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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 change 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.

Keywords: body size, body condition, selective logging, land-use change, tropical birds, phenotypic plasticity

1. 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 understorey 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. 2013; Woodcock et al. 2013). Moreover, some bird species show differences between forest types in their physiological status (Messina et al. 2020a; Messina et al. 2020b).

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 (Irwin et al. 2019; Janin et al. 2011; Tellería et al. 2013). 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 grey-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 proximal 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 show 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 (Caizergues et al. 2021; Liker et al. 2008) 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*) (Kraft et al. 2019; Muller et al. 2009). 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 forest 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.

2. Materials and Methods

2.1 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). Mean tarsus length (mm) ± SD of each species for each forest type can be found in the supplementary material (Table S10).

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)).

2.2 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).

2.3 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*.

2.4 Species' ecological traits

Feeding guilds and foraging strata of birds are important traits affecting species responses to selective logging (Burivalova et al. 2015; Gray et al. 2007; 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 lower 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), Vulnerable (VU) or Endangered (EN) by the International Union for Conservation of Nature (IUCN) Red List classification, than those classified as Least Concern (LC) (Costantini et al. 2016). 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.

2.5 Statistical Analyses

2.5.1 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. As the response variable, we used tarsus length because it is classically used as a proxy for body size (Senar and Pascual 1997; Subasinghe et al. 2021). 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 concern. 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.

To test if the inclusion of species with a low sample size affected the results, we re-ran the model excluding from the database 15 species with fewer than six individuals per forest type. Results were similar to those of the model including all species (Supplementary Tables S4-S5).

2.5.2 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).

2.5.3 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.

2.5.4 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.

2.5.5 Morphometric changes 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. 2020b). 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).

3. Results

3.1 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.

3.2 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).

3.3 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 S11). 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 S12-S13). We also found that body size did not differ between juveniles and adults (Supplementary Table S14), indicating that there was no post-fledging selective mortality in juvenile individuals owing to a given body size.

3.4 Abundance changes

Changes in abundance between forest types were not related with changes in body size in insectivore species (coefficient estimate±SE = -0.058±0.102; t-value = -0.568; $P = 0.572$), and non-obligate insectivore species (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).

4. 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 changes in body size and population abundance across forest types, although there was among species variation. Overall, our results point to changes in body size indicating altered developmental conditions in response to new environmental conditions experienced after forest logging.

4.1 Body size changes 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 (Kraft et al. 2019; Muller et al. 2009). We found no correlation between changes 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.

4.2 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. 2013), 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 understory-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.

4.3 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 S15), 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.

4.4 Changes in 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.

4.5 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. 2013), ii) reduced or increased singing behaviours in accordance with their population trend (Pillay et al. 2019), and iii) physiological resilience (Messina et al. 2020a). 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.

5. 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.

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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**

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)**	**Effective sample size**	***p*MCMC**
		Intercept	-6.82	-26.7	12.7	1998	0.466
Species variation		Between-species	2.47	1.92	2.96	1998	**<5e-04**
		Within-species	0.736	0.640	0.826	1822	**<5e-04**
Year	2015	Year 2016	0.235	0.001	0.434	1998	**0.027**
		Year 2017	-0.088	-0.346	0.167	1998	0.511
		Year 2018	-0.175	-0.167	-0.435	1998	0.450
	2016	Year 2017	-0.321	-0.570	-0.088	1919	**0.005**
		Year 2018	-0.118	-0.408	0.171	1998	0.401
	2017	Year 2018	0.202	-0.115	0.520	2208	0.225
Forest	LOG	Forest UNL	0.021	-0.184	0.226	1998	0.835
Feeding guild	Frugivores	Insectivores	-9.462	-22.490	4.127	2197	0.159
		Omnivores	-2.266	-12.680	7.181	1998	0.657
	Omnivores	Insectivores	-7.452	-18.700	4.018	1998	0.214
Feeding strata	Higher level	Mixed level	2.408	-3.719	8.252	1998	0.427
		Lower level	-4.110	-9.549	1.526	1998	0.151
	Mixed level	Lower level	-6.416	-12.360	0.464	1998	**0.054**
IUCN	LC	CC	1.965	-1.632	5.476	1998	0.270
Date			-0.008	-0.497	0.343	1998	0.689

Figures legends

Fig. 1 – Estimates and highest posterior density (HPD) intervals of body size changes 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.

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.

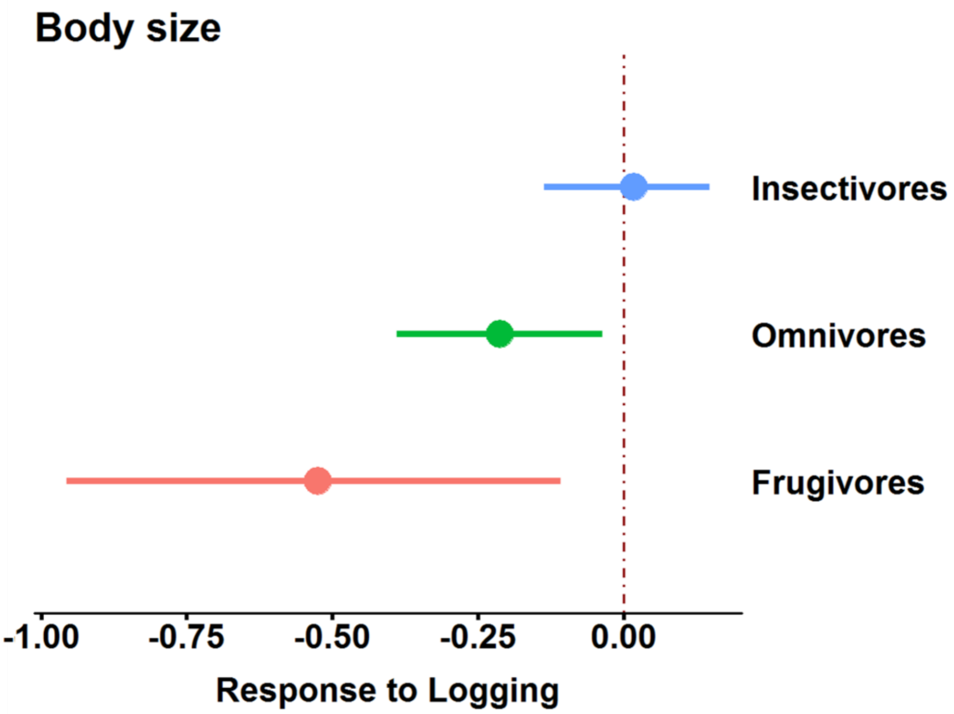
Body size
Insectivores
Omnivores
Frugivores
-1.00
-0.75
-0.50
-0.25
0.00
Response to Logging

