higher quality.

Data on within-individual variation in fCORT across years (range 3.5 to 109.2 %, average 46.5 %, Supplementary Table S7) indicates high individual plasticity of the individual CORT response in tackling the concomitant metabolic demands. The strength of the physiological stress response to environmental challenges can be affected by life-history stages, such as moult and reproduction (Romero 2002, Cyr et al. 2008, Dantzer et al. 2014). Many tropical birds, including our study species, replace feathers opportunistically and gradually over a period of months, with a peak of feather moult soon after breeding (Mulyani et al. 2017). Evidence suggests that CORT levels do not change in birds with extended moult periods during feather replacement (Cornelius et al. 2011, Buttemer et al. 2015). Moreover, overlap between moult and reproduction has been found extremely rare in Bornean birds (Mulyani et al. 2017), thus we can assume that birds involved in this study were not reproductively active when they moulted feathers.

Seasons prior to fieldwork in 2016 and 2017 were affected by El Niño-Southern Oscillation (ENSO) events. ENSO events are composed by the El Niño warming phase and La Niña cooling counterpart. Compared to 2018 and to the average values in the last thirty years, the weather conditions (mean temperatures and total rainfalls) in the study area were substantially warmer and drier in 2016 and less warm but rainier in 2017 (climate data of DVCA provided by South East Asia Rainforest Research Partnership). Such extreme changes in weather conditions affect CORT production in vertebrates (Romero and Wikelski 2001, Wingfield et al. 2018). We found that fCORT levels for 2016 and 2017 were significantly lower than in 2018 for seven bird species out of ten (Fig. 2). It is possible that the prolonged situation of stress due to unpredictable climatic events induced a dampened HPA-axis activity, with consequent decrease in CORT production, probably because too energetically demanding to sustain (Wingfield and Sapolsky 2003, Hau et al. 2010, Angelier and Wingfield 2013). Further studies are needed to clarify the link between CORT production and direct (e.g., rainfall, temperature, or wind) and indirect (e.g., food availability) effects of weather conditions.

Another possible factor that might have changed fCORT levels between years and forest types lies with population density variation. It is well documented in vertebrates that population density may affect HPA axis activity (reviewed in Creel et al. 2013). A positive relationship between intra-specific population density and glucocorticoids levels may be expected owing to reduced food availability per individual and/or increased conspecific aggressiveness to access resources available in the environment (Silverin 1993, 1998, Landys et al. 2007, Landys et al. 2010). A behavioural and hormonal study conducted on the buff-breasted wren (*Thryothorus leucotis*), a Neotropical species, found that birds responded aggressively to intruders and males increased plasma levels of CORT in accordance with the duration of the challenge (Gill et al. 2008).

The RPA Index in our study can be considered indicative for relative population density, with some limitations. For example, we have no information on factors that may affect species density estimation based on mist-netting data, such as species' home ranges and patterns of movement (Efford et al. 2016) in logged forest compared to unlogged. We found significant within-year relationships between fCORT and RPA Index, indicating that production of CORT might also reflect the current conditions in the forests. The cause of these relationships between fCORT and RPA Index is currently unknown, but it might be that annual variation in local relative densities of birds affected the HPA axis activity. Future studies will need to estimate the local density of species to test the extent to which this could be one route through which CORT production affects population size.

In conclusion, this study provides evidence that production of CORT might mediate the carry-over effects of given forest characteristics on the variation in relative abundance of co-specific populations between old-growth and selectively logged forests. This result would also indicate that fCORT may be an important physiological tool to predict directional population changes. This result has strong conservation implications because it indicates that quantification of fCORT might be employed to determine which silvicultural practises impact less on understorey birds. Future work should focus on (i) how the individual physiological status translates in population size or population growth rates, (ii) how different practices and intensities of forest management impact on stress physiology of understorey birds, and (iii) the density-dependent and independent mechanisms through which forest management impact on the individual physiology and population dynamics.

Supporting information

Phylogenetic signal analysis

Interspecies data analysis often requires accounting for phenotypic similarities due to common ancestry. However, phylogenetic dependence of phenotypic traits can be weaker than expected due to evolutionary constraints (e.g., selection; Martins et al. 2002), and incorporating phylogenetic information in statistical analysis might not be always necessary (Blomberg and Garland 2003, Rheindt et al. 2004). We tested for phylogenetic signal, namely a measure of statistical non-independence among species trait values, of the species-specific RPA Index, to assess whether a phylogenetically based statistical method was needed for our linear regression model.

To assess the phylogenetic relationship among study species, we obtained 500 probable phylogenies from www.birdtree.org (Jetz et al. 2012). First, using the R package *phytools* (Revell 2012), we obtained the best average phylogenetic tree based on a quadratic path difference method. Then, we used the Blomberg's *K* statistic (Blomberg and Garland 2003) to estimate the phylogenetic signal of the RPA Index. In order to avoid the repetition of species within the database, we calculated the phylogenetic signal of the RPA Index separately for the three years, and for the overall RPA Index between years. RPA Values of *K* range between 0 and ∞, with $K = 1$ indicating that traits have evolved as in Brownian motion model (that is a model for evolution of continuous characters based on simple randomization procedures; Revell et al. 2008). When closely related species resemble each other less than expected, values of $K < 1$ indicate a loss of phylogenetic signal. On the other hand, values of $K > 1$ reflect an excess of statistical dependence between species for the evolution of the considered trait (Blomberg and Garland 2003). In our database, the phylogenetic signals of the RPA Index measured as overall 2017-18, and separately for each year were low and not statistically different from 0 (Table S9). Thus, in accordance with previous studies (Blomberg and Garland 2003, Rheindt et al. 2004), we did not include phylogeny in our multispecies model.

Table S1 – Study species and relative sample sizes for fCORT analysis.

Species Name	Family	2016		2017		2018	
		LOG	UNL	LOG	UNL	LOG	UNL
Little spiderhunter *Arachnothera longirostra*	Nectariniidae	14	14	14	13	12	12
Hairy-backed bulbul *Tricholestes criniger*	Pycnonotidae	11	10	5	3	10	9
Brown fulvetta *Alcippe brunneicauda*	Leiotrichidae	12	12	9	8	3	8
Chestnut-winged babbler *Stachyris erythroptera*	Timaliidae	11	12	10	6	10	6
Fluffy-backed tit-babbler *Macronus ptilosus*	Timaliidae	8	9	11	3	7	10
Rufous-crowned babbler *Malacopteron magnum*	Pellorneidae	9	9	5	4	6	10
Ferruginous babbler *Trichastoma bicolor*	Pellorneidae	13	12	10	12	10	9
Black-capped babbler *Pellorneum capistratum*	Pellorneidae	12	10	10	6	7	6
Horsfield's babbler *Malacocincla sepiaria*	Pellorneidae	10	10	7	8	10	9
Short-tailed babbler *Malacocincla malaccensis*	Pellorneidae	12	12	11	11	10	7

Tables from S2 to S9 can be find online at:

https://besjournals.onlinelibrary.wiley.com/doi/full/10.1111/1365-2435.13586

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Chapter IV

Impacts of selective logging on the oxidative status of tropical understorey birds

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Abstract

1. Selective logging is the dominant form of human disturbance in tropical forests, driving changes in the abundance of vertebrate and invertebrate populations relative to undisturbed old-growth forests.

2. A key unresolved question is understanding which physiological mechanisms underlie different responses of species and functional groups to selective logging. Regulation of oxidative status is thought to be one major physiological mechanism underlying the capability of species to cope with environmental changes.

3. Using a correlational cross-sectional approach, we compared a number of oxidative status markers among 15 understorey bird species in unlogged and selectively logged forest in Borneo in relation to their feeding guild. We then tested how variation of markers between forest types was associated with that in population abundance.

4. Birds living in logged forests had a higher activity of the antioxidant enzyme superoxide dismutase and a different regulation of the glutathione cycle compared to conspecific birds in unlogged forest. However, neither oxidative damage nor oxidized glutathione differed between forest types. We also found that omnivores and insectivores differed significantly in all markers related to the key cellular antioxidant glutathione irrespective of forest type. Species with higher levels of certain antioxidant markers in a given type of forest were less abundant in that forest type compared to the other.

5. Our results suggest that there was little long-term effect of logging (last logging rotation occurred ~15 years prior to the study) on the oxidative status of understorey bird species. However, it is unclear if this was owing to plasticity or evolutionary change. Our correlative results also point to a potential negative association between some antioxidants and population abundance irrespective of forest type.

Introduction

Forest logging is one of the major causes of biodiversity loss worldwide (Tilman et al. 2017). In tropical regions, selective logging is the most common form of timber extraction for commercial exploitation. More than 400 million hectares (~25%) of remaining tropical forests are designated for selective logging (Blaser et al. 2011), most of which is being done unsustainably (Edwards et al. 2014b, Edwards et al. 2019). As a consequence, selectively logged tropical forests are more prevalent than intact old-growth forests in most tropical countries (Laurance et al. 2014, Lewis et al. 2015).

Selectively logged forests are less heterogeneous than old-growth forests (Okuda et al. 2003, Senior et al. 2018), their canopy is lower, thinner and frequently interrupted by large forest gaps that allow solar radiation to directly reach the forest floor (Hardwick et al. 2015) boosting growth of vines and bamboos (Cerullo and Edwards 2019). Although selectively logged forests may retain high levels of animal and plant species richness (Sodhi et al. 2010, Edwards et al. 2011, Putz et al. 2012), it is increasingly realised that the impact of selective logging differs significantly among species (Gibson et al. 2011, Arbainsyah et al. 2014, Ewers et al. 2015), with local abundances of vertebrate and invertebrate species increasing, remaining similar, or declining after logging. A major question then is which proximate mechanisms make species resilient or vulnerable to such changes. There is presently very limited knowledge about the physiological responses of species to selective logging and how these responses are linked to differences in population abundance between primary and logged forests.

Trophic ecology is a crucial ultimate factor that determines the persistence of species in selectively logged tropical forests (Gray et al. 2007, Burivalova et al. 2015, Costantini et al. 2016b, LaManna and Martin 2017) and that can also affect physiological status (Raubenheimer et al. 2009, Costantini 2014). Generally, species from lower trophic levels or with a broader trophic niche tend to undergo less pronounced changes in abundance in logged forest (Hamer et al. 2015). In Bornean understorey birds, higher trophic position was found in selectively logged than unlogged forests (Edwards et al. 2013a), suggesting that birds altered their diets (i.e., omnivores feeding less on fruit and nectar in logged forest, and insectivores feeding more on predatory arthropods) or there was increased trophic position of prey owing to more complex food webs.

Changes in abiotic and biotic conditions of selectively logged forests also require species to physiologically respond to the new conditions to avoid any decrease in reproductive success or survival (Messina et al. 2018). Regulation of cellular oxidative status in changing environments is proposed as one major physiological mechanism for maintaining homeostasis because changes in oxidative status may impact on a number of fitness traits, such as growth, reproduction or lifespan (reviewed in Costantini 2014). Among-species variation in oxidative status is due to different levels of reactive oxygen species (ROS) production, oxidative damages caused by ROS to biomolecules (e.g., lipids, proteins), and/or enzymatic and non-enzymatic (dietary and endogenous) antioxidant molecules (Costantini 2019). Antioxidants differ in their mode and tempo of action, and low availability of some antioxidants may be compensated by the upregulation of others in a complex and multifaceted system (Costantini 2014). Moreover, food types differ in their antioxidant content, indicating a significant link between feeding ecology and the antioxidant status of species (Costantini 2014). For example, a comparative study of 95 bird species showed that carotenoids (a type of dietary antioxidant) were negatively associated with invertebrate consumption (Cohen et al. 2009). Similarly, omnivorous bats had lower plasma oxidative damage and higher plasma non-enzymatic antioxidant capacity than insectivorous bats (Schneeberger et al. 2014).

Environmental challenges can affect the oxidative status in different ways. For example, the antioxidant defenses can be weakened by a reduced intake of dietary antioxidants in poor quality habitat or during adverse seasons (Catoni et al. 2008, Isaksson et al. 2011). On the other hand, deficiency in dietary antioxidants may be compensated by upregulation of endogenous antioxidants (Vertuani et al. 2004, Isaksson 2013). Changes in oxidative status may not necessarily translate into fitness costs. For example, an experimental study on free-living jackdaws (*Coloeus monedula*) found that brood size manipulation affected only markers of antioxidant status that were not associated with survival. This finding supported the hypothesis that physiological variables might be robust against changes when related to fitness traits (Boonekamp et al. 2018).

In this correlative, cross-sectional, multi-species study, we have tested for the first time the effects of forest logging on the oxidative status of birds. To this end, we measured multiple blood-based markers to examine the long-term effects of forest logging (last logging rotation occurred ~15 years prior the study) on the oxidative status of 15 understorey bird species in Borneo during two years. We also tested if the feeding guild of species explained the effect of logging on their oxidative status, because feeding ecology might also affect oxidative status (e.g., through a different intake of antioxidants; Cohen et al. 2009, Costantini 2014) and insectivorous birds show a stronger trophic change in response to logging compared to other feeding guilds (Edwards et al. 2013a). We tested the following predictions: (i) birds living in logged forests will have higher oxidative damage if the new environmental conditions are metabolically stressful; (ii) birds in selectively logged forests will have similar antioxidant levels to those in primary forests if they are physiologically adapted (through plasticity or genetic change) to the new environment; (iii) feeding guilds will differ in oxidative status depending on forest type because logging affects the trophic position of birds with a stronger response of insectivorous birds and (iv) higher abundance of birds in a given type of forest will be negatively associated with oxidative damage levels owing to its detrimental effects on reproduction or survival and antioxidant levels if the need to upregulate them is costly for the individual.

Materials and Methods

Study species

We studied 15 understorey bird species belonging to six different passerine families and two distinct feeding guilds (i.e. insectivores and omnivores), whose mean body mass ranges from 11.42 g (purple-naped sunbird, *Hypogramma hypogrammicum*) to 40.88 g (white-crowned shama, *Copsychus stricklandii*; Table S1). Species were selected based on their capture rates and local changes in abundance during the years previous to our fieldwork, and they are representative of the understorey avifauna of the forest (Ansell et al. 2011, Edwards et al. 2011). Tropical understorey birds are highly sedentary and forage predominantly in the lower stratum of the forest (Wilman et al. 2014). The reproduction of the study species occurs opportunistically throughout wide reproductive windows (Billerman et al. 2020).

Study area and data collection

The study area is located within the Yayasan Sabah logging concession, in Sabah, Malaysian Borneo. Unlogged old-growth forest is located within the Danum Valley Conservation Area (DVCA) (4°57045.2″N, 117°48010.4″E) and is bordered by selectively logged forests in a single contiguous lowland rainforest (Fig. 1). Trees of the Family Dipterocarpaceae, which dominate these forests, are valuable timber species. Selective logging in the Ulu Segama-Malua Forest Reserve (4°57042.8″N, 117°56051.7″E) occurred in the late 80’s and early 90’s at high rate of timber removal (~115 m^3 ha^{-1}), and again about 15 years prior to our study (~31 m^3 ha^{-1} of additional wood extracted) leaving a heavily disturbed forest. After the last logging rotation, the forest was left to recover naturally.

Fieldwork took place from early June to late August in the years 2017-2018. We set three plots in unlogged old-growth forests and three plots in twice-selectively logged forests. Plots were at least 1.8 km apart (mean unlogged forest = 6.64 km; mean logged forest = 4.04 km) and 500 m from the nearest road. Within each plot, three independent parallel transects (spaced at 250 m intervals; Hill and Hamer 2004) containing fifteen nets (12 x 2.7 m; 25-mm mesh size) erected end-to-end, were run simultaneously from 06:00 to 12:00 h. Each net was checked within one hour, thus samples of blood were collected in a timeframe during which the measured markers do not change significantly following stress exposure (reviewed in Costantini et al. 2011). Each plot was visited three times per field-season (estimated 1,944 mist-net hours in total) following a rotation among plots to minimise potential temporal effects.

Every captured bird was marked with an individual numbered ring. Species, ring number, day and time of capture were recorded. Blood samples (≤ 100 μl) were taken from the brachial vein of adult birds only using Microvette CB 300 lithium-heparine tubes (Sarstedt, Numbrecht, Germany), and were stored in ice during the time of mist netting. After transfer to the field laboratory, tubes were centrifuged (10,000 rpm for 5 minutes) to separate plasma from red blood cells which were pipetted in different tubes and stored at cryogenic temperatures in a vapour-shipper (MVE CryoShipper SC 20/12V). In our main laboratory at the University of Antwerp, samples were stored at -80 °C prior to analysis.

All experimental procedures were approved by the Sabah Biodiversity Council (access licence number: JKM/MBS.1000-2/2 JLD.6(39) and JKM/MBS.1000-2/2 JLD.7(57)). Samples were exported under the export licences JKM/MBS.1000-2/2 JLD.3(45) and JKM/MBS.1000-2/3 JLD.3(64).

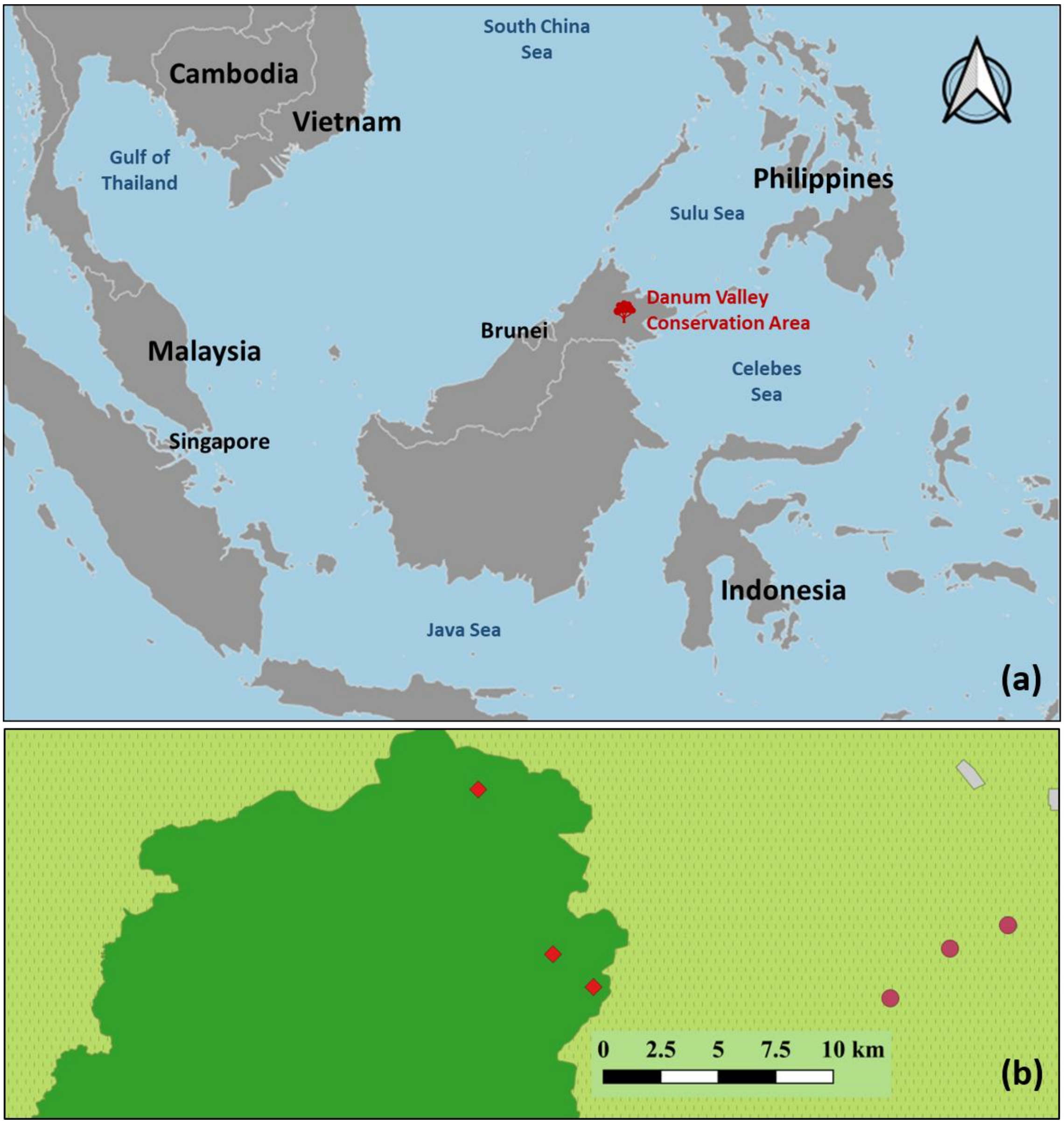


Figure 4 – (a) Study area in the Malaysian state of Sabah, Borneo and (b) distribution of study plots between old-growth unlogged forest (uniform green area, diamond symbols) and selectively logged forest (dotted light green area, circle symbols); grey areas are plantations.

Markers of oxidative status

We collected blood samples from 451 birds, of which 224 samples were from selectively logged and 227 from old-growth forest, and 255 were insectivores and 196 were omnivores. Due to limited sample volumes, we were not able to measure all markers of oxidative status for each individual, therefore relative sample sizes vary among markers of oxidative status (Table S2).

Markers of oxidative status were analysed in duplicate following established protocols for birds (see Supporting Information). Briefly, we quantified: (i) the plasma lipid oxidative damage using the Thiobarbituric Acid Reactive Substances (TBARS) method (El-Shafey and AbdElgawad 2012); TBARS values are strongly correlated with estimates of malondialdeyde (MDA) made by HPLC methods, however, they may be slightly overestimated owing to contributions of several lipid peroxidation aldehydes and formation of aldehydes at working conditions. To protect samples from possible oxidation due to heating, we added 0.01% of the synthetic antioxidant butylated hydroxyl toluene (BHT) to the extraction buffer (Esterbauer and Cheeseman 1990; see Supplementary Information); (ii) the non-enzymatic antioxidant capacity in erythrocytes using a ferric ion reducing antioxidant power (FRAE) assay (Benzie and Strain 1996); (iii) the activities of the two antioxidant enzymes superoxide dismutase (SOD) and glutathione peroxidase (GPx) in erythrocytes (Dhindsa et al. 1981, Drotar et al. 1985); (iv) the concentrations of the reduced glutathione (GSH), oxidised glutathione (GSSG) and total glutathione (tGSH) in erythrocytes using reversed-phase high-performance liquid chromatography with electrochemical detection (Shimadzu, Hai Zhonglu, Shanghai; Sinha et al. 2014); and (v) the redox state of the glutathione system GSH/GSSG, which is the ratio between the availability of the antioxidant GSH and the product of its oxidation GSSG, according to Jones (2006). We also measured plasma triglycerides because they are important substrates of lipid oxidative damage, thus higher levels of TBARS might be due to higher amounts of triglycerides in blood (Perez-Rodriguez et al. 2015). Mean values (±SD) of markers of oxidative status per each species are shown in Table S3.

Statistics

Forest type and feeding guilds

Linear mixed models (LMMs) were applied to the data for each marker of oxidative status, separately, to test the effects of the main factors forest type and feeding guild. We also included in the model an interaction term between forest type and feeding guild to test for any difference in a given marker between insectivorous and omnivorous species across the two types of forest. In each model, we included a number of potential confounding factors: year of sampling to control for any annual variation in marker values; day and time of blood sampling to control for any seasonal and daily variation in marker values, respectively. In each model, we also included the random factor species to account for conspecific individuals; the factor species was nested within taxonomic family to control for phylogenetic non-independence (as in Koh et al. 2004, Hamer et al. 2015). The random factor plot, necessary to assess possible variability due to local topographic differences within each forest type, was not included in the models because preliminary analyses showed that it did not improve the fitting of any model. The random factor plate, necessary to control for variation in the markers due to unpredictable effects of laboratory analyses, was included in the models for FRAE and GPx only, because only for these two markers it improved the fitting of the models as determined by a decrease of the Akaike Information Criterion over a value of 2.

The concentration of TRIG was not included in the model for TBARS because a preliminary model including the fixed effect TBARS, the covariate TRIG and the species as random factor, did not detect any significant covariation between the two variables (LMM: $F = 0.05$, $P = 0.81$). The factor individual was also not included in the models because we only had repeated measurements for 14 birds within a same year and 12 birds between years (or fewer depending on the marker). For these individuals, we calculated the coefficient of variation for each marker of oxidative status (Table S4 and S5). Significance threshold of our models was set at $P < 0.05$ and non-significant interaction terms were removed only if the fitting of the model improved as estimated by a decrease of the Akaike Information Criterion over a value of 2. Distribution of model residuals was checked using the Shapiro-Wilk test. When model residuals did not meet the assumption of normal distribution, data were square-root or log-transformed ($\log_{10} + 1$) and normality was tested again. Heteroscedasticity was assessed by plotting residuals vs. fitted values.

Analyses of outliers were implemented for every model by measuring the Cook's distance with fixed cut-off at 4/n (n = sample size). Detected outliers were removed from the database and the respective models were run again. Results were generally similar between models with or without outliers except in two cases. We reported models including all individuals, specifying if removal of outliers affected the outcomes. Given the low number of samples in some species (Table S2), we re-ran the models excluding from the database those species with less than five samples for type of forest, for any given marker. Results are shown in Table S8. All statistical analyses were performed using R (R Core Team 2013).

Relationship between oxidative status and population abundance

To obtain measures of the effect of forest logging weighted for confounding variables, we calculated least square means (LSMs) for each species and marker of oxidative status in logged and unlogged forests, from the interaction term of LMMs, which included forest type, species and their interaction as fixed factors. Potential confounding variables included in the LMMs were year, date and hour of sampling. We used the family of the species as random factor to control for phylogenetic non-independence.

Then, to standardize the measures of the effect of forest logging on markers of oxidative status across species, we used LSMs, their standard deviations and sample sizes to calculate Hedges' *g* effect sizes for each bird species and marker of oxidative status. Standardized effect sizes calculated from LSMs measure the magnitude and direction of a change, weighed for the effect of confounding factors included in the model. In our study, a positive effect size estimate indicates that a given marker of oxidative status is higher in logged than in unlogged forest. Small effect sizes (Hedges $g = 0.2$) explain 1% of the variance, intermediate (Hedges $g = 0.5$) explain 9% of the variance, and large (Hedges $g = 0.8$) explain 25% of the variance (Cohen 1988). Effect sizes were calculated in R (R Core Team 2013) using the *compute.es* package (Del Re 2013). Then, we reduced the number of variables by performing a Principal Components Analysis (PCA) on the correlation matrix between effect size estimates of markers of oxidative status. We extracted the first two main axes (PC1 and PC2, see results) and tested their correlation with values of effect sizes of each marker of oxidative status to assess how markers loaded on each of the two axes.

To test for relationships between changes in effect size estimates of oxidative status and population abundance between unlogged and logged forests, PC1 and PC2 were included in two separate linear regression models (LMs) with the Relative Population Abundance (RPA) index of each species as response variable. The inclusion of phylogeny in the LMs (see Supporting Information) did not change significantly the outcomes, thus we report only results of non-phylogenetic models. To estimate the RPA index of each species, we used captures data of birds for each type of forest relative to our study period, as follow: [(captures in logged forest – captures in unlogged forest) / (captures in logged forest + captures in unlogged forest)] (inverse of Logging Sensitivity Index; Hamer et al. 2015, Messina et al. 2020c). Positive values of the RPA index indicate higher abundance of the species in selectively logged forest compared to unlogged forest. Captures data were corrected for sampling effort [Number of captures / (Expected Effort (nets*hours)]. The patterns of species abundances we found are broadly similar to those observed in the region from both mist-netting and point count survey methods (Edwards et al. 2011). We are therefore confident that the method we used to estimate population abundances is reliable.

Correlations between markers of oxidative status and body mass

We used Pearson's correlation to test for relationships between markers of oxidative status and species mean body masses. Given that species body condition does not differ between old-growth unlogged and selectively logged forests (paper in preparation), we used pooled data per species to calculate mean values of markers of oxidative status.

Results

Effects of forest type and trophic guild on oxidative status

Birds living in selectively logged forests had higher activity of SOD than birds living in primary forests (Table 1). We also found higher GSH/GSSG ratios in selectively logged forests (after removing two outliers; Table S6, Fig. 2). All other markers did not differ between forests (Table 1, Fig. 2).

Insectivores and omnivores did not differ between forest types for any of the oxidative status markers (non-significant interaction term, Table 1). However, feeding guilds showed significant differences in all markers related to the glutathione cycle (see Fig. S1 for explanation of the glutathione cycle): insectivores had higher GPx, GSSG, and tGSH than omnivores across both forest types (Table 1, Fig. 3). Differences in GSH values between feeding guilds were marginally significant, but after removal of outliers, the value of GSH was significantly higher in insectivores than omnivores ($F = 8.41$, d.f. = 1,3.91, $P = 0.04$). The value of GSH/GSSG was significantly higher in insectivores than omnivores only after removal of outliers ($F = 8.96$, d.f. = 1,9.22, $P = 0.01$). TBARS, SOD and FRAE did not differ between insectivores and omnivores (Table 1).

Values of FRAE, SOD, GSH, GSSG and tGSH were higher in 2018 than 2017 (coefficient estimates ± SE: FRAE = -1.33±0.09, $P = <0.01$; SOD = -0.02±0.01, $P = <0.01$; GSH = -0.52±0.03, $P = <0.01$; GSSG -0.45±0.03, $P = <0.01$; tGSH = -0.69±0.03, $P = <0.01$), whereas TBARS and GPx were higher in 2017 than 2018 (TBARS = 0.020±0.01, $P = <0.01$;

Table 2 – Outcomes of linear mixed models implemented for markers of oxidative status. Significant *P*-values are indicated by an asterisk. The interaction term was retained in the models even if it was never significant because its removal did not improve the fitting of the model according to the Akaike Information Criterion.

		Full Models		
Variable	**Factors**	**d. f.**	***F*-value**	***P*-value**
TBARS	Forest	1,407.94	0.524	0.469
	Guild	1,10.80	1.682	0.221
	Year	1,411.46	8.078	0.004*
	Date	1,406.11	2.237	0.135
	Time	1,409.79	12.178	<0.001*
	Forest*guild	1,407.83	0.255	0.613
FRAE	Forest	1,364.62	1.601	0.206
	Guild	1,13.52	2.224	0.158
	Year	1,4.93	6.893	0.047*
	Date	1,336.00	9.142	0.002*
	Time	1,366.26	2.164	0.142
	Forest*guild	1,361.13	0.104	0.746
SOD	Forest	1,361.78	5.139	0.023*
	Guild	1,3.47	0.208	0.674
	Year	1,361.87	8.122	0.004*
	Date	1,361.93	8.571	0.003*
	Time	1,358.49	0.626	0.429
	Forest*guild	1,361.53	2.041	0.153
GPx	Forest	1,359.89	0.638	0.424
	Guild	1,12.38	9.057	0.010*
	Year	1,2.97	30.700	0.011*
	Date	1,346.28	0.098	0.753
	Time	1,355.35	0.548	0.459
	Forest*guild	1,357.72	0.029	0.863
GSH	Forest	1,327.78	0.751	0.386
	Guild	1,3.89	7.717	0.051
	Year	1,327.96	240.801	<0.001*
	Date	1,324.99	7.535	0.006*
	Time	1,331.29	1.063	0.303
	Forest*guild	1,328.07	1.995	0.158
GSSG	Forest	1,333.95	2.717	0.100
	Guild	1,3.65	8.879	0.045*
	Year	1,333.90	192.455	<0.001*
	Date	1,328.66	1.339	0.247
	Time	1,329.22	2.885	0.090
	Forest*guild	1,334.06	0.485	0.486
tGSH	Forest	1,328.05	0.173	0.677
	Guild	1,3.85	8.301	0.047*

	Year	1,328.12	343.672	<0.001*
	Date	1,325.07	5.883	0.015*
	Time	1,331.81	3.169	0.075
	Forest*guild	1,328.38	0.546	0.460
GSH/GSSG	Forest	1,333.98	2.993	0.084
	Guild	1,9.40	4.687	0.057
	Year	1,334.59	0.165	0.684
	Date	1,327.29	2.160	0.142
	Time	1,332.20	0.002	0.959
	Forest*guild	1,333.87	0.794	0.373

GPx = 0.11±0.01, *P* = <0.01; Table S7). Birds sampled later in the field-season had higher values of FRAE (8.03±2.65, *P* = <0.01), GSH (1.96±7.1, *P* = <0.01), tGSH (1.94±7.99 *P* = 0.01) and lower values of SOD (-4.73±1.61 *P* = <0.01). Values of TBARS were also lower in birds sampled later in the morning (-1.27±3.65 *P* < 0.01). The within-individual coefficient of variation in markers ranged from 8.9 % (SOD, n = 28) to 48.3 % (GSSG, n = 24) within the same year, and from 8.4 % (TBARS, n = 24) to 73.3 % (GSH, n = 14) between years.

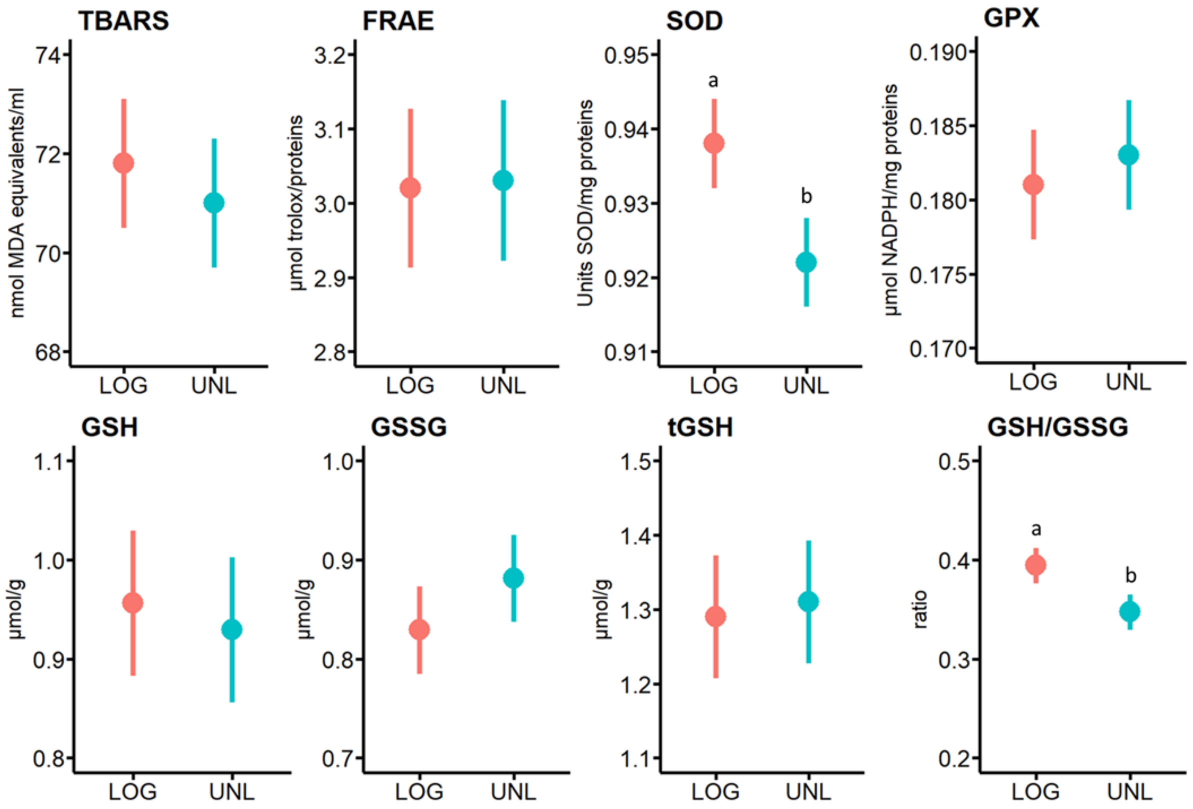


Fig. 2 – least square means +/- standard error of the mean markers level between selectively logged (LOG) and unlogged (UNL) forests. GSH/GSSG is represented after removal of outliers. Different superscripts (a and b) represent significant differences (*P* < .05).

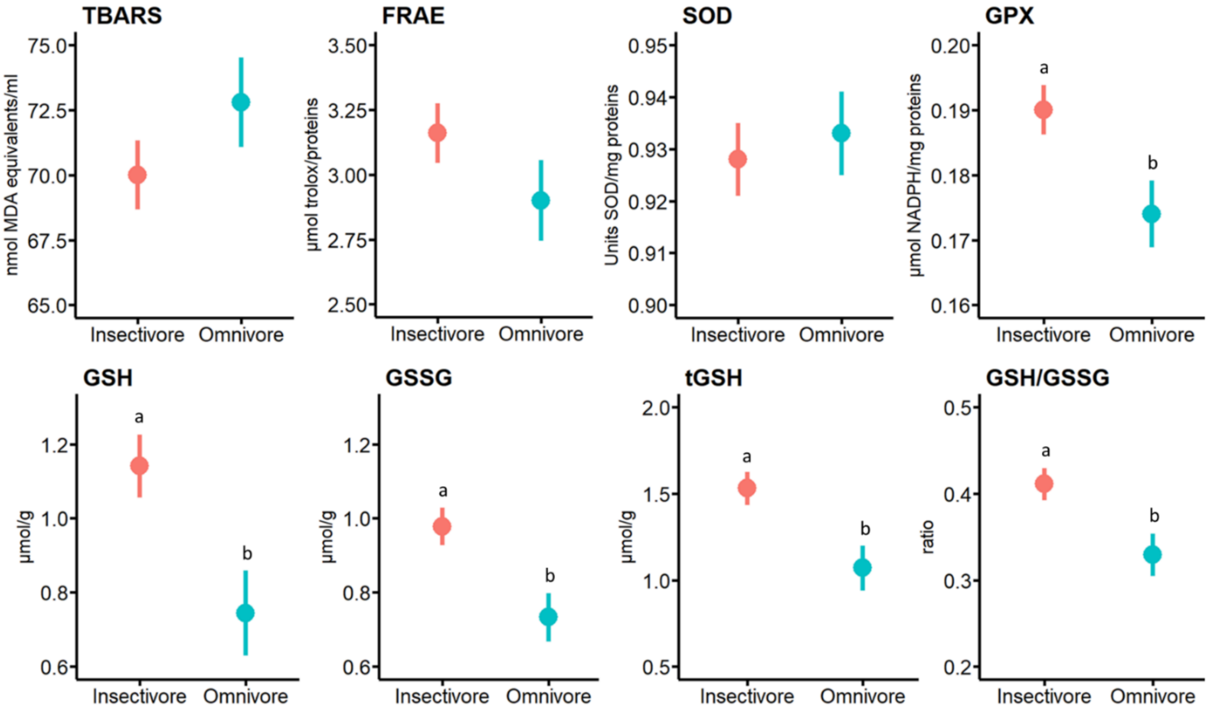


Fig. 3 – least square means +/- standard error of markers of glutathione system between feeding guilds. Significant differences were found for all markers involved in glutathione system (*P* < 0.05).