Figure 1

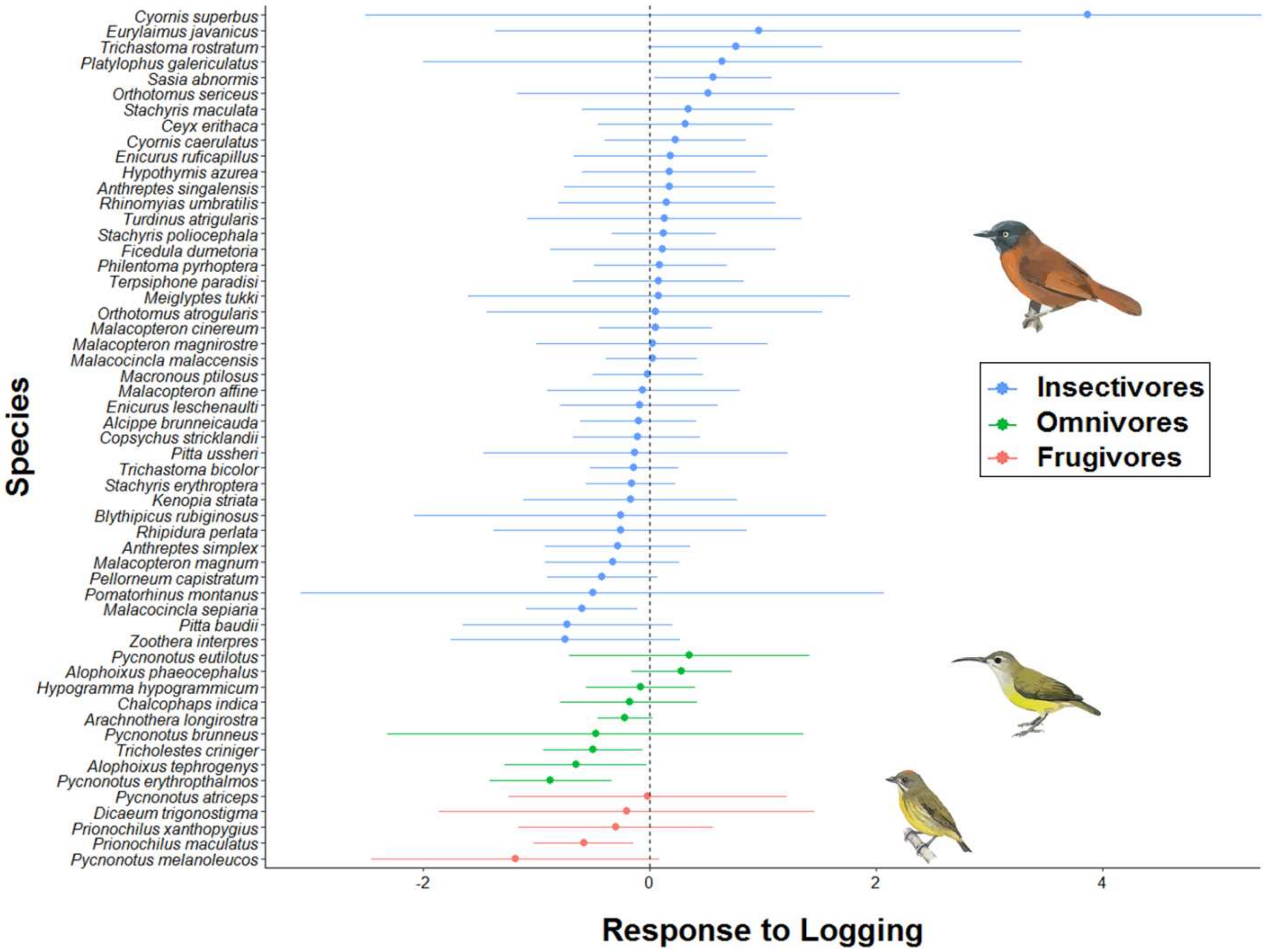
Species
Cyornis superbus
Eurylaimus javanicus
Trichastoma rostratum
Platylophus galericulatus
Sasia abnormis
Orthotomus sericeus
Stachyris maculata
Ceyx erithaca
Cyornis caerulatus
Enicurus ruficapillus
Hypothymis azurea
Anthreptes singalensis
Rhinomyias umbratilis
Turdinus atrigularis
Stachyris poliocephala
Ficedula dumetoria
Philentoma pyrhoptera
Terpsiphone paradisi
Meiglyptes tukki
Orthotomus atrogularis
Malacopteron