Oxidative status and population abundance

The first two principal components of the PCA explained 63.7 % of the variance in oxidative status markers. The PC1 explained 36.7 % of the variance; it was significantly correlated with (from higher to lower absolute values) TBARS (r = 0.92, *P* = <0.01), GSH/GSSG (r = -0.85, *P* = <0.01), GSSG (r = 0.71, *P* = <0.01), SOD (r = -0.64, *P* = <0.01) and GSH (r = -0.55, *P* = 0.03). The PC2 explained 27.0 % of the variance; it was significantly correlated with (from higher to lower absolute values) tGSH (r = 0.73, *P* = <0.01), FRAE (r = 0.68, *P* = <0.01), GSH (r = 0.65, *P* = <0.01) and GPx (r = 0.61, *P* = 0.01). Estimates of effect sizes obtained from PC1 did not predict variation in population abundance between forest types, indicating that, contrary to our expectation, markers reflecting oxidation levels (TBARS and GSSG) were not associated with changes in population abundance. In contrast, estimates of effect sizes obtained from PC2 were negatively correlated with RPA index (coefficient estimate±SE = -5.25±1.72, *P* = <0.01; Fig. 4), indicating that levels of particular dietary and endogenous antioxidants in a given forest type were associated with lower population abundance in the same forest type compared to the other.

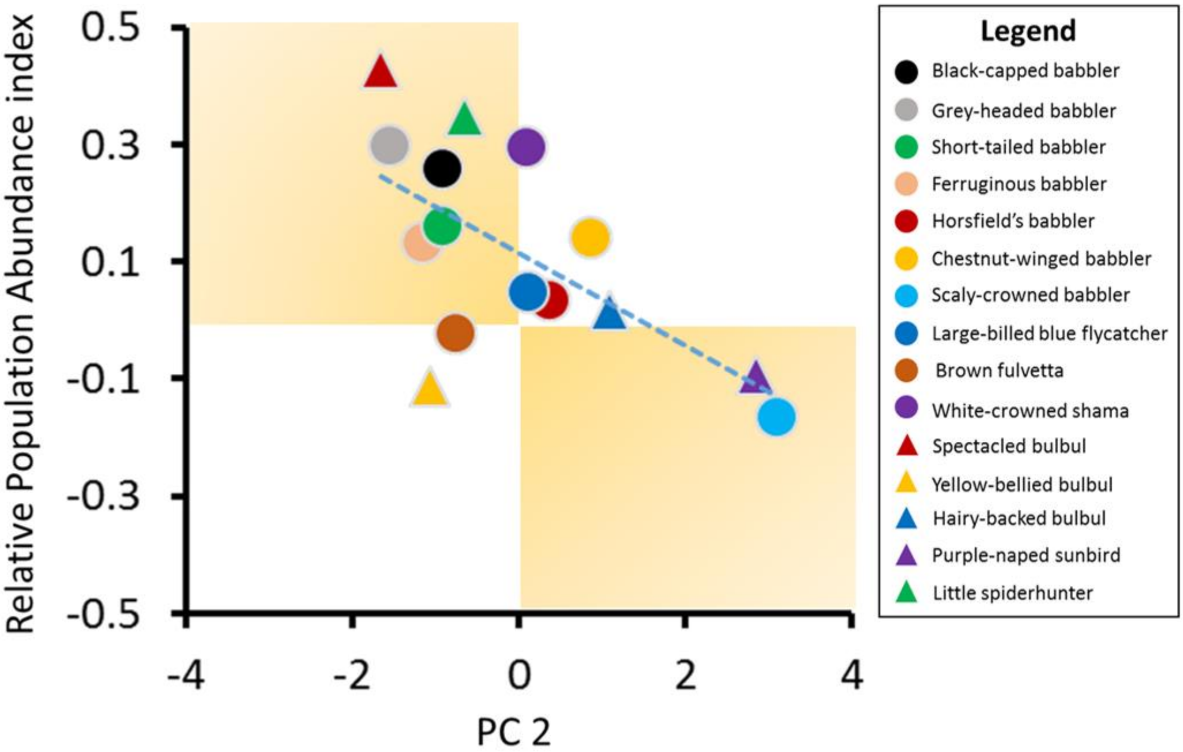


Fig. 4 – Relationship between changes in the relative population abundance (RPA) of species (positive values indicate higher abundance of a given species in logged than in unlogged forest) and markers of antioxidant capacity represented by the Principal Component axis (PC2). Principal Component Analysis were run on the effect sizes (ESs) of least square means of each marker (ES; positive values mean higher marker of oxidative status of a given species in logged than in unlogged forest), between unlogged and selectively logged forest. The PC2 explained 27.0 % of the variance. Data relate markers of oxidative status effect sizes and RPA index of 15 understorey bird species for the years 2017 and 2018. Circles = insectivores; triangles = omnivores.

Correlations

We found that larger bird species had lower levels of TBARS (cor = -0.61, $P = 0.01$) and higher GSH/GSSG ratio (cor = 0.82, $P = <0.01$). TBARS and GSH/GSSG ratio were negatively correlated (cor = -0.78, $P = <0.01$). Higher activity of the antioxidant enzyme SOD was negatively correlated with FRAE (cor = -0.51, $P = 0.04$).

Discussion

Our study used correlative cross-sectional data to investigate the effects of selective logging on the oxidative status of tropical understorey birds. We found that birds living in logged forests had higher values of SOD and of the GSH/GSSG ratio than in old-growth unlogged forests, partially supporting our hypothesis. However, contrary to our expectations, the other markers of antioxidant capacity and oxidative damage did not differ between forest types. Insectivores had higher levels of markers related to the glutathione cycle. Neither TBARS nor SOD differed between feeding guilds. Moreover, we lacked support for the hypothesis that the oxidative status of insectivores and omnivores was differentially affected by logging. Importantly, we found correlative support for our hypothesis that higher levels of particular antioxidants in a given type of forest were negatively associated with relative population abundances of birds in the same forest type, suggesting that implicit costs of maintaining cellular homeostasis might translate into population effects.

Forest logging and oxidative status

The results of our work suggest a possible physiological adaptation of the oxidative status of birds to logging. However, in logged forests, birds had higher activity of SOD, probably to cope with the new environmental conditions. We do not know if this difference in SOD reflects phenotypic plasticity or adaptation (e.g. higher mortality of birds with low SOD in logged forests). Prior work on other bird species did not find support for a link between SOD and survival (Koivula et al. 2011, Messina et al. 2020a), indicating low selective mortality. Future studies will be needed to determine the roles of phenotypic plasticity and microevolutionary processes in driving the physiological adaptation of birds to the new environmental conditions within logged forests.

SOD is an important intracellular enzyme primarily involved in the inactivation of the free radical superoxide anion produced during normal cellular respiration by mitochondria

(Halliwell and Gutteridge 2015). Although it is not possible to determine the environmental factors that explain the higher SOD in logged forest birds, this higher activity might be owing to higher basal mitochondrial production of the free radical superoxide (Sylvie et al. 2012). In line with our results, a recent study showed that great tits (*Parus major*) living in urban habitats had higher SOD as compared to birds living in rural habitats (Salmon et al. 2018); this suggests the importance of SOD for the physiological response to new environmental conditions.

One potential factor that can increase the metabolic activity, and thus SOD activity in birds from selectively logged forests, might be the risk of predation. Large forest openings and less dense canopy cover may affect the risk of predation in birds (Hua and Sieving 2016, Williamson and Fagan 2017). For example, scaly-crowned babbler (*Malacopteron cinereum*, one of our study species) is a more likely victim of nest-predation by pig-tailed macaques (*Macaca leonina*) when their nest is surrounded by saplings and a lower density of tall trees (Somsiri et al. 2019). Such environmental conditions can be found in selectively logged forests, where the abundance of pig-tailed macaques is similar to that in primary forest (Granados et al. 2016). The oxidative cost of predation risk hypothesis is supported by a recent work that found an increased activity of SOD in willow tits (*Poecile montanus*) exposed to higher avian predation risk (Morosinotto et al. 2018). However, Ruuskanen et al. (2017) found no effect of nest predation risk on SOD and other antioxidant enzymes in pied flycatchers (*Ficedula hypoleuca*).

Birds living in selectively logged forests also showed higher GSH/GSSG values than those in old-growth forests, indicating a different regulation of the GSH redox cycle. The activity of SOD in mitochondria converts superoxide anions into hydrogen peroxide, which is then reduced into water by the GSH redox cycle (Halliwell and Gutteridge 2015). Thus, the higher GSH/GSSG values might indicate an upregulation of the glutathione system to counteract accumulation of hydrogen peroxide (Ault and Lawrence 2003), despite levels of total glutathione (tGSH) remained unchanged between the two forest types. Our results are partly in accordance with a study on great tits in rural and urban habitats, where lower levels of GSH/GSSG ratio were not followed by changes in tGSH level (Isaksson et al. 2005). The higher GSH/GSSG ratio in logged forests appears to be mainly driven by either lower oxidation of GSH into GSSG or higher recycling of GSSG into the reduced form (GSH) by the enzyme glutathione reductase. While we are unable to infer the mechanism underlying the regulation of levels of GSH, GSSG and tGSH, our results point to the regulation of glutathione system (i.e., GSH/GSSG ratio) as another major pathway to physiologically adjust to the new conditions of logged forests.

Birds from logged and unlogged forests had similar levels of oxidation markers (TBARS and GSSG) and non-enzymatic antioxidants (FRAE, GSH, GSSG, tGSH). Food availability may affect the oxidative status, for example increasing levels of oxidative damage when antioxidants occur in limited supply in food (van de Crommenacker et al. 2011, Giordano et al. 2015). Elevated trophic flexibility of our study species in selectively logged forest compared to unlogged (Edwards et al. 2013a, Hamer et al. 2015, Corlett 2017, Mansor et al. 2018), and a large abundance of invertebrates in both old-growth and naturally regenerating selectively logged forests (Edwards et al. 2012), might determine similar foraging efforts of birds in both forest types. We do not know, however, if damages to proteins or nucleic acids are similar between unlogged and selectively logged forests.

Feeding guild and temporal variation

Although the effects of forest type on oxidative status were independent of trophic guild, we found higher levels of markers related to the glutathione cycle (i.e. GPx, GSH, GSSG, tGSH and GSH/GSSG) in insectivores than omnivores. This suggests that the glutathione cycle underlies the link between physiological organisation and diet, but that this link does not affect the physiological response to forest logging. The synthesis of GSH in cells depends on the availability of the amino acid cysteine, which can be obtained directly from food or by metabolism of the essential amino acid methionine (Isaksson et al. 2011, Sikalidis et al. 2014). Animal proteins generally contain larger quantities of cysteine and methionine than plant proteins (Wiesenborn 2012, Brede et al. 2018). Thus, relative to omnivores, insectivorous birds could have a surplus of cysteine to relocate for cellular production of GSH. Furthermore, the foraging behaviour of insectivore birds is considered energetically very expensive as compared to omnivores (McNab 1988, Hambly et al. 2004, Yap et al. 2017). Therefore, maintenance of high levels of glutathione cycle molecules in insectivore birds might be needed to neutralize increased ROS production due to high metabolic costs of their feeding behaviour.

We also found daily and annual variation in oxidative damage and in different antioxidant markers. Environmental conditions may explain a large quota of the variance in markers of oxidative status (e.g., Costantini and Dell'Omo 2006, Cohen et al. 2009, Isaksson 2013, North et al. 2017). Changes in weather conditions may, for example, affect the individual oxidative status owing to a direct effect of temperature and rainfalls on the organism's metabolism, or indirectly affecting availability of prey (i.e., invertebrates) and timing of flowering and fruiting of tropical plants. We also found higher levels of oxidative damage later in the morning. Circadian rhythm of oxidative status markers may follow patterns of physical activity, secretion of stress hormones and melatonin, or respond to environmental stimuli (Hardeland et al. 2003, Costantini 2014). Further work will be needed in order to determine which factors drive the daily variation of oxidative damage.

Meteorological data collected in Danum Valley showed that 2018 was drier than 2017 (Table S9). Endotherms eliminate extra heat actively increasing basal metabolism to maintain inner temperature constant (Lin et al. 2008, Angilletta 2009). If such increased metabolism results in higher production of the superoxide anion, birds would need to upregulate SOD to control its pro-oxidant effects. An increase of glutathione and non-enzymatic antioxidant capacity might also be needed to reduce increased levels of hydrogen peroxide produced by SOD reaction with superoxide anion (Fig. S1). Lower level of TBARS in 2018 compared to 2017 could actually be an effect of the higher antioxidant defences. Although we do not have information about different production and access to food sources between 2017 and 2018, annual variation in abiotic conditions might be another important factor involved in the regulation of antioxidants to investigate further.

Population abundance and antioxidants

Although we found significant changes between unlogged and logged forest for two out of eight markers, effect size estimates enabled us to detect several small to large differences among forest types, indicating that the effects of logging varied among markers. Small changes in physiological traits may be biologically important (Møller and Jennions 2002, Garamszegi 2006). We found correlative evidence that variation in four markers (FRAE, GSH, tGSH, and GPx) between forest types was significantly associated with differences in local abundance of birds between forests. Specifically, species with higher levels of these four antioxidant markers in a given type of forest were less abundant there than in the other forest type. This result may suggest that a higher investment in certain antioxidant mechanisms (e.g. glutathione cycle) might be part of a trade-off between self-maintenance and fitness traits (e.g., reproduction), which translates into population effects. For example, energetic constraints might rise from increased consumption of molecules of ATP for the synthesis of both GSH and GPx (Halliwell and Gutteridge 2015). However, we expect that other physiological mechanisms were also involved in the response of birds to selectively logged forests (e.g., the regulation of the hypothalamic-pituitary-adrenal axis), concurring to the trade-off between self-maintenance and fitness traits.

Markers of oxidative status that appear to be associated with the population abundance did not differ significantly between forest types. In contrast, SOD and GSH/GSSG were not related to the population abundance, but differed between forest types. An explanation for this result might lie with a differential canalisation, a biological process by which traits with larger fitness effects show weaker responses to environmental perturbations owing to preferential resource allocation to such traits (Nijhout et al. 2017, Boonekamp et al. 2018). Thus, the effect of an environmental perturbation, like forest logging, would be stronger on those oxidative status markers whose deviations from the optimal trait value are less costly in fitness terms (i.e., are less well canalised). The response of markers of antioxidant capacity to changes in forest characteristics does not, however, appear to be consistent across studies. Previous studies on wild birds did not find any association between habitat or territory quality and plasma non-enzymatic antioxidant capacity (van de Crommenacker et al. 2011, Isaksson 2013). However, Isaksson (2013) found that great tits (*Parus major*) living in deciduous forests have lower tGSH than in evergreen forests. It might be that the ecological meaning of oxidative status markers varies across species and contexts.

White-crowned shama and yellow-bellied bulbul (*Alophoixus phaeocephalus*), which are the largest birds included in this study (respectively, 40.88 grams and 32 grams; Wilman et al. 2014), showed a slight deviation from the correlation between antioxidants and changes in population abundance (Fig. 4). In particular, white-crowned shama was the only species that increased in abundance in selectively logged forests without showing a substantial change in antioxidant levels (PC2 = 0.11, RPA index = 0.29). In contrast, yellow-bellied bulbul was less abundant in selectively logged forest but its antioxidant levels were higher in old-growth forest (PC2 = -1.05, RPA index = -0.11). Both results suggest between species variation in physiological adaptability and its fitness consequences. Cohen et al. (2008) suggested that antioxidant protection could assume higher importance in smaller birds because they might experience higher levels of daily stress and thus invest in a strategy that assumes stress as unavoidable. In line with the hypothesis of Cohen et al. (2008), we found that larger species have lower levels of oxidative damage (TBARS) and higher levels of GSH/GSSG ratio. In Borneo, larger birds are those that are less resilient to forest logging (Costantini et al. 2016b). Srinivasan and Quader (2019) also reported that changes in demographic vital rates of sub-tropical understorey birds along a gradient of selective logging intensity were dependent on the body mass of the species.

Conclusions

Our cross-sectional study provides correlative evidence that bird species had similar levels of most oxidation and antioxidant markers in the two forest types regardless of their feeding ecology. These results suggest that the oxidative status of species was not generally affected by the new environmental conditions of logged forests approximately 15 years after the last logging event took place. Our study also suggests that an increase of particular endogenous antioxidants in understorey birds might contribute to mediate the physiological adaptation of species to the environmental conditions encountered in selectively logged forests, possibly to avoid decreases in reproductive performance.

The results of our work also provide correlative support to the hypothesis that a higher investment in some antioxidant mechanisms may come at a cost for population abundance, possibly through a trade-off between individual self-maintenance and fitness traits. Finally, our data show a correlation between glutathione metabolism and feeding ecology. Future work will be needed to identify the processes (phenotypic plasticity and adaptation) and the abiotic or biotic factors that are responsible for the differences among species in specific markers of oxidative status between undisturbed and logged forests. It will also be crucially important to determine the extent to which variation in oxidative status markers translates into fitness outcomes to determine the role of oxidative status in explaining among-species variation in persistence in logged forests.

Supporting information

Analyses of biomarkers of oxidative status

Protein concentration and markers of oxidative status (glutathione excluded) were measured on five plates, in duplicate. Quality controls (QCs) were used to measure inter-assay variation. In order to measure the protein concentration, the non-enzymatic antioxidant capacity (FRAE), and the activity of antioxidant enzymes superoxide dismutase (SOD) and glutathione peroxidase (GPx) in erythrocytes, we produced haemolysates by diluting 5 µl of red blood cells (RBCs) in 350 µl of extracting buffer (pH 7.4; 1.15% KCl and 0.02 M EDTA in 0.01 M PBS) and processing the samples through a MagNALyser to break cells (Roche, Vilvoorde, Belgium).

The protein concentration was determined by adding 180 µl of Biuret reagent to 20 µl of haemolysate and, after 2 minutes, 20 µl of Folin reagent. Bovine serum albumin (BSA) was used as a reference standard. Readings of absorbances were taken at 660 nm and the protein concentration was expressed as µg BSA/ml. We quantified the FRAE by mixing 180 µl of ferric ion reducing antioxidant power reagent (pH 3.6; 0.3 M acetate buffer, 0.01 mM TPTZ in 0.04 mM HCl and 0.02 M $FeCl_3 \cdot 6H_20$) with 20 µl of haemolysate. Readings of absorbances were taken at 600 nm after 30 minutes. 6-Hydroxy-2,5,7,8-tetramethylchroman-2-carboxylic acid (Trolox) was used as the standard and FRAE concentration was expressed as µmol trolox/proteins (Benzie and Strain 1996). Although this method was originally developed for plasma (FRAP; Benzie and Strain 1996), the generality of the assay principle makes it suitable to be applied to any kind of biological matrix, including haemolysates, tissue homogenates, plant extracts or beverages (e.g., Benzie and Strain 1999, Benzie and Devaki 2017). SOD activity was determined by adding 20 µl of SOD reaction buffer (50 mM sodium carbonate buffer (pH 10.2); xanthine 0.1 mM; NBT 0.025 mM and EDTA 0.1 mM) and 20 µl of xanthine oxidase (0.24 U, units) to 20 µl of haemolysate. The inhibition of nitro blue tetrazolium (NBT) reduction made by SOD was measured at 560 nm. The activity of SOD was expressed as Units/mg protein (Dhindsa et al. 1981). To measure the activity of GPx we added 140 µl of GPx reaction buffer (50 mM PBS (Ph 7.1); sodium azide 3.6 Mm; GSH 3.6 mM; NADPH 0.2 mM) to 20 µl of haemolysate. GPx activity was determined by measuring the decrease in NADPH absorbance measured at 340 nm and calculated from the 6.22 mM^{-1} cm^{-1} extinction coefficient. GPx activity was expressed as µmol NADPH/mg protein (Drotar et al. 1985). The average inter-assay coefficients of variation, measured by the use of QCs, were 3.56% for proteins, 3.22% for FRAE, 0.72% for SOD, 3.99% for GPx. The average intra-assay coefficients of variation were 8.08% for proteins, 6.13% for FRAE, 0.56% for SOD, and 10.77% for GPx.

Reduced glutathione (GSH) and oxidized glutathione (GSSG) were measured by Reversed-Phase HPLC of Shimadzu (Hai Zhonglu, Shanghai) in RBCs, following the protocol developed by Sinha et al. (2014). Briefly, 1 ml of 6% metaphosphoric acid (MPA) solution was added to 2 µl of RBCs, quickly frozen in liquid nitrogen and crushed into powder trough a MagNALyser at 5000 rpm for 10s (freezing and crushing repeated three times). Samples were then centrifuged for 12 minutes at 14000 rpm at 4 ºC. The supernatants of the resulting lysates were used for the Reversed-Phase HPLC of Shimadzu and the concentrations of GSH and GSSG were expressed as µM per gram fresh weight of RBCs. Samples were not analyzed in duplicate given the high reproducibility of data obtained with HPLC methods. When the total amount of RBCs in a sample was lower than 5 µl, we gave priority to measures of glutathione because of the strong antioxidant role and possibility to measure both the reduced and oxidized form of this molecule.

As marker of oxidative damage, we measured the thiobarbituric acid reactive substances (TBARS) in plasma to quantify lipid peroxidation following the protocol developed by El-Shafey and AbdElgawad (2012) and validated for bird species (Raap et al. 2016, Casasole et al. 2017, Sebastiano et al. 2017). We mixed 5 µl of plasma with 0.5 ml of thiobarbituric acid (TBA) reagent (0.5% TBA in 20% trichloroacetic acid) and placed the samples in oven at 90 ºC for 45 minutes. To protect samples from potential oxidation caused by heating, we added 0.01% of the synthetic antioxidant butylated hydroxyl toluene (BHT) to the extraction buffer (Esterbauer and Cheeseman 1990)**.** The reaction was then stopped by placing samples in ice bath for 5 minutes. The supernatant (200 µl) of the resulting product was used in the assay and absorbance was measured at 532, 600 and 440 nm in a micro-plate reader. The concentration of TBARS was calculated using the following formula: $6.45 \times (A_{532} - A_{600}) - 0.56 \times A_{450}$. Values of TBARS were expressed as nmol malondialdeyde (MDA) equivalents/ml; we expressed values as an equivalence instead of a concentration because the TBARS method measures a number of aldehydes generated by lipid peroxidation, so that MDA is not the only lipid peroxidation compound measured (Halliwell and Gutteridge 2015). TBARS values are strongly correlated with lipid peroxidation values obtained using HPLC methods (e.g., Moselhy et al. 2013, Kil et al. 2014, Reitznerova et al. 2017), indicating that the formation of aldehydes at working conditions is generally negligible. The average intra- and inter-assay coefficients of variation were 10.45 and 9.07%.

Analysis of Triglycerides

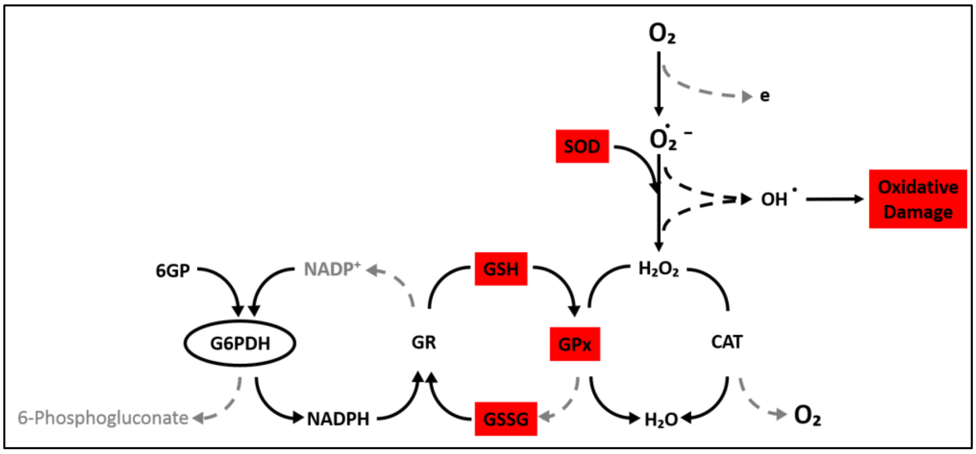
For the analysis of triglycerides (TRG) we used a commercial kit (WAKO LabAssay Triglycerides) according to manufacturer's instructions. The assay is based on an enzymatic method using *N*-ethyl-*N*-(2-hydroxy-3-sulfopropyl)-3,5-dimethoxyaniline sodium salt (DAOS) as a blue pigment. Two µl of plasma of each sample (in duplicate) were mixed with 300 µl of color reagent. The color reagent was previously prepared by dissolving 1 vial of chromogen substrate in 105 ml of buffer (color reagent components provided in the kit). After 15 minutes of incubation at room temperature, we measured the absorbance at 600 nm. Results of the absorbance were plotted against a standard curve of known concentrations to obtain the

TRG concentrations expressed as mg/dl. The average intra- and inter-assay coefficients of variation were, respectively, 7.5% and 12.06%.

Phylogenetic Linear Models

Prior to run the phylogenetic models, we calculated least square means (LSMs) for each species and marker of oxidative status in logged and unlogged forests from the interaction term of linear models (LMs). Differently from linear mixed models for LSMs calculation described in the main text, in LMs we did not include the family of the species as random factor because it can be considered a proxy for phylogenetic non-independence control. Then, we calculated Hedges' *g* effect sizes of LSMs for each marker of oxidative status, and we used their correlation matrix to perform a principal component analysis. To assess the phylogenetic relationship among study species, we used 500 probable phylogenies obtained from www.birdtree.org (Jetz et al. 2012) to calculate the best average phylogenetic tree. Finally, the first two principal component axes and the Relative Population Abundance Indexes were correlated in phylogenetic linear models (PGLS) in which the best combination of phylogenetic signals calculated as lambda (λ), kappa (*K*) and delta (δ) was determined by maximum likelihood. PGLS were ran using the R package *phytools* (Revell 2012).

Figure S1 – Glutathione redox cycle.



Tables from S1 to S9 can be found online at:

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Chapter V

Selective logging reduces body size in omnivorous and frugivorous tropical forest birds

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Abstract

Selective logging is the main anthropogenic disturbance in tropical forests, driving shifts in species abundances. Body size and body condition are important metrics of fitness that may be affected by habitat degradation. We conducted a four-year study to investigate how selective logging impacted the body size and body condition index (BCI) of 55 Bornean bird species and whether changes in body metrics were associated with shifts in relative population abundance. Frugivorous and omnivorous birds had reduced body size in selectively logged versus unlogged forest, but we found no evidence for selective removal of individuals driven by sex differences or post-fledging body size, indicating different developmental conditions for frugivores and omnivores in logged forest. Change in body size between forest types showed no clear patterns for insectivorous birds, and did not differ between IUCN categories. BCI of birds was affected by study year, suggesting an effect of climatic conditions on food availability, but not by logging. At the community level, post-logging difference in population abundance was not associated with reduced body size, although between species variation suggests that adverse environmental conditions and different coping strategies underlie body size reductions in logged forest. Our study suggests that body size is a valuable metric to assess how logging impacts forest birds, pointing towards potential functional consequences related to seed dispersal within logged forests and need for improved silvicultural practices.

Introduction

Anthropogenic land-use changes are major drivers of biodiversity loss. Biodiversity-rich tropical forests are primarily degraded by logging, via the selective harvesting of large, commercially valuable trees (Edwards et al. 2014b). Over 400 million hectares (~25%) of remaining tropical forests are designated as logging concession, with selectively logged forests more prevalent than unlogged forests in most regions (Blaser et al. 2011). Determining how species respond to selective logging and which traits make species more or less resilient to logging is thus a research frontier.

Selective logging opens large forest gaps, increasing sunlight penetrating the understory and boosting vines and climbing bamboos (Edwards et al. 2014b). The local abundance of many taxa, including both invertebrates and vertebrates, changes post-logging, shifting species richness and community composition (e.g. Edwards et al. 2011, Ewers et al. 2015). As a consequence of altered trophic interactions, birds and ants feed at higher trophic levels in selectively logged forest (Edwards et al. 2013a, Woodcock et al. 2013). Moreover, some bird species show differences between forest types in their physiological status (Messina et al. 2020b, Messina et al. 2020c).

Changes in body size and body condition are sub-lethal effects of habitat degradation that may act as early signals to predict future population responses (Janin et al. 2011, Irwin et al. 2019). How selective logging impacts body size and condition remain key unresolved questions for several taxa. Previous studies found that body fat storage of dung beetles increased as a stress response to selectively logging (França et al. 2016), whereas the mass of gray-cheeked mangabey (*Lophocebus albigena*) of similar body size, was higher in unlogged compared to selectively logged forest, likely due to increased investment in tissue mass (Olupot 2000). Understanding proximate mechanisms underlying species responses to selective logging may provide useful tools for the monitoring of the actual population status and for predicting long-term viability (Ewers and Didham 2006).

Environmental changes may also affect skeletal growth and development of vertebrates, generating large among-individual variation in adult phenotype (Yom-Tov and Geffen 2011). For example, forest fragmentation has been shown to reduce body size in small temperate mammals (Lomolino and Perault 2007), sub-tropical skink lizards (Tuff et al. 2019), and tropical tree-frogs (Neckel-Oliveira and Gascon 2006). Similarly, birds living in secondary tropical forests (Smith et al. 2008) or in cities (Liker et al. 2008, Caizergues et al. 2021) were of smaller body size than those living in undisturbed forests.

Nutritional restrictions and other stressful events experienced during early-life development can reduce growth rate, so that individuals are of smaller body size in adulthood. For example, artificially induced developmental stress through corticosterone administration constrained tarsus growth in nestling common kestrels (*Falco tinnunculus*) and in zebra finches (*Taeniopygia guttata*) (Muller et al. 2009, Kraft et al. 2019). Such phenotypic effects are not necessarily negative. For example, while little greenbuls (*Andropadus virens*) living in secondary forests had reduced tarsus length compared to those living in mature forests, they were five-fold more abundant than in mature rainforest (Smith et al. 2008).

Body condition index (BCI; body mass normalised for body size differences) is an indirect estimate of the energy stores (mainly fat mass) accumulated in the body, and thus available to support energetically demanding life processes, such as reproduction (Peig and Green 2009). Changes in diet could affect BCI through differential intake in nutrients or indirectly through a change in metabolic rate owing to altered foraging activity (Köhler et al. 2012). For example, diademed sifakas (*Propithecus diadema*) spend more time foraging in forest fragments, and have lower nutrient intake and BCI than in continuous forest (Irwin et al. 2019). Nwaogu et al. (2019) demonstrated experimentally a causal effect of diet composition on BCI: adult common bulbuls (*Pycnonotus barbatus*), a tropical omnivorous bird, were in better condition when fed on fruits than invertebrates.

Focusing on birds and Borneo, where selective logging has been very intensive, we carried out a four-year research program to test: (i) whether birds in selectively logged forests had reduced body size (using tarsus length as a proxy; Senar and Pascual 1997) and BCI compared to those in unlogged old-growth forest; and (ii) whether differences in these two body metrics were linked to changes in relative population abundance between the two forest types. If environmental conditions in selectively logged forest were detrimental for birds, we expected to find (i) reduced body size and/or BCI, along with (ii) lower population abundance.

Materials and Methods

Data collection

The study was conducted within the Yayasan Sabah logging concession, in Sabah, Malaysian Borneo. Unlogged forest was located in a 45,200 ha block within the Danum Valley Conservation Area (DVCA) (4°57´45.2″N, 117°48´10.4″E) and adjacent Palum Tambun Watershed Reserve. This is contiguous with selectively logged forest in the Ulu Segama-Malua Forest Reserve (4°57´42.8″N, 117°56´51.7"E). Trees of the Family Dipterocarpaceae, which dominate these lowland forests, are valuable timber species. Selective logging in the study area occurred in the late 80’s and early 90’s at high rates of timber removal (~115 m^3 ha^{-1}), and again between 2000 and 2007 (~31 m^3 ha^{-1} of additional wood extracted) leaving a heavily disturbed forest (Fisher et al. 2011). After the last logging rotation, the forest was left to recover naturally.

Fieldwork took place between June and August from 2015 to 2018. Mist netting of the avian understorey community was performed in three plots in unlogged old-growth forests and three plots in twice-selectively logged forests (Fig. S1), to have replicates within each forest type. Plots were placed at least 1.8 km apart (mean unlogged forest = 6.64 km; mean logged forest = 4.04 km) and 500 m from the nearest road. Distance between unlogged and logged forest plots was >10 km, ensuring that dispersal of juveniles between forest types is rare (we had no recaptures between forest types; Cosset et al. under review). Each plot contained three independent parallel transects containing fifteen nets (12 x 2.7 m; 25-mm mesh size, overall 45 nets per plot) erected end-to-end. Based on previous studies, our data from mist netting in different transects are statistically independent (distance between transects > 200 m; Hill and Hamer 2004) and our transects are representative of the different environmental conditions found in unlogged and selectively logged forests (Senior et al. 2018).

Transects were run simultaneously from 06:00 to 12:00 h and nets were checked hourly. Each plot was visited for two consecutive days, three times per field season in fine weather, with rotation among plots to minimise potential temporal effects, equating to 38,800 mist-net hours in total. Mist nets were closed in case of rain.

All captured birds were marked with individual numbered rings. Species and capture date were recorded, with sex recorded for dimorphic species. We discerned between adults and juveniles following an aging system for tropical birds based on moult cycle and plumage (Johnson et al. 2011). We considered ‘juvenile’ birds as those in juvenile plumage, pre-formative moult (first pre-basic), or formative plumage. Body mass of birds was measured with a spring scale (Pesola) to the nearest 0.5 g. Tarsus length was measured with a calliper (0.1 mm). Measurements of tarsus length for birds recaptured multiple times were highly consistent across ringers (2.38% of variation). Tables with species information and data on recaptures can be found in Supplementary Information (Supplementary Tables S1-S2, respectively).

All experimental procedures were approved by the Sabah Biodiversity Council (access licence number: JKM/MBS.1000-2/2 JLD.6(39) and JKM/MBS.1000-2/2 JLD.7(57)).

Data Analysis

We included in our study all species that were represented by a minimum of two individuals per forest type. Samples sizes were as follows: 2,634 birds belonging to 55 different species for tarsus length; and 2,377 birds belonging to 51 species for BCI (Supplementary Table S3).

Phylogenetic control

Statistical analysis based on multi-species comparison may require the inclusion of species' phylogenetic information to control for non-independence of a given trait. To take into account phylogenetic uncertainty, we built least consensus trees based on 1000 phylogenetic trees from the backbone of Hackett et al. (2008) of the complete phylogeny of birds available at www.birdtree.org. The species *Alophoixus tephrogenys* was until recently considered conspecific with *Alophoixus bres*, and phylogenetic data are available only for the older classification. Thus, to include *Alophoixus tephrogenys* in our phylogenetic models, we used its former classification as *Alophoixus bres*.

Species ecological traits

Feeding guilds and foraging strata of birds are important traits affecting species responses to selective logging (Gray et al. 2007, Burivalova et al. 2015, Hamer et al. 2015), thus we considered species' feeding traits in our models testing for the relationship between body size or BCI with selective logging. Data on feeding guilds and strata (Supplementary Table S1) were obtained from Wilman et al. (2014). 'Insectivores' were species feeding >50% of their diet on invertebrates; 'Frugivores' for species feeding >50% on fruits, or fruits and nectar; and 'Omnivores' for species in which no main food category reached 50% of the diet. Feeding strata categories were: 'Lower level', for species spending >65% of time feeding between ground and understory strata; 'Higher level', for species spending >65% of the time feeding between mid-high and canopy strata; or 'Mixed level' for species spending less than 65% of the time feeding in understory or higher level strata. Since mist netting occurred in the understorey, we consider all study species as part of the understorey avian community.

A recent meta-analysis found that selective logging in Borneo has stronger negative impact on population abundance of avian species classified as Near Threatened (NT) or Vulnerable (VU) by the International Union for Conservation of Nature (IUCN) Red List classification, than those classified as Least Concern (LC) (Costantini et al. 2016b). We considered species IUCN conservation status as a fixed factor to assess whether the body size and the BCI of species of conservation concern (CC; NT x16, VU x3 and EN x1 species; Supplementary Table S1) are more adversely affected by forest selective logging than LC species.

Statistical Analyses

Models for body size

To test for differences in body size between the two types of forest we used multiple-measurements phylogenetic Bayesian models, implemented in R by *MCMCglmm* package (Hadfield 2010). This approach allows the inclusion of the phylogeny in a model with unbalanced numbers of observations. We used tarsus length as response variable. Fixed factors were forest type, feeding guild, feeding strata and IUCN Red List status. Forest type included unlogged and logged forests. Feeding guild and strata were included to control for an effect of feeding habits on body size changes between forests, and the IUCN Red List status to control for an effect of species' conservation status. The model also included three interaction terms between forest type and feeding guild, forest type and feeding strata, and forest type and IUCN, to test for any difference in body size between feeding and conservation categories (i.e., feeding guild: insectivores, frugivores, omnivores; feeding strata: understory, higher levels, mixed levels; IUCN: least concern, conservation concern) across the two types of forest. Since we had no information on the year of birth of captured adult birds, the model did not include the fixed factor 'year'.

Random factors were: individual identity, to account for individuals recaptured within and between years; phylogeny, to deal with non-independence of species due to common ancestry; and species, to account for any other possible effect independent from the phylogenetic relationship between species (e.g. environmental effects; Garamszegi 2014). The random factor plot was not included in our models because it showed low variance in preliminary models. Interaction terms were explored by Tukey's multiple comparison test on least square means. Interactions were considered significant when the highest posterior density (HPD) interval did not overlap zero. The final model did not include the interaction term between IUCN Red List category and forest type because it was not significant in a preliminary model.

To test if the inclusion of species with a low sample size affected the results, we re-ran the model excluding from the database 14 species with fewer than six individuals per forest type. Results were similar to those of the model including all species (Supplementary Tables S4-S5).

Model for body condition index

We used multiple-measurements phylogenetic Bayesian models also to test for differences in BCI between the two types of forest. Differently from the model for body size, we used body mass as the response variable and tarsus length as covariate for an estimation of the effect of forest logging on BCI (García-Berthou 2001). In so doing, we rely on least square means, which indicate values of body mass normalised by body size. However, by using individual measurements in the covariate we cannot discern which relationship (between- or within-species) the slope is measuring. We obtained the between-species and within-species slopes separating the predictor (i.e. tarsus length) in two components: one containing the species-level mean and another containing the within-species variability (within-group centring technique; Garamszegi 2014).

As fixed factors, we included forest type, feeding guild, feeding strata and IUCN Red List status. We also included fixed factors year (categorical variable) and date (continuous variable) of sampling in the model, to control for potential temporal variation in BCI due to body mass changes. Interaction terms between forest and feeding guild, forest and feeding strata, and forest and IUCN Red List category, were not included in the final model because they were non-significant in a preliminary model. Random factors were individual identity, phylogeny, and species, as in the model for body size.

To test if the inclusion of species with low sample size affected the results, we re-ran the model excluding from the database 14 species with less than six individuals per type of forest. Results were similar to those of the model including all species (Supplementary Table S6).

Models setting

For both models on body size and BCI, the Monte Carlo Markov chains were run for 1,000,000 iterations, with a burn-in interval of 1,000 to ensure satisfactory convergence. A total of 500 iterations were sampled to estimate parameters for each model. Following Garamszegi (2014), we calculated the inverse of our matrix of phylogenetic correlation and we set prior distributions corresponding to an inverse-Gamma distribution with shape and scale parameters equal to 0.01. We checked for model convergence and auto-correlation visually inspecting trace plots of fixed and random factors. In addition, we checked that levels of autocorrelation among samples were lower than 0.1.

Models for sex and age

Our database included 12 dimorphic species for which we could determine sex and eight species for which we had more than one juvenile and one adult per forest type. Such species were used to test for an effect of sex and age, respectively, on body size and, with the exception of one species (*Chalcophaps indica*), for BCI differences between unlogged and selectively logged forest (Supplementary Table S7-S8). Information on the building of the Linear Mixed Models (LMMs) testing for an effect of sex or age on body size and BCI can be found in Supplementary Information.

Morphometric differences and population abundance

To compare measures from different species, we calculated standardized effect sizes of body size and BCI differences, for each species, between unlogged and logged forests (Fig. 1). Details on the calculation of the effect sizes can be found in Supporting Information.

We used data of species captures in unlogged and logged forest to calculate an index of species' relative abundance between the two types of forest (Supplementary Table S9). The Relative Population Abundance (RPA) Index was calculated as follow: [(abundance in logged forest – abundance in unlogged forest) / (abundance in logged forest + abundance in unlogged forest)] (Messina et al. 2020c). Positive values of the RPA index indicate higher abundance of the species in selectively logged forest compared to unlogged forest. Abundance data were corrected for sampling effort [Number of captures / (Expected Effort (nets*hours)]. Recaptured individuals within-year, but not between years, were excluded from the abundance counts.

To test for relationships between changes in relative population abundance between forest types and body size, we ran Phylogenetic Linear Models (PGLS) separately for each feeding guild. RPA index of the species, calculated over the study period, was included as the response variable and the effect size estimates of body size as a covariate. Models were run separately for insectivores and non-obligate insectivorous birds (omnivores and frugivores pooled together to increase the sample size). Since the RPA index of species feeding above understorey may be biased by higher capture rates in the logged forest, we also run separate models including all species feeding at lower levels, and at both lower and mixed levels. The model testing for relationships between changes in relative population abundance between types of forest and BCI was not run because 45 species out of 51 had low effect sizes with low variation among them (range: -0.14 – 0.21).

Results

Body size

Selective logging had a significant effect on body size of tropical birds (posterior mean = -0.61; 95% CI: -1.04, -0.14). Lower level feeding birds were larger than those feeding at mixed (posterior mean = -3.73; 95% CI: -7.76, -0.41) and higher (posterior mean = -4.21; 95% CI: -7.14, -1.21) level strata. Differences in body size between IUCN categories were marginally significant (Ref. level LC: posterior mean = 2.17; 95% CI: -0.30, 4.84), indicating larger species as those of major concern for conservation.

Post-hoc analysis of interaction terms showed a significant reduction of body size in logged forest compared to unlogged forest in omnivore (estimate = -0.23; 95% CI: -0.42,-0.03) and frugivore species (estimate = -0.53; 95% CI: -0.95,-0.12; Fig. 1), in species feeding at lower (estimate = -0.30; 95% CI: -0.53,-0.09) and higher (estimate = -0.35; 95% CI: -0.58,-0.12) strata, and in both IUCN categories (LC: estimate = -0.23; 95% CI: -0.38,-0.08; CC: estimate = -0.26; 95% CI: -0.51,-0.03). Body size of insectivorous species and of species feeding at mixed levels showed no clear patterns of changes between forest types (Table 1). However, visual inspection of effect sizes (Fig. 2) shows either reduced or increased body size for several insectivore species in selectively logged compared to unlogged forest.

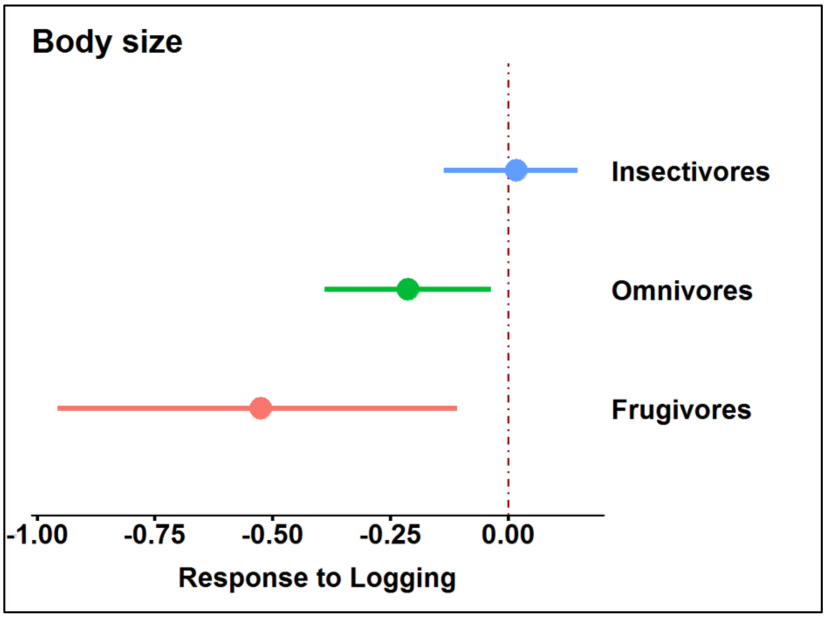


Fig. 1 –Estimates and highest posterior density (HPD) intervals of body size differences between unlogged and selectively logged forests, in different feeding guilds. Negative values indicate smaller body size in selectively logged forest. When the HPD intervals do not overlap zero, the effect size is significant.

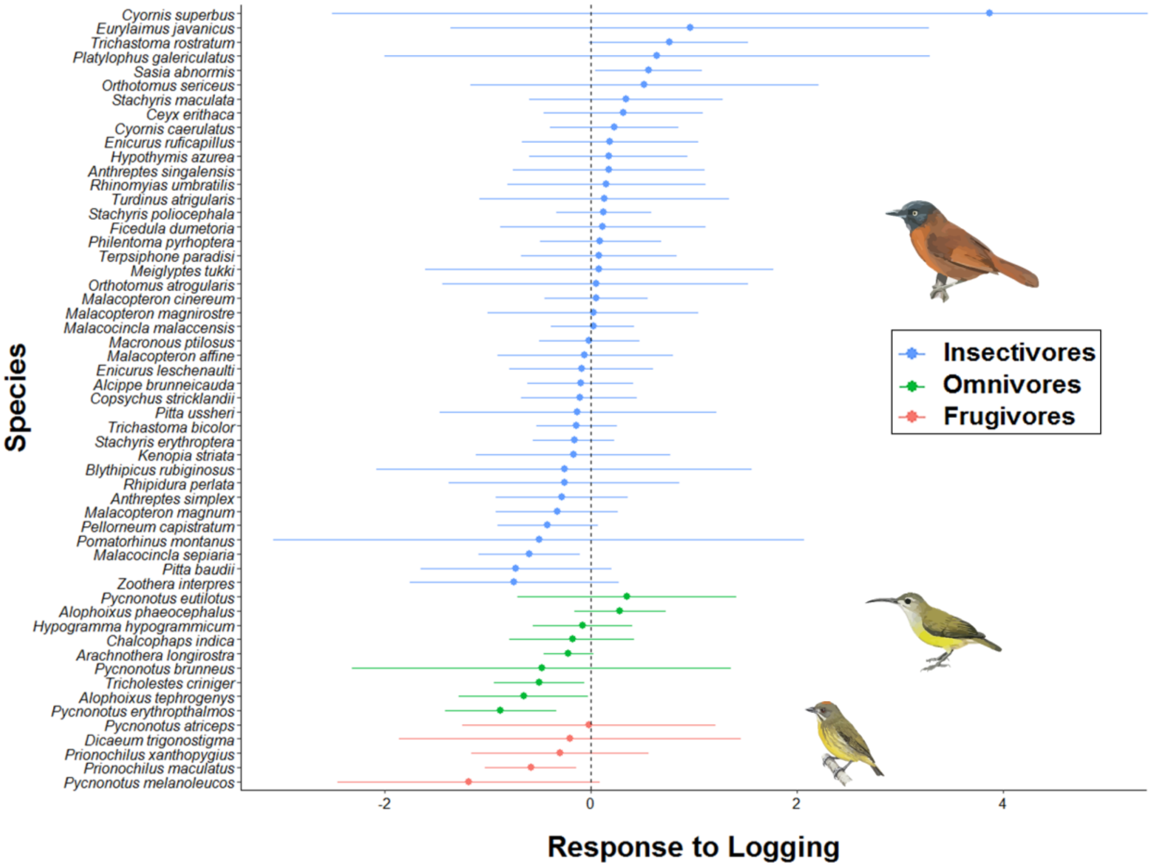


Fig. 2 – Effect size estimates of body size per species. Negative values indicate smaller body size in selectively logged forest. When the confidence intervals do not overlap zero, the effect size is significant.

Table 1 – Pairwise comparison between least square means of the interaction term between forest and feeding guild, included in the multiple-measurements phylogenetic Bayesian model for body size. Significant levels of the interactions are shown in bold. HPD = highest posterior density.

Interaction term	Pairwise comparison	Estimate	Lower (HPD)	Upper (HPD)
Forest*Feeding guild	LOG,Frugivores – UNL,Frugivores	-0.522	**-0.908**	**-0.111**
	LOG,Insectivores – UNL,Insectivores	0.020	-0.129	0.146
	LOG,Omnivores – UNL,Omnivores	-0.210	**-0.378**	**-0.039**
Forest*Feeding strata	LOG,Lower level – UNL,Lower level	-0.293	**-0.500**	**-0.106**
	LOG,Mixed level – UNL,Mixed level	-0.088	-0.312	0.126
	LOG,Higher level – UNL,Higher level	-0.332	**-0.561**	**-0.126**
Forest*IUCN	LOG,LC – UNL,LC	-0.230	**-0.383**	**-0.085**
	LOG,CC – UNL,CC	-0.268	**-0.512**	**-0.037**

Body Condition Index (BCI)

Avian BCI was not affected by logging, feeding guild, feeding strata, IUCN categories or sampling date. However, we found a significant effect of year. In particular, BCI was significantly higher in 2016 compared to 2015 and 2017 (Table 2; Fig. 3).

Table 2 – Outcomes of the comparative phylogenetic Bayesian model implemented for body condition. Significant *p*MCMC-values are shown in bold. LOG = logged forest; UNL = unlogged forest; LC = least concern; CC = conservation concern.

Variable	Reference level	Factors	Posterior mean	Lower (CI)	Upper (CI)	*p*MCMC
		Intercept	-6.82	-26.7	12.7	0.466
Species variation		Between-species	2.47	1.92	2.96	**<5e-04**
		Within-species	0.736	0.640	0.826	**<5e-04**
Year	2015	Year 2016	0.235	0.001	0.434	**0.027**
		Year 2017	-0.088	-0.346	0.167	0.511
		Year 2018	-0.175	-0.167	-0.435	0.450
	2016	Year 2017	-0.321	-0.570	-0.088	**0.005**
		Year 2018	-0.118	-0.408	0.171	0.401
	2017	Year 2018	0.202	-0.115	0.520	0.225
Forest	LOG	Forest UNL	0.021	-0.184	0.226	0.835
Feeding guild	Frugivores	Insectivores	-9.462	-22.490	4.127	0.159
		Omnivores	-2.266	-12.680	7.181	0.657
	Omnivores	Insectivores	-7.452	-18.700	4.018	0.214
Feeding strata	Higher level	Mixed level	2.408	-3.719	8.252	0.427
		Lower level	-4.110	-9.549	1.526	0.151
	Mixed level	Lower level	-6.416	-12.360	0.464	**0.054**
IUCN	LC	CC	1.965	-1.632	5.476	0.270
Date			-0.008	-0.497	0.343	0.689

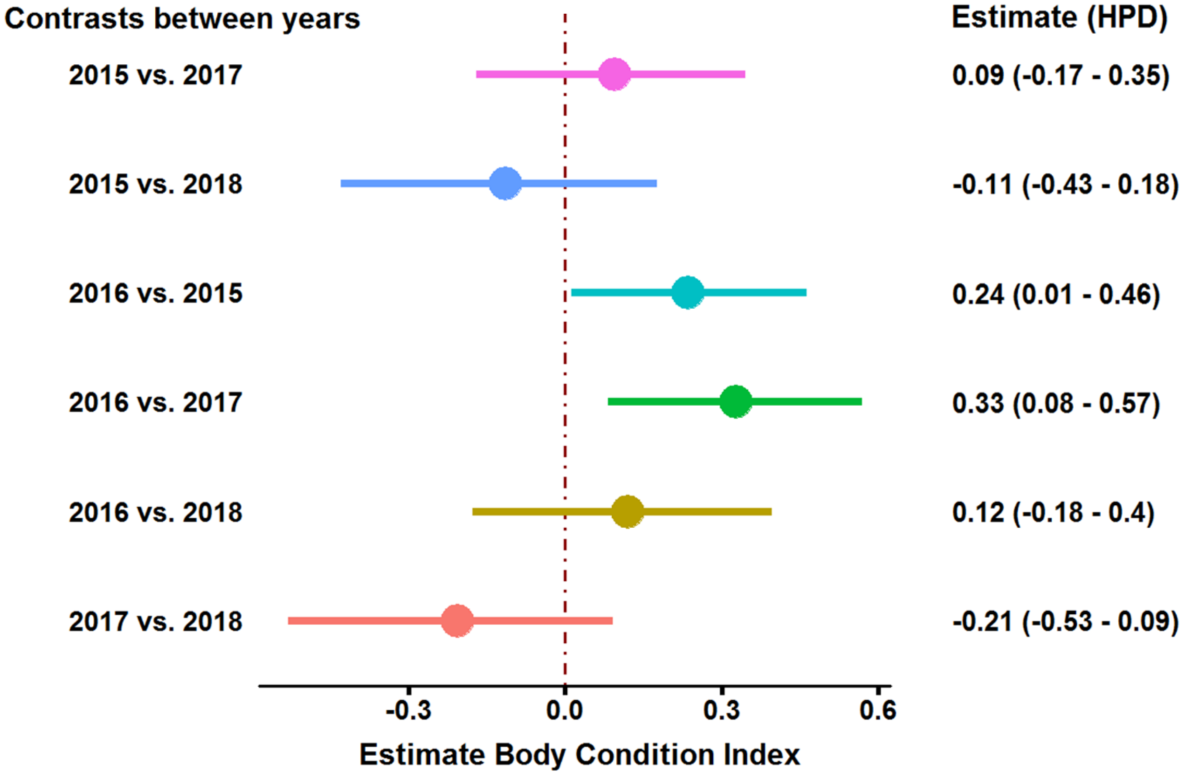


Fig. 3 – Estimates and highest posterior density (HPD) intervals of body condition index contrasts between years. When the HPD intervals do not overlap zero, the effect size is significant.

Sex and age

Males were larger than females (estimate±SE = 0.79±0.10; $P < 0.01$) and had higher BCI (estimate±SE = 1.55±0.18; $P < 0.01$). For body size, the lack of a significant interaction between forest type and sex showed that sexual differences were similar in both types of forest (Supplementary Table S10). For BCI, the interaction between forest type and sex was marginally significant ($F = 3.78$; d.f. = 1,660.05; $P = 0.052$), although post-hoc analysis showed that this result was driven by differences between sexes, and there was no effect of forest type on a given sex (Supplementary Table S11-S12). We also found that body size did not differ between juveniles and adults (Supplementary Table S13), indicating that there was no post-fledging selective mortality in juvenile individuals owing to a given body size.

Population abundance and body size

Differences in abundance between forest types were not related with differences in body size in insectivore species (coefficient estimate±SE = -0.058±0.102; t-value = -0.568; *P* = 0.572). Similarly, non-obligate insectivorous species showed no association between relative population abundances and body size effect size estimates (coefficient estimate±SE = -0.161±0.145; t-value = -1.113; *P* = 0.287). Similarly, species feeding at lower strata, and at lower plus mixed strata, showed no association between relative population abundance and body size effect size estimates (lower levels: coefficient estimate±SE = 0.010±0.150; t-value = 0.070; *P* = 0.944; lower and mixed levels: coefficient estimate±SE = -0.073±0.095; t-value = -0.773; *P* = 0.444).

Discussion

We presented novel evidence that omnivorous and frugivorous birds in logged forest attain a smaller body size than conspecifics living in unlogged forest. This difference in body size was not due to a higher post-fledging mortality of juveniles with longer tarsi in logged forest because body size was similar between juveniles and adults in both types of forest. The reduced body size in logged forest was also consistent between sexes, suggesting the absence of directional sexual selection. Further, BCI was not affected by selective logging, indicating that birds have comparable energy reserves in the two types of forest. However, the BCI of birds was higher in 2016 than in 2015 and 2017, possibly due to an effect of weather conditions on food abundance. Finally, we found no general patterns of causality between differences in body size and population abundance across forest types, although there was among species variation. Overall, our results point to reduction in body size indicating altered developmental conditions in response to new environmental conditions experienced after forest logging.

Body size reduction in selectively logged forest

The body size of birds is determined during development and can be affected, directly or indirectly, by food provisioning and environmental conditions (Muller et al. 2009, Kraft et al. 2019). We found no correlation between differences in body size and population abundance, and significantly smaller species in selectively logged forest (Fig. 2) show increasing or stable population trend, as compared to unlogged forest. Our results suggest that there is no direct link between body size changes and population abundance. However, further studies are needed to assess more precisely whether changes in body size affect population demography and dynamics.

Morphological variation across forests of different quality may also occur via the exclusion of lesser quality individuals from the species' preferred habitat (Camacho et al. 2013). For a subset of species, we found that both males and females are smaller in selectively logged forest, indicating the absence of selection driven by sexual preferences. Further, we found no evidence for selective mortality of individuals with longer or shorter tarsi during the post-fledging period because young and adult birds did not differ in tarsus length. These results suggest that conditions experienced during development (e.g. *in ovo* maternal effects, parental care) might contribute to explain the reduced body size. We cannot, however, exclude that selection could have operated within the nest, for instance if metabolic demands of larger nestlings were not met by parents. Below we discuss possible ways through which selective logging may indirectly have led to reduced body size of birds.

Body size shaped by early-life conditions

Studies on avian nutritional ecology have found that higher protein content and favourable amino acid balance in the diet increase the egg production (Murphy 1994, Ramsay and Houston 1998). As a consequence, increased sibling competition owing to reduced food availability may be a way through which nestlings attain a smaller body size at fledging (Raberg et al. 2005).

Although birds living in our study area have higher-protein diet in selectively logged forest (Edwards et al. 2013a), we found no studies investigating differences in nutritional quality and brood size between unlogged and selectively logged forests.

The risk of predation may also constrain birds' development. Parents feeding their chicks face a trade-off between the risk of nest predation and the provisioning rate of food to the nest (Martin 1995). In southeast Asian evergreen forests, most nest predators are visually oriented (i.e., rodents, monkeys, and birds) or olfactory oriented (i.e., snakes) (Pierce and Pobprasert 2013). For understorey-nesting birds, denser regrowth vegetation might reduce parental control against snakes, inducing higher perceived risk of predation in parents (Chotprasertkoon et al. 2017). Similarly, for birds nesting at mid-storey, lower tree density could increase the risk of predation towards visually-oriented predators (Somsiri et al. 2019). To reduce the risk of nest location by predators, parent birds may reduce the rate of food provisioning or the nestling rearing period (Hua et al. 2014), with associated reduction of nutrients intake and skeletal growth.

Glucocorticoid hormones (e.g. corticosterone) might be one important proximate link between predation risk and phenotype development (Groothuis and Schwabl 2008). Avian body size has been constrained by risk of predation through adaptive maternal effects (Coslovsky and Richner 2011). Increased levels of corticosterone in mothers due to high predation risk can be transferred to the eggs, and these hormones would affect skeletal growth rates in offspring (Hayward and Wingfield 2004). Higher maternal glucocorticoid levels can also increase growth rates in offspring under high-density conditions (Dantzer et al. 2013). Future studies should focus on the regulation of plasma corticosterone levels in response to stressors in breeding tropical birds, and their effects on phenotype development of the offspring.

Body Condition Index in tropical birds

We found no difference in BCI between birds living in unlogged and logged forests, indicating that energy reserves in birds are comparable between the two forest types. We also found no effect of IUCN conservation status on BCI, and no association between BCI and relative population abundance (RPA) index, suggesting the lack of a linear relationship between BCI and fitness in tropical birds (Barnett et al. 2015). Milenkaya et al. (2015) found that combined indices of energy reserves in a tropical bird (*Neochmia phaeton*) predict reproductive success, but only in some years. Thus, condition indices may be meaningful predictors of fitness only under certain circumstances. Unfortunately, sample sizes of our data did not allow us to test for annual relationships between BCI and RPA Index.

Birds had higher BCI in summer 2016 than 2015 and 2017. Environmental conditions affect dipterocarp production of seed and fruit (Curran and Leighton 2000), determining fluctuations in the invertebrate community (Goldman et al. 2020). During summer 2016, the total amount of rainfall in Danum Valley was higher than in the other study years (Table S14), and was coincident with the end of an extremely dry year caused by El Niño event. High post-drought rainfall likely increased food availability, leading to a surplus of fat storage compared to other years.

Relative population abundance and body size

Mist netting is a robust technique for measuring relative abundances of cryptic understorey birds, avoiding biases of censusing techniques using visual or auditory abilities (Dunn and Ralph 2004). Nonetheless, behavioural changes across different forest types may differentially affect species capture rates (Remsen and Good 1996). Our data were not impacted by habitat-induced changes in peak activity, because mist-netting encompassed the entire morning foraging period, while recapture rates of understory birds were similar between unlogged and selectively logged forests, indicating that habitat characteristics have limited impact on species recapture probability (Cosset et al. *under review*).

The understorey avian community is composed of ground- and strictly-understorey foragers, but also by species that spend variable time foraging above the understorey. For this latter group, a lower canopy and higher presence of small trees in selectively logged forest may induce more activity at lower height compared to the unlogged forest. It is thus possible that capture rates of species foraging above the understorey are overestimated in logged forest, although communities of lower, or lower plus mixed strata species (i.e. excluding species from higher strata) also revealed no impact of change in body size on change in abundance for both insectivores and non-obligate insectivores. It instead appears likely that differential responses among species, with increases, no change, and decreases in abundance with reduced body size hide a community-wide response.

Implications for conservation

Our work suggests that body size is a valuable metric to assess how logging affects forest birds. Results indicate that logging in Borneo impacts the development of understorey birds, including some species of conservation concern. Reduced body size of omnivorous and frugivorous birds, plus of some insectivore species after logging, points to lower food quality or quantity for nestlings, and potentially to important functional consequences related to seed dispersal and predation services within logged forest (Zwolak 2018).

Some understorey bird species show reduced body size and higher population abundance in logged forest (e.g., *Arachnothera longirostra* and *Pellorneum capistratum*), suggesting that smaller body size may be part of a successful strategy to cope with the environmental conditions. For example, smaller birds tend to have lower metabolic demands than larger birds, so that a reduced food availability in logged forest would still meet metabolic needs (Hudson et al. 2013). On the other hand, we observed a reduced body size in some species that were also less abundant in selectively logged forest (e.g., *Pitta baudii* VU and *Zoothera interpres* EN) or with stable population trends between forest types (e.g., *Malacocincla sepiaria*, *Prionochilus maculatus*, and *Tricholestes criniger*). Differential resilience of species with similar feeding habits to logging points to the need for further understanding of optimal logging strategies, especially related to logging intensity and the retention of primary forest reserves (i.e. land-sharing and land-sparing logging; Edwards et al. 2014a).

Previous studies conducted in lowland tropical forests of Borneo also found that understorey birds in selectively logged forest compared to undisturbed old-growth forest show i) higher mean trophic level (Edwards et al. 2013a), ii) reduced or increased singing behaviours in accordance with their population trend (Pillay et al. 2019), and iii) physiological resilience (Messina et al. 2020b). Our result on body size together with those of previous findings on phenotypic changes, emphasize the importance of assessing multiple phenotypic metrics to assess how selective logging impacts species' vital rates (Cosset et al. 2019) and population connectivity (Gilroy and Edwards 2017). Such information is critical to implement management practises that minimize losses and facilitate long-term recovery of biodiversity.

Conclusions

Frugivore and omnivore bird species have reduced body size in selectively logged forests, indicating different developmental conditions compared to the unlogged forest. Variation in body size reduction and relative population abundance points to either adverse environmental conditions or different coping strategies between species. For a subset of species, body size was similar between adults and fledged juveniles, indicating the absence of selective mortality of birds with longer or shorter tarsi in the post-fledging period. BCI differed significantly only among years, suggesting an effect of climatic conditions on food availability. These results indicate that skeletal size, but not current energy stores (i.e. BCI), might be a relevant trait that could affect the long-term viability of populations in logged forests. Future experimental studies should focus on which ecological factors and physiological mechanisms are leading to smaller body size of frugivorous and omnivorous birds in selectively logged forests. Our data indicate that ensuring the protection of logged forests from further disturbance and the improvement of silvicultural practices are likely to be of critical importance for conserving biodiversity, particularly within Southeast Asia, where most forests have been or are designated to be logged.

Supporting information

Models for sex and age

Our database included 12 species for which we could determine sex and for which we had more than one male and one female per forest type. Such species were used to test for an effect of sex on body size and, with the exception of 1 species (*Chalcophaps indica*), for BCI differences between unlogged and selectively logged forest (Supplementary Table S7). We run two Linear Mixed Models (LMMs): one for body size including tarsus length as explanatory variable, and one for BCI including body mass as explanatory variable and tarsus length as covariate (García-Berthou 2001). Both LMMs included forest, feeding guild, feeding strata, and sex as fixed factors. The interaction term between forest and sex was also included to test for any effect of sex on body size and BCI across the two types of forest. Only the LMM for BCI included the fixed factor year. In LMMs with individual measurements it is not possible to include phylogenetic control. However, given the low number of avian species, we included in the model the random factors species and family as proxy for phylogenetic non-independence (Koh et al. 2004, Edwards et al. 2013a). Interaction terms were explored by Tukey's multiple comparison test on least square means.

We also run a model to test for any differences in body size between juveniles and adults, across the two types of forest. This model was run to assess if any differences in body size among adults were owing to (i) directional selection of juveniles with short or long tarsi or (ii) developmental conditions. This LMM was based on eight species with more than one juvenile and one adult per type of forest (Supplementary Table S8). The building of the LMM was similar as that used for sex (see above) but with age as a fixed factor. We did not run this model for BCI because sample sizes of juveniles per year were too low, not allowing a control for year effect.

Effect sizes calculation

Hedges' *g* effect sizes (Cooper et al. 2009) were calculated in R through the *compute.es* package (Del Re 2013) using mean values, standard deviations, and sample sizes of a given trait for each species in both type of forests. Based on Cohen (1988), we considered effect sizes as small (Hedges g = 0.2, explaining 1% of the variance), intermediate (Hedges g = 0.5, explaining 9% of the variance) or large (Hedges g = 0.8, explaining 25% of the variance). Negative effect size estimate indicates smaller body size in logged compared to unlogged forest (Fig. S1).

For the calculation of effect sizes of body size, we used average measurements of tarsus length across years since we could not assess in which year the birds had developed. We also used mean tarsus length of recaptured birds to consider recaptures in the calculation of species effect sizes. To calculate effect sizes of BCI, we run a LMM including body mass as explanatory variable, tarsus length as co-variable, year, species, forest type, and the interaction between species and forest as fixed factors. We included the random factor family as proxy for phylogenetic control. Then, we used least square means and standard deviations of the interaction term between forest and species, together with sample sizes per type of forest, to calculate Hedges' *g* effect sizes.

Table S1 – Study species, their feeding guild and strata, and IUCN classification. *Blythipicus rubiginosus, Chalcophaps indica, Pitta ussheri, Pomatorhinus montanus* were not included in analyses of body condition index. Species classified as Vulnerable (VU) by the IUCN where considered together with Near Threatened (NT) species in our analyses; LC = Least Concern.

Species latin name	Species common name	Family	Feeding guild	Feeding strata	IUCN
Alcippe brunneicauda	Brown fulvetta	Leiotrichidae	Insectivores	Higher level	NT
Alophoixus tephrogenys	Grey-cheeked bulbul	Pycnonotidae	Omnivores	Mixed level	VU
Alophoixus phaeocephalus	Yellow-bellied bulbul	Pycnonotidae	Omnivores	Mixed level	LC
Anthreptes simplex	Plain sunbird	Nectariniidae	Insectivores	Higher level	LC
Anthreptes singalensis	Ruby-cheeked sunbird	Nectariniidae	Insectivores	Higher level	LC
Arachnothera longirostra	Little spiderhunter	Nectariniidae	Omnivores	Understory	LC
Blythipicus rubiginosus	Maroon woodpecker	Picidae	Insectivores	Understory	LC
Ceyx erithaca	Oriental dwarf kingfisher	Alcedinidae	Insectivores	Understory	LC
Chalcophaps indica	Emerald dove	Columbidae	Omnivores	Understory	LC
Copsychus stricklandii	White-crowned shama	Muscicapidae	Insectivores	Understory	LC
Cyornis caerulatus	Large-billed blue-flycatcher	Muscicapidae	Insectivores	Mixed level	VU
Cyornis superbus	Bornean blue-flycatcher	Muscicapidae	Insectivores	Understory	LC
Dicaeum trigonostigma	Orange-bellied flowerpecker	Dicaeidae	Frugivores	Higher level	LC
Enicurus leschenaulti	White-crowned forktail	Muscicapidae	Insectivores	Understory	LC
Enicurus ruficapillus	Chestnut-naped forktail	Muscicapidae	Insectivores	Understory	NT
Eurylaimus javanicus	Banded broadbill	Eurylaimidae	Insectivores	Mixed level	NT
Ficedula dumetoria	Rufous-chested flycatcher	Muscicapidae	Insectivores	Understory	LC
Hypogramma hypogrammicum	Purple-naped sunbird	Nectariniidae	Omnivores	Mixed level	LC
Hypothymis azurea	Black-naped monarch	Monarchidae	Insectivores	Higher level	LC
Kenopia striata	Striped wren-babbler	Pellorneidae	Insectivores	Understory	NT
Macronous ptilosus	Fluffy-backed tit-babbler	Timaliidae	Insectivores	Understory	NT
Malacocincla malaccensis	Short-tailed babbler	Pellorneidae	Insectivores	Understory	NT
Malacocincla sepiaria	Horsfield’s babbler	Pellorneidae	Insectivores	Understory	LC
Malacopteron affine	Sooty-capped babbler	Pellorneidae	Insectivores	Higher level	LC

Malacopteron cinereum	Scaly-crowned babbler	Pellorneidae	Insectivores	Higher level	LC
Malacopteron magnirostre	Moustached babbler	Pellorneidae	Insectivores	Higher level	LC
Malacopteron magnum	Rufous-crowned babbler	Pellorneidae	Insectivores	Higher level	NT
Meiglyptes tukki	Buff-necked woodpecker	Picidae	Insectivores	Higher level	NT
Orthotomus atrogularis	Dark-necked tailorbird	Cisticolidae	Insectivores	Mixed level	LC
Orthotomus sericeus	Rufous-tailed tailorbird	Cisticolidae	Insectivores	Understory	LC
Pellorneum capistratum	Black-capped babbler	Pellorneidae	Insectivores	Understory	LC
Philentoma pyrhoptera	Rufous-winged philentoma	Vangidae	Insectivores	Higher level	LC
Pitta baudii	Blue-headed pitta	Pittidae	Insectivores	Understory	VU
Pitta ussheri	Black-headed pitta	Pittidae	Insectivores	Understory	NT
Platylophus galericulatus	Crested jay	Corvidae	Insectivores	Higher level	NT
Pomatorhinus montanus	Chestnut-backed scimitar	Timaliidae	Insectivores	Understory	LC
Prionochilus maculatus	Yellow-breasted flowerpecker	Dicaeidae	Frugivores	Mixed level	LC
Prionochilus xanthopygius	Yellow-rumped flowerpecker	Dicaeidae	Frugivores	Mixed level	LC
Pycnonotus atriceps	Black-headed bulbul	Pycnonotidae	Frugivores	Mixed level	LC
Pycnonotus brunneus	Red-eyed bulbul	Pycnonotidae	Omnivores	Higher level	LC
Pycnonotus erythropthalmos	Spectacled bulbul	Pycnonotidae	Omnivores	Higher level	LC
Pycnonotus eutilotus	Puff-backed bulbul	Pycnonotidae	Omnivores	Higher level	NT
Pycnonotus melanoleucos	Black-and-white bulbul	Pycnonotidae	Frugivores	Higher level	NT
Rhinomyias umbratilis	Grey-chested jungle-	Muscicapidae	Insectivores	Mixed level	NT
Rhipidura perlata	Spotted fantail	Rhipiduridae	Insectivores	Higher level	LC
Sasia abnormis	Rufous piculet	Picidae	Insectivores	Understory	LC
Stachyris erythroptera	Chestnut-winged babbler	Timaliidae	Insectivores	Higher level	LC
Stachyris maculata	Chestnut-rumped babbler	Timaliidae	Insectivores	Higher level	NT
Stachyris poliocephala	Grey-headed babbler	Timaliidae	Insectivores	Understory	LC
Terpsiphone paradisi	Asian paradise-flycatcher	Monarchidae	Insectivores	Mixed level	LC
Trichastoma bicolor	Ferruginous babbler	Pellorneidae	Insectivores	Understory	LC

Trichastoma rostratum	White-chested babbler	Pellorneidae	Insectivores	Understory	NT
Tricholestes criniger	Hairy-backed bulbul	Pycnonotidae	Omnivores	Higher level	LC
Turdinus atrigularis	Black-throated wren-babbler	Pellorneidae	Insectivores	Understory	NT
Zoothera interpres	Chestnut-capped thrush	Turdidae	Insectivores	Higher level	EN

Table S2 – Mean coefficient of variation (CV) of tarsus length measurements for species with more than 3 recaptured individuals. N = sample size recaptured individuals.

Species	N	Mean CV %
Alcippe brunneicauda	7	2.41
Alophoixus bres	6	4.4
Alophoixus phaeocephalus	16	2.59
Arachnothera longirostra	46	2.39
Cyornis caerulatus	13	1.88
Enicurus leschenaulti	6	1.59
Enicurus ruficapillus	6	1.06
Hypogramma hypogrammicum	12	1.47
Macronus ptilosus	8	1.97
Malacocincla malaccensis	16	1.46
Malacocincla sepiaria	15	1.57
Malacopteron cinereum	13	3.19
Malacopteron magnum	8	4.54
Pellorneum capistratum	16	0.9
Philentoma pyrhoptera	7	4.23
Prionochilus maculatus	24	2.68
Sasia abnormis	7	6.07
Stachyris erythroptera	10	1.9
Stachyris maculata	4	2.17
Stachyris poliocephala	8	0.78
Trichastoma bicolor	21	1.69
Trichastoma rostratum	6	1.4
Tricholestes criniger	10	2.31
Mean total		**2.38**

Table S3 – Sample sizes of species included in our study for the analyses of body size and body condition index, respectively; N LOG = sample size in logged forest, N UNL = sample size in unlogged forest.

Species	Body Size		Body Condition	
	N LOG	N UNL	N LOG	N UNL
Alcippe brunneicauda	30	37	27	35
Alophoixus bres	31	20	24	18
Alophoixus phaeocephalus	39	65	35	62
Anthreptes simplex	21	19	19	18
Anthreptes singalensis	9	10	9	10
Arachnothera longirostra	209	131	202	124
Blythipicus rubiginosus	2	6		
Ceyx erithaca	15	15	15	15
Chalcophaps indica	18	26		
Copsychus stricklandii	27	25	24	25
Cyornis caerulatus	26	31	22	31
Cyornis superbus	2	2	2	2
Dicaeum trigonostigma	4	4	4	4
Enicurus leschenaulti	28	17	24	16
Enicurus ruficapillus	8	24	8	22
Eurylaimus javanicus	2	3	2	2
Ficedula dumetoria	7	10	7	9
Hypogramma	37	44	35	41
Hypothymis azurea	13	15	12	13
Kenopia striata	8	19	6	17
Macronous ptilosus	39	38	36	37
Malacocincla malaccensis	61	56	58	51
Malacocincla sepiaria	41	43	41	41
Malacopteron affine	12	10	11	10
Malacopteron cinereum	29	52	28	52
Malacopteron magnirostre	9	10	9	10
Malacopteron magnum	29	25	27	23
Meiglyptes tukki	8	2	5	2
Orthotomus atrogularis	3	7	3	6
Orthotomus sericeus	5	3	5	3
Pellorneum capistratum	53	36	48	33
Philentoma pyrhoptera	31	23	28	22
Pitta baudii	7	17	4	10
Pitta ussheri	10	3		
Platylophus galericulatus	2	2	2	2
Pomatorhinus montanus	2	2		
Prionochilus maculatus	57	54	53	47
Prionochilus xanthopygius	16	9	11	8
Pycnonotus atriceps	9	4	9	4
Pycnonotus brunneus	5	2	5	2
Pycnonotus erythropthalmos	40	23	39	23
Pycnonotus eutilotus	7	10	6	9
Pycnonotus melanoleucos	8	5	8	4
Rhinomyias umbratilis	7	17	7	16
Rhipidura perlata	4	20	4	20
Sasia abnormis	36	32	32	29
Stachyris erythroptera	59	51	54	44
Stachyris maculata	8	17	6	16
Stachyris poliocephala	43	38	41	36
Terpsiphone paradisi	17	12	13	10
Trichastoma bicolor	65	61	64	57
Trichastoma rostratum	25	15	23	14
Tricholestes criniger	41	54	40	47
Turdinus atrigularis	4	10	3	6
Zoothera interpres	6	14	5	14

Table S4 – Outcomes of the comparative phylogenetic Bayesian model implemented for body size with reduced number of species. This model included only species with more than five individuals per type of forest. Results of the interactions between forest and feeding guild, are shown below in the Table S5. Significant *p*MCMC-values are shown in bold.

Variable	Reference level	Factors	Posterior mean	Lower (CI)	Upper (CI)	Effective sample size	*p*MCMC
		Intercept	14.371	1.235	26.586	2040	**0.026**
Forest	LOG	Forest UNL	0.630	0.058	1.167	1998	**0.027**
Feeding guild	Frugivores	Insectivores	3.724	-7.362	13.934	1998	0.496
		Omnivores	1.914	-8.384	12.832	1998	0.686
	Omnivores	Insectivores	1.762	-4.307	7.804	1998	0.557
Feeding strata	Higher level	Mixed level	0.002	-4.085	4.793	1998	1.00
		Lower level	4.091	0.820	7.717	1998	**0.022**
	Lower level	Mixed level	-4.080	-8.626	0.919	1998	0.099
IUCN	LC	CC	0.728	-1.404	3.301	1759	0.543

Table S5 – Pairwise comparison between least square means of main levels of the interaction terms included in the multiple-measurements phylogenetic Bayesian model for body size, with reduced number of species. Significant levels of the interactions are shown in bold. HPD = highest posterior density.

Interaction term	Pairwise comparison	Estimate	Lower (HPD)	Upper (HPD)
Forest*Feeding guild	LOG,Frugivores – UNL,Frugivores	-0.551	**-1.048**	**-0.041**
	LOG,Insectivores – UNL,Insectivores	0.004	-0.140	0.151
	LOG,Omnivores – UNL,Omnivores	-0.227	**-0.426**	**-0.038**
Forest*Feeding strata	LOG,Lower level – UNL,Lower level	-0.316	**-0.559**	**-0.063**
	LOG,Mixed level – UNL,Mixed level	-0.109	-0.316	0.132
	LOG,Higher level – UNL,Higher level	-0.348	**-0.598**	**-0.058**
Forest*IUCN	LOG,LC – UNL,LC	-0.241	**-0.403**	**-0.063**
	LOG,CC – UNL,CC	-0.276	**-0.536**	**-0.005**

Table S6 – Outcomes of the comparative phylogenetic Bayesian model implemented for body condition index with reduced number of species. This model included only species with more than five individuals per type of forest. Significant *p*MCMC-values are shown in bold.

Variable	Reference level	Factors	Posterior mean	Lower (CI)	Upper (CI)	*p*MCMC
		Intercept	-11.631	-29.328	5.082	0.194
Species variation		Between-species	1.730	1.231	2.339	**<0.01**
		Within-species	0.772	0.696	0.854	**<0.01**
Year	2015	Year 2016	0.226	0.045	0.428	**0.021**
		Year 2017	-0.179	-0.407	0.059	0.134
		Year 2018	0.079	-0.180	0.345	0.551
	2016	Year 2017	-0.407	-0.616	-0.189	**0.001**
		Year 2018	-0.147	-0.400	0.106	0.241
	2017	Year 2018	0.254	-0.014	0.522	0.062
Forest	LOG	Forest UNL	0.017	-0.163	0.198	0.851
Feeding guild	Frugivores	Insectivores	0.776	-13.841	14.305	0.909
		Omnivores	7.568	-5.347	21.164	0.242
	Omnivores	Insectivores	-7.028	-14.721	1.819	0.084
Feeding strata	Higher level	Mixed level	4.191	-1.051	10.307	0.145
		Lower level	-2.018	-6.625	2.785	0.398
	Mixed level	Lower level	-6.255	-12.713	0.045	**0.047**
IUCN	LC	CC	1.198	-1.738	6.184	0.422
Date			-0.001	-0.004	0.002	0.522

Table S7 – Sample sizes of the species included in Linear Mixed Models testing for an effect of sex on body size and condition across unlogged and logged forests. Data on body mass of *Chalcophaps indica* were not available because above the upper limit of our spring scale.

Species	Forest	Sex	Sample size	
			Body size	BCI
Anthreptes simplex	LOG	F	11	10
		M	7	6
	UNL	F	10	10
		M	6	5
Anthreptes singalensis	LOG	F	4	4
		M	5	5
	UNL	F	3	3
		M	7	7
Arachnothera longirostra	LOG	F	109	107
		M	98	94
	UNL	F	70	69
		M	59	53
Chalcophaps indica	LOG	F	9	
		M	9	
	UNL	F	14	
		M	12	
Cyornis caerulatus	LOG	F	16	13
		M	9	8
	UNL	F	12	12
		M	18	18
Ficedula dumetoria	LOG	F	4	4
		M	3	3
	UNL	F	5	4
		M	5	5
Hypogramma hypogrammicum	LOG	F	14	13
		M	22	21
	UNL	F	12	10
		M	31	30
Hypothymis azurea	LOG	F	4	3
		M	9	9
	UNL	F	6	5
		M	8	7
Philentoma pyrhoptera	LOG	F	17	16
		M	14	12
	UNL	F	7	6
		M	13	14
Pitta baudii	LOG	F	4	2
		M	3	2
	UNL	F	2	2
		M	15	8
Prionochilus xanthopygius	LOG	F	7	5
		M	8	6
	UNL	F	3	2
		M	6	6
Sasia abnormis	LOG	F	27	25
		M	7	6
	UNL	F	23	22
		M	8	6

Table S8 – Sample sizes of the species included in Linear Mixed Models testing for an effect of age on body size across unlogged and logged forests.

Species	Forest	Age	
		Adult	Juveniles
Alcippe_brunneicauda	LOG	30	2
	UNL	37	3
Alophoixus_phaeocephalus	LOG	39	3
	UNL	65	3
Arachnothera_longirostra	LOG	209	49
	UNL	131	29
Hypogramma_hypogrammicum	LOG	37	7
	UNL	44	8
Malacopteron_affine	LOG	12	5
	UNL	10	3
Malacopteron_cinereum	LOG	29	5
	UNL	52	6
Malacopteron_magnirostre	LOG	9	3
	UNL	10	4
Sasia_abnormis	LOG	36	3
	UNL	32	4

Table S9 –Data of birds captures for the entire study period (2015 to 2018). Data of captures have been previously corrected for each annual sampling effort. Log = logged forest; Unl = unlogged forest; Tot = the sum of captures in logged and unlogged forests.

Species	**Family**	**Feeding guild**	**Captures Log**	**Captures Unl**	**Captures Tot**
Pycnonotus melanoleucos	Pycnonotidae	Frugivores	11.94	7.46	19.40
Pycnonotus atriceps	Pycnonotidae	Frugivores	32.06	22.89	54.95
Dicaeum trigonostigma	Dicaeidae	Frugivores	16.18	5.71	21.89
Prionochilus maculatus	Dicaeidae	Frugivores	100.74	85.80	186.54
Prionochilus xanthopygius	Dicaeidae	Frugivores	36.06	17.16	53.22
Chalcophaps indica	Columbidae	Omnivores	53.91	59.10	113.01
Alophoixus bres	Pycnonotidae	Omnivores	65.69	32.04	97.74
Tricholestes criniger	Pycnonotidae	Omnivores	98.21	86.34	184.54
Arachnothera longirostra	Nectariniidae	Omnivores	549.35	236.27	785.61
Pycnonotus eutilotus	Pycnonotidae	Omnivores	20.01	13.95	33.96
Hypogramma hypogrammicum	Nectariniidae	Omnivores	87.57	78.88	166.45
Pycnonotus brunneus	Pycnonotidae	Omnivores	14.45	2.99	17.44
Pycnonotus erythropthalmos	Pycnonotidae	Omnivores	92.40	40.73	133.13
Alophoixus phaeocephalus	Pycnonotidae	Omnivores	75.06	83.40	158.46
Terpsiphone paradisi	Monarchidae	Insectivores	35.43	26.01	61.44
Cyornis superbus	Muscicapidae	Insectivores	3.00	3.00	6.00
Eurylaimus javanicus	Eurylaimidae	Insectivores	2.09	3.09	5.18
Pellorneum capistratum	Pellorneidae	Insectivores	102.35	52.64	154.98
Alcippe brunneicauda	Leiotrichidae	Insectivores	75.08	70.69	145.77
Pitta ussheri	Pittidae	Insectivores	22.30	6.80	29.10
Pitta baudii	Pittidae	Insectivores	11.07	27.30	38.36
Hypothymis azurea	Monarchidae	Insectivores	28.92	31.84	60.76
Meiglyptes tukki	Picidae	Insectivores	18.74	3.49	22.23
Turdinus atrigularis	Pellorneidae	Insectivores	8.96	18.58	27.54
Pomatorhinus montanus	Timaliidae	Insectivores	4.00	2.08	6.08
Zoothera interpres	Turdidae	Insectivores	15.88	23.05	38.93
Platylophus galericulatus	Corvidae	Insectivores	4.72	3.13	7.85

Enicurus ruficapillus	Muscicapidae	Insectivores	13.15	26.97	40.13
Stachyris maculata	Timaliidae	Insectivores	17.21	27.24	44.45
Stachyris erythroptera	Timaliidae	Insectivores	101.52	83.89	185.41
Orthotomus atrogularis	Cisticolidae	Insectivores	16.26	11.78	28.04
Trichastoma bicolor	Pellorneidae	Insectivores	120.62	81.52	202.13
Macronous ptilosus	Timaliidae	Insectivores	69.07	58.13	127.21
Rhinomyias umbratilis	Muscicapidae	Insectivores	15.93	40.64	56.56
Stachyris poliocephala	Timaliidae	Insectivores	79.74	53.27	133.02
Malacocincla sepiaria	Pellorneidae	Insectivores	73.41	67.52	140.93
Cyornis caerulatus	Muscicapidae	Insectivores	40.88	52.89	93.76
Malacopteron magnirostre	Pellorneidae	Insectivores	27.23	25.66	52.89
Blythipicus rubiginosus	Picidae	Insectivores	9.35	8.29	17.64
Ceyx erithaca	Alcedinidae	Insectivores	93.23	75.09	168.32
Anthreptes simplex	Nectariniidae	Insectivores	64.45	29.12	93.57
Malacopteron magnum	Pellorneidae	Insectivores	57.21	47.24	104.45
Ficedula dumetoria	Muscicapidae	Insectivores	26.00	30.45	56.46
Anthreptes singalensis	Nectariniidae	Insectivores	25.83	10.78	36.60
Sasia abnormis	Picidae	Insectivores	95.53	82.34	177.87
Orthotomus sericeus	Cisticolidae	Insectivores	12.11	9.95	22.06
Philentoma pyrhoptera	Vangidae	Insectivores	61.40	34.66	96.06
Malacopteron affine	Pellorneidae	Insectivores	24.91	21.03	45.95
Malacopteron cinereum	Pellorneidae	Insectivores	68.72	81.94	150.66
Rhipidura perlata	Rhipiduridae	Insectivores	6.78	29.70	36.47
Malacocincla malaccensis	Pellorneidae	Insectivores	108.86	86.38	195.24
Kenopia striata	Pellorneidae	Insectivores	23.33	43.88	67.21
Trichastoma rostratum	Pellorneidae	Insectivores	41.30	23.60	64.90
Enicurus leschenaulti	Muscicapidae	Insectivores	49.41	22.00	71.41
Copsychus stricklandii	Muscicapidae	Insectivores	71.23	36.54	107.77

Table S10 – Data on tarsus length (mm) for each species in logged and unlogged forest. N = sample size, Mean = mean tarsus length (mm), and SD = standard deviation.

Tarsus length (mm)						
Species	**Logged forest**			**Unlogged forest**		
	N	**Mean**	**SD**	**N**	**Mean**	**SD**
Alcippe brunneicauda	28	20.97	1.18	31	21.1	1.26
Alophoixus tephrogenys	26	21.9	1.06	18	22.66	1.25
Alophoixus phaeocephalus	33	20.84	1.09	51	20.53	1.08
Anthreptes simplex	20	14.56	0.51	19	14.69	0.4
Anthreptes singalensis	9	16.36	0.82	10	16.22	0.75
Arachnothera longirostra	184	16.42	1.01	102	16.63	0.83
Blythipicus rubiginosus	2	22.65	0.49	5	23.05	1.45
Ceyx erithaca	15	10.8	1.67	12	10.23	1.87
Chalcophaps indica	18	25.46	3.72	26	26	2.1
Copsychus stricklandii	26	26.93	1.23	23	27.08	1.36
Cyornis caerulatus	18	16.98	0.99	23	16.77	0.84
Cyornis superbus	2	16.3	0.14	2	15.55	0.07
Dicaeum trigonostigma	4	12.88	0.53	3	13.05	0.95
Enicurus leschenaulti	22	28.52	1.31	13	28.66	1.69

Enicurus ruficapillus	8	29.15	0.54	18	28.9	1.52
Eurylaimus javanicus	2	25.8	0.14	3	25.53	0.23
Ficedula dumetoria	7	16.89	0.84	10	16.76	1.21
Hypogramma hypogrammicum	32	16.68	0.68	35	16.77	1.39
Hypothymis azurea	13	16.1	0.76	14	15.95	0.91
Kenopia striata	6	21.54	1.12	18	21.71	0.91
Macronous ptilosus	33	23.29	0.83	33	23.31	1.45
Malacocincla malaccensis	51	29.36	1.29	45	29.34	1.34
Malacocincla sepiaria	34	27.12	1	34	27.73	1.01
Malacopteron affine	12	21.27	0.89	10	21.35	1.82
Malacopteron cinereum	25	20.63	1.3	43	20.57	1.09
Malacopteron magnirostre	7	21.56	1.13	9	21.54	0.75
Malacopteron magnum	25	23.49	1.1	21	23.83	0.87
Meiglyptes tukki	7	22.1	1.06	2	22	1.41
Orthotomus atrogularis	3	18.67	1.27	6	18.6	1.32
Orthotomus sericeus	4	21.33	0.87	3	20.27	2.48
Pellorneum capistratum	45	30.11	1.04	26	30.58	1.24
Philentoma pyrhoptera	27	16.93	0.59	20	16.87	0.68
Pitta baudii	7	38.36	2.06	17	39.62	1.51
Pitta ussheri	10	39.96	1.96	3	40.2	0.36
Platylophus galericulatus	2	31.75	0.35	2	30.65	1.34
Pomatorhinus montanus	2	27.6	0.57	2	28.1	0.57
Prionochilus maculatus	39	13.65	0.67	42	14.09	0.81
Prionochilus xanthopygius	14	13.64	0.42	9	13.81	0.7
Pycnonotus atriceps	9	14.29	0.53	4	14.3	0.63
Pycnonotus brunneus	5	19.82	1	2	20.4	1.13
Pycnonotus erythropthalmos	40	16.2	0.6	23	16.7	0.48
Pycnonotus eutilotus	7	19.77	0.59	8	19.48	0.92
Pycnonotus melanoleucos	8	13.64	0.8	5	14.66	0.8
Rhinomyias umbratilis	6	17.81	0.9	16	17.68	0.83
Rhipidura perlata	4	14.5	0.78	17	14.73	0.86
Sasia abnormis	31	13.31	0.89	29	12.81	0.86
Stachyris erythroptera	53	19.69	0.87	46	19.83	0.81
Stachyris maculata	7	25.14	0.57	14	24.65	1.63
Stachyris poliocephala	38	23.77	0.92	34	23.64	1.16
Terpsiphone paradisi	17	16.79	0.51	12	16.74	0.78
Trichastoma bicolor	53	29.71	1.26	49	29.9	1.37
Trichastoma rostratum	20	26.11	1.26	11	24.95	1.86
Tricholestes criniger	36	15.37	0.61	48	15.68	0.61
Turdinus atrigularis	4	34.33	0.96	10	34.12	1.63
Zoothera interpres	6	26.92	0.96	14	27.79	1.17

Table S11 – Results of the Linear Mixed Model testing for an effect of sex on body size across unlogged and logged forests. Significant *P*-values are shown in bold.

Full Models				
Variable	**Factors**	**d. f.**	***F*-value**	***P*-value**
Tarsus length	Forest	1,760.11	1.063	0.302
	Feeding strata	2,2.00	0.225	0.816
	Feeding guild	2,5.03	0.387	0.697
	Sex	1,760.61	71.903	**<0.001**
	Forest*Sex	1,760.01	1.878	0.171

Table S12 – Results of the Linear Mixed Model testing for an effect of sex on body condition index across unlogged and logged forests. Significant *P*-values are shown in bold.

Full Models				
Variable	**Factors**	**d. f.**	***F*-value**	***P*-value**
Weight	Tarsus	1,663.93	43.837	**<0.001**
	Forest	2,659.97	1.692	0.193
	Feeding strata	2,2.06	0.713	0.581
	Feeding guild	2,4.23	0.552	0.612
	Sex	1,661.15	79.901	**<0.001**
	Year	3.660.15	1.984	0.114
	Forest*Sex	1.660.05	3.788	0.052

Table S13 – Pairwise comparison between least square means of levels of the interaction term between forest type and sex included in the Linear Mixed Model for body condition index. Significant levels of the interactions are shown in bold. LOG = logged forest; UNL = unlogged forest; F = females; M = males; SE = standard error.

Interaction term	Pairwise comparison	Estimate	SE	t-value	*P*-value
Forest*Sex	LOG,F – UNL,F	-0.083	0.184	-0.454	0.969
	LOG,F – LOG,M	-1.555	0.187	-8.324	**<0.001**
	LOG,F – UNL,M	-1.128	0.194	-5.815	**<0.001**
	UNL,F – LOG,M	-1.472	0.199	-7.401	**<0.001**
	UNL,F – UNL,M	-1.045	0.204	-5.109	**<0.001**
	LOG,M – UNL,M	0.427	0.188	2.265	0.107

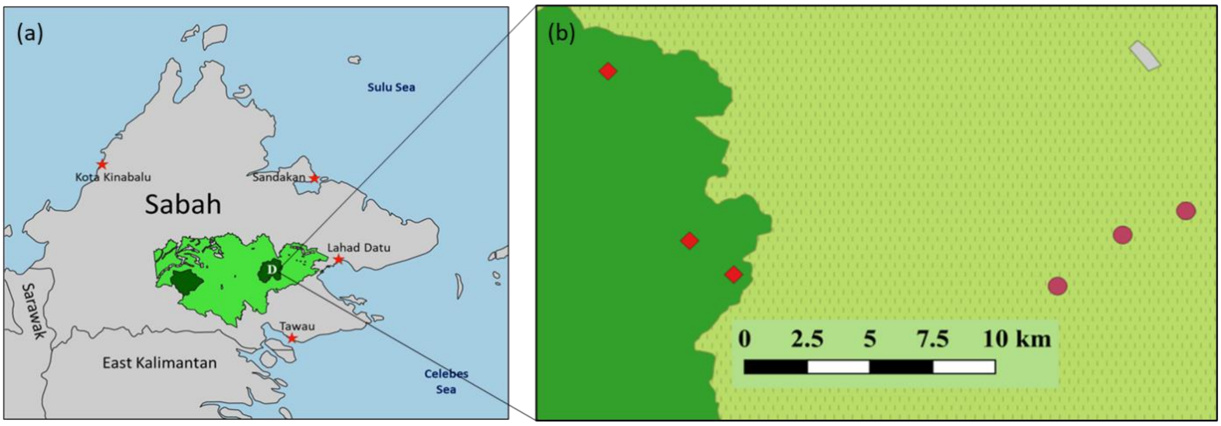
Table S14 – Results of the Linear Mixed Model testing for an effect of age (juveniles vs. adults) on body size across unlogged and logged forests.

Full Models				
Variable	**Factors**	**d. f.**	***F*-value**	***P*-value**
Tarsus length	Forest	1,908.43	0.697	0.403
	Feeding strata	2,2.00	5.991	0.143
	Feeding guild	1,2.19	4.831	0.147
	Age	1,908.88	1.320	0.250
	Forest*Age	1,908.26	0.079	0.778

Table S15 – Climatic conditions in Danum Valley Conservation Area during summer months of the study years, and over a period of 33 years (1985-2018). tmax = mean maximum temperatures; tmin = mean minimum temperatures. Data are provided by SEARRP project and can be downloaded in: https://www.searrp.org/

Summer season	tmax	tmin	Mean tot. rainfall	hours of sun
1985-2018	**31.5**	**22.6**	**625.5**	**5**
2015	**34.1**	**20.8**	**435.6**	**5.6**
2016	**32.9**	**22.5**	**719.4**	**5.1**
2017	**31.07**	**22.33**	**644**	**4.3**
2018	**32.20**	**23.27**	**490.6**	**5.0**

Figure S1 – Map of the study area with plots location. (a) Yayasan Sabah logging concession in the Malaysian state of Sabah in Borneo. Dark green areas correspond to protected areas of undisturbed old-growth forests; Light green correspond to selectively logged forests. The letter 'D' indicates the Danum Valley Conservation Area. (b) Dark green area corresponds to unlogged forest within the Danum Valley Conservation Area; light green area corresponds to selectively logged forest. Red squares and pink circles correspond, respectively, to study plots in unlogged and selectively logged forests. The grey area is a plantation.



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Chapter VI

General Discussion

The study of the effects of habitat changes on species' physiological and morphological traits is a critical first step to understand the current and future viability of wildlife. The integration of disciplines of ecology and molecular physiology is one main route by which unravelling proximate mechanisms that make species resilient or vulnerable to environmental conditions of human-modified habitats. In this context, the emerging field of conservation physiology aims to measure changes in individual physiological status in response to anthropogenic disturbance in order to have a functional understanding of the effects of environmental changes on organisms (Wikelski and Cooke 2006, Cooke et al. 2013). In this Ph.D. project, I investigated the effects of selective logging on HPA axis activity (through production of GC hormones), oxidative status, body condition, and body size of tropical understorey birds. The main results of my work indicate long-term effects of selective logging on (i) the antioxidant enzyme superoxide dismutase, (ii) the regulation of the glutathione cycle, and (iii) the body size of frugivorous and omnivorous birds. Importantly, results of **Chapters III** and **IV** provide correlative support that glucocorticoids (GCs) and levels of certain antioxidants underlie differences in population abundance between unlogged and selectively logged forests.

Drivers of population differences between forest types

I found little evidences for long-term effects of selective logging on mechanisms of stress physiology in tropical understorey birds. In **Chapter III** I found no differences in fCORT levels between unlogged and logged forests, while in **Chapter IV** I found that birds living in selectively logged forests had higher activity of the antioxidant enzyme superoxide dismutase (SOD) and higher values of the ratio of reduced glutathione onto oxidized glutathione (GSH/GSSG). I do not know whether differences in SOD activity in my study species are due to adaptation or phenotypic plasticity. Previous studies on birds living in urban and rural habitat found evidences for a main role of phenotypic plasticity of antioxidant enzymes levels. A recent study on great tits (*Parus major*) found higher levels of gene expression related to antioxidant protection in urban environment compared to rural, suggesting a key role for epigenetics in mediating environmentally induced physiological variation (Watson et al. 2017). Cross-fostering studies in wild birds found little heritability of antioxidant levels (Costantini and Dell'Omo 2006, Losdat et al. 2014). In particular, Salmon et al. (2018) found that SOD level changes in urban-reared great tits were independent from the nest of origin, pointing to post-hatching environment as the main driver of the physiological change.

In **Chapter V** I found reduced body size of frugivorous and omnivorous birds in selectively logged forest compared to unlogged. I also found no support for selection driven by sexual preferences or body size differences at fledging state, suggesting a major role of phenotypic plasticity in determining body size differences between forest types. Environmental conditions experienced during development can shape the adult phenotype (Young et al. 2017, e.g. Kraft et al. 2019). For example, Zhang et al. (2019) found that medium to low proportions of optimal food in the diet of Asian short-toed lark (*Calandrella cheelensis*) inhibited the growth of nestlings. Furthermore, increased sibling competition owing to reduced food availability may also be a way through which nestlings attain a smaller body size at fledging (Raberg et al. 2005). In a recent experimental study, urban nestlings of great tits receiving supplementary insect food achieved similar body size to that of nestlings in forest control broods (Seress et al. 2020). Thus, it is possible that frugivorous and omnivorous nestlings in selectively logged forests, are smaller due to lower nutritional values of their diets or reduced food availability.

Constrained skeletal development due to nutritional stress in early-life may also depend on increased risk of predation. Parents feeding their chicks face a trade-off between the risk of nest predation and the provisioning rate of food to the nest (Martin 1995, Martin et al. 2011). A recent study on the tropical bird red-whiskered bulbul (*Pycnonotus jocosus*) found a strong positive correlation between daily parental visit rate at nest and events of predation (Li et al.

2019). Furthermore, Eggers et al. (2008) showed that the negative relationship between risk of predation and parents' feeding rates may be further enhanced by lower nest concealment from surrounding vegetation. It is possible that the high presence of lianas and saplings in selectively logged forest facilitate movement of small predators in the understorey (Magrach et al. 2016), increasing the risk of nest predation. This predation risk hypothesis is further supported by differences in SOD between forest types (see below). However, given the lack of studies investigating differences in nest predation rates between unlogged and selectively logged forests, I suggest that future studies will cover this knowledge gap and test for an effect of vegetation cover on parental provisioning rate and nestling development.

Maternal effects mediated by GC hormones might be one important mechanism linking predation risk and phenotype development (Love et al. 2013, Groothuis et al. 2019). Increased levels of CORT in mothers can be transferred to the eggs, affecting skeletal growth rate in offspring (Hayward and Wingfield 2004). Weber et al. (2018) found that offspring of female house wrens (*Troglodytes aedon*) experiencing experimentally increased CORT were larger than offspring of control females. Differently, eggs of barn swallows (*Hirundo rustica*) injected with CORT produced fledglings with smaller body size (Saino et al. 2005). Both studies suggests that maternally derived CORT prepare offspring for the environment their mother encountered. Future studies should focus on the regulation of plasma CORT levels in response to stressors in breeding tropical birds, and their effects on phenotype development of the offspring.

Endocrine system and population abundance

Quantification of GCs in biological matrices (e.g., plasma, faeces, feathers) is one of the most widely used approaches to assess the physiological stress state of organisms following anthropogenic habitat changes (Wikelski and Cooke 2006, Coristine et al. 2014). In **Chapter II** I used a meta-analytical approach to show how different types of habitat degradation, including selective logging, induce consistent changes in the production of GCs in birds and mammals. Results of the meta-analyses suggested that stress physiology might be an important mediator of the long-term species response to changing forests. On the other hand, hormonal systems are powerful physiological mechanisms by which organisms can flexibly adjust behavioural, physiological, and morphological phenotypes to variation in the current environmental conditions (Hau et al. 2016). For example, GCs are involved in coordinating adjustments to variation in climate, resource abundance, social and internal conditions.

In **Chapter III**, I found significant correlations between fCORT effect sizes and differences in population abundance between unlogged and selectively logged forests. In particular, relatively higher concentrations of fCORT in a given forest type at year (x), were associated with lower abundances of the study species in the same type of forest the following year (x+1), and vice versa. Such result suggests that carry-over effects mediated by fCORT could have impacted on some processes of population dynamics.

Higher levels of baseline CORT may sustain increased request of energy for foraging, reproduction and chick rearing (e.g., Love et al. 2014, Apfelbeck et al. 2017). However, according to the pace-of-life syndrome hypothesis, tropical birds tend to prioritize future reproduction over current attempts if costs of rearing the brood exceed the expected benefits (Ricklefs and Wikelski 2002, Mathot and Frankenhuis 2018). A study on tropical house wrens showed that breeding individuals with experimentally increased workload reduced their nestling feeding rate, but maintained unaltered body mass and metabolic rate (Tieleman et al. 2008). Thus, the association between higher fCORT effect size and lower relative population abundance might depend on the smaller reproductive investment of individuals with prolonged higher CORT production, which preferentially invest energy into self-maintenance. Alternatively, it is also possible that survival decreases in individuals whose baseline CORT levels cause long-term energy needs that exceed energy intakes (McEwen and Wingfield 2003).

A recent phylogenetic meta-analytical study found that baseline GCs in vertebrates are negatively associated with reproductive success and survival, with stronger effects on survival in long-lived species (Schoenle et al. 2021).

Although it is not possible to exactly determine the environmental factors driving annual fCORT variation in our study species, I suggest that weather conditions and population density might be two relevant factors involved. Seasons prior to fieldwork in 2016 and 2017 were affected by El Niño-Southern Oscillation (ENSO) events, and fCORT levels in those years were significantly lower than in 2018 for seven species out of 10. Previous studies found that ENSO events affect CORT production on vertebrates (Romero and Wikelski 2001, Wingfield et al. 2018). It is possible that the prolonged situation of stress due to unpredictable climatic events induced a dampened HPA-axis activity, with consequent decrease in CORT production (Hau et al. 2010, Angelier and Wingfield 2013). Further, I found significant within-year relationship between fCORT and RPA index (the direction of this relationship changed between years). Thus, assuming that RPA index in our study is indicative of relative population density, it is possible that annual variation in local relative densities of birds affected the HPA-axis activity. It is well documented in vertebrates that population density may affect HPA-axis activity (Creel et al. 2013, Dantzer et al. 2020). For example, the CORT production in prairie voles (*Microtus ochrogaster*) is higher at lower population densities (Blondel et al. 2016). Differently, king penguins (*Aptenodytes patagonicus*) have higher baseline CORT levels in the centre of the colony, where the social density is higher, compared to peripheral areas (Viblanc et al. 2014). Given the lack of studies investigating how population density affect CORT production in free-living forest birds, I recommend that future studies cover this knowledge gap.

Endogenous factors can also affect circulating levels of GCs. For example, moult and reproduction can affect the CORT response of birds to environmental challenges (Romero

2002, Cyr et al. 2008, Dantzer et al. 2014). My study species replace feathers gradually over a period of months (Mulyani et al. 2017), and evidences suggest that CORT levels do not change in birds with extended moult periods during feather replacement (Cornelius et al. 2011, Buttemer et al. 2015). Moreover, overlap between moult and reproduction has been found extremely rare in Bornean birds (Mulyani et al. 2017). Therefore, I can assume that birds involved in my study were not reproductively active when they moulted feathers. Other important endogenous factors that may link with GCs concentrations are body condition and cellular oxidative status. As regulator of metabolism and behaviour, GC secretion is responsive to the body condition of an individual, and can affect the oxidative status of an organism via increased cellular metabolic activity (Costantini et al. 2011, Beaulieu and Costantini 2014). Future studies are needed to understand the density-dependent and independent mechanisms through which the forest management impacts on the physiology of individuals and population dynamics.

Corticosterone, body condition and oxidative status

One of the main functions of GCs is the regulation of behaviours that control energy intake and expenditure, such as locomotor activity and food seeking (McEwen and Wingfield 2003). Thus, individuals with lower body condition, a proxy for the amount of energy reserves of an organism, often have increased baseline GC concentrations (e.g., Love et al. 2005, Jenni-Eiermann et al. 2008, Angelier et al. 2009). In my studies it was not possible to directly measure the link between CORT levels and body condition index (BCI), because the fCORT levels reflected a precedent period to that of body condition measurements. However, in **Chapter V** I found overall similar BCI of birds between unlogged and selectively logged forest. This result is in accordance with similar levels of fCORT between birds from unlogged and logged forests, found in **Chapter III**. Both results indicate that energy reserves in birds are comparable between unlogged and selectively logged forests.

In **Chapters III** and **IV** I found that species with relatively higher levels of fCORT and certain antioxidant markers (i.e., FRAE, GSH, tGSH, and GPx) in a given forest type, were associated with lower abundances in the same type of forest, and vice versa. The regulation of the HPA-axis might concur with a higher investment in certain antioxidant mechanisms (e.g., glutathione cycle) for a trade-off between self-maintenance and fitness traits, which translates into population effects. For example, higher baseline CORT levels can reduce the efficiency of mitochondria at producing ATP (Stier et al. 2019, Casagrande et al. 2020), reinforcing the energetic constraints rising from increased consumption of molecules of ATP for the synthesis of GSH and GPx (Fig. 1; Halliwell and Gutteridge 2015). In accordance, a study on king penguins (*Aptenodytes patagonicus*) found that individuals with higher baseline CORT levels had higher activity of the glutathione antioxidant system (tGSH and GPx activity), and less efficient mitochondria at producing ATP (Stier et al. 2019). Future experimental studies should test how increased CORT levels and activity of the glutathione antioxidant system affect survival and reproduction of tropical birds.

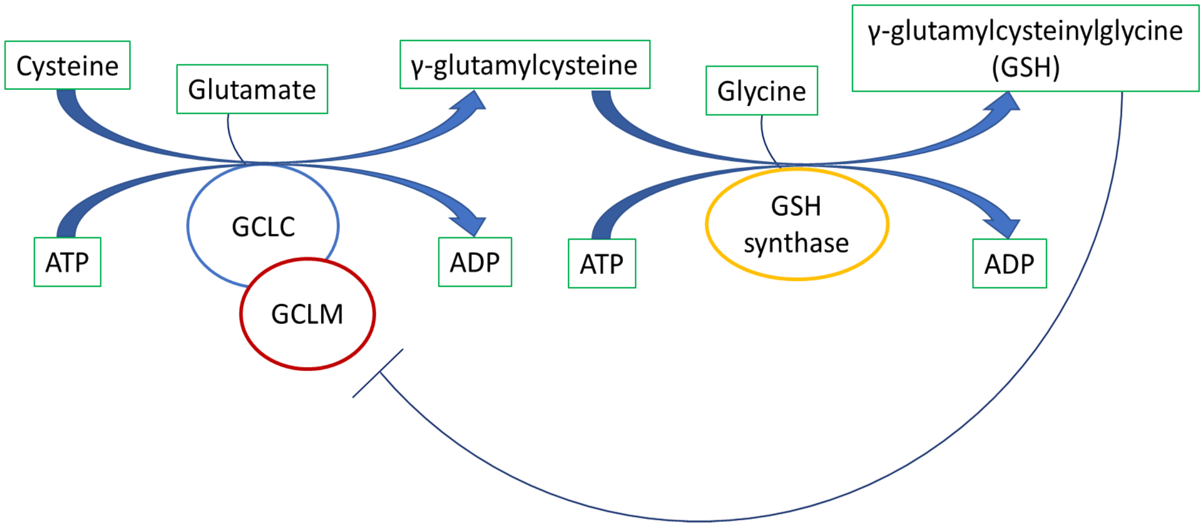

Fig. 1 – GSH synthesis occurs via a two-step ATP-requiring enzymatic process. The first step is catalyzed by glutamate-cysteine ligase (GCL), which is composed by catalytic and modifier subunits (GCLC and GCLM), to generate γ-glutamylcysteine. The second step is catalyzed by glutathione (GSH) synthase which adds glycine to γ-glutamylcysteine to form γ-glutamylcysteineglycine or GSH.

Pace-of-life syndrome

Most of our knowledge about trade-offs between fitness traits and baseline CORT production, or oxidative status, comes from studies on temperate species which differ in life history traits from those living at tropical latitudes. Life history traits have coevolved in response to environmental conditions along a “pace-of-life” axis (Ricklefs and Wikelski 2002, Mathot and Frankenhuis 2018). Tropical birds have a slow pace of life, for example via a slower metabolism, smaller clutches and a slower growth rate, and higher rates of adult survival than temperate birds (Wiersma et al. 2007).

Growing evidence suggests that trade-offs between GCs and oxidative status with reproduction and survival work differently for temperate and tropical species. This slow pace of life might help explaining some of the results found in this project. For example, the lack of differences in the oxidative damage levels in birds between forests may be partly due to the higher resistance of tropical birds to oxidative challenges, and lower contents of polyunsaturated fatty acids in cellular membranes of tropical birds which make them less susceptible to oxidative damage to lipids (Williams et al. 2010, Calhoon et al. 2014, Jimenez et al. 2014). Furthermore, a recent meta-analysis showed that seasonal changes in baseline glucocorticoid levels between non-breeding and breeding seasons are more marked in temperate than tropical passerines (Casagrande et al. 2018), suggesting that tropical birds might limit any increase of baseline GCs to avoid harmful effects on their body condition (i.e., metabolizing energy from muscles). Moreover, Schoenle et al. (2021) recently found that higher baseline GCs in slow pace of life vertebrates negatively correlates with survival, possibly owing to greater phenotypic costs (e.g., accelerated telomere shortening) which may reduce lifespan. This may explain lower levels of fCORT during years of El Niño events, and the effect sizes showing a trend for higher fCORT levels in unlogged forest compared to selectively logged forest. Finally, it is important to point out that the lack of significant differences between forest types for many physiological markers may simply indicate that adult birds are physiologically acclimatized to the new environmental conditions created by logging.

Implications for rainforests conservation

Selectively logged forests deserve particular attention from conservationists and politicians, because they are too vast and vulnerable to deforestation, despite their high conservation value. Although they cannot replace primary forests, selectively logged forests can enhance conservation at landscape and regional scales, act as buffer zones around protected areas, and help maintain forest connectivity for wildlife (Edwards and Laurance 2013). Nonetheless, recent meta-analyses indicated logging intensity and practices as important drivers of biodiversity decline. In particular, lower logging intensity and reduced-impact logging practices have less impacts on biodiversity compared, respectively, to higher intensity of timber removal (Burivalova et al. 2014) and conventional methods of selective logging (Bicknell et al. 2014).

The use of occurrence or count data to measure population responses to habitat alteration may have a bias due to time-lagged responses that obscure the actual status of the populations. Because the effects of environmental alterations often manifest in an organism’s physiology before changes can be detected at population level, physiological measures can provide greater predictive capacity than traditional demographic methods (Wikelski and Cooke 2006, Ellis et al. 2012). Results of this project indicate that quantification of fCORT may be an important physiological tool to predict directional population changes, and that fCORT might be employed to determine how different silvicultural practises impact on understorey birds. Further studies are needed to test how the individual physiological status translates in population size or population growth rates, and how different practises and intensities of forest management impact on stress physiology of understory birds.

The study of physiological mechanisms underlying population abundance change can help understanding which conditions constitute a disturbance following habitat modifications (Madliger and Love 2014). Although I did not directly investigate possible ecological factors affecting understory birds' physiology in selectively logged forests, the integration of results from my studies with that from other published researches (e.g., Hua and Sieving 2016, Somsiri et al. 2019) suggests that changes in the risk of predation between unlogged and selectively logged forests may be one main driver of population abundance changes in understory birds. Thus, I recommend that future studies will investigate differences in the frequency of nest predation events between unlogged and selectively logged forests, and test how different rates of predation affect birds' strategies for chicks rearing.

Another asset of integrating population abundance data with physiological information is the potential for determining most susceptible species to disturbance. In my studies, most of the species appear to be positively affected by selective logging. This is one important limit of my project, due to low capture rates of most declining species in selectively logged forests despite the consistent sampling effort carried out each year. Nonetheless, results from my studies indicate that the black-capped babbler (*Pellorneum capistratum*; Fig. 2) is particularly responsive to the environmental effects of selective logging, and seems well acclimatized to the new habitat conditions. The relative population abundance index of black-capped babbler for the period 2015-2018 showed no marked oscillations, and the species was each year more abundant in selectively logged forest compared to primary (mean RPA Index = 0.32). For the same study

Figure 2 – Black-capped babbler

period, the species showed reduced body size in logged forest compared to unlogged (mean Body size effect size = -0.42; $CI_{95\%}$ = -0.91, 0.06), and for the period 2016-2018 it showed significantly lower concentrations of fCORT in logged forest compared to primary forest (mean fCORT effect size = -0.72; $CI_{95\%}$ = -1.29, -0.14). Furthermore, a recent study investigating movement patterns of 71 species of understory birds in Borneo found that the black-capped babbler is one of seven species showing significantly higher probability of moving shorter distance in selectively logged forest compared to unlogged, suggesting that the species may have reduced home range size in selectively logged forest (Cosset et al., under submission). Taken together, these results indicate the black-capped babbler as a promising indicator species for further investigation into the mechanisms of adaptation, or acclimation, of understorey birds to selectively logged forests.

Concluding remarks

There is growing evidence that selectively logged tropical forests might be important habitat to preserve for the conservation of tropical biodiversity. There is a need for the creation of large-scale protected areas in the tropics, which include both unlogged and sustainably managed selectively logged forests, to reach goals of biodiversity conservation (Edwards et al. 2019). Within this frame, the study of physiological mechanisms underlying species acclimatization or adaptation to selectively logged forests have the potential to provide new tools for monitoring the impact of different types of forest management and conservation strategies on wildlife (Madliger et al. 2018).

My work is a first step towards the understanding of the proximate mechanisms underlying the responses of birds to forest disturbance and the differences in population abundance between selectively logged forests and unlogged forests. Relying on a multi-species approach, I found long-term effects of selective logging on oxidative status and body size. Importantly, the results of my Ph.D. project indicated a link between glucocorticoids and population abundance, suggesting that forest conditions might impact on birds through the energetic balance. This result also indicates that the concentration of CORT in feathers might be one candidate tool for monitoring and predicting changes in population abundance, and for determining the impacts of different sylvicultural practices on understorey avifauna. However, further studies are needed to clarify how the individual physiological status translates in population size or population growth rates.

Overall, the phenotypic differences I found between forest types raise important questions about the roles of phenotypic plasticity and genetic adaptations in driving conspecific populations differentiation. On one hand, the boundary between pristine and logged forests may affect the movement ecology and gene flow (Fahrig 2007), leading to genetically impoverished sub-populations (Cros et al. 2020). On the other hand, forest abiotic and biotic conditions are likely to vary dramatically owing to climate change, suggesting that rapid plastic responses of birds might be particularly relevant. Thus, a better understanding of avian community (e.g. source-sink dynamics, gene flow) is urgently needed to (i) identify the eco-evo mechanisms affecting community structure, (ii) better assess the conservation value of selectively logged forests, and (iii) drive policy makers on more robust plans for tropical forests' conservation.

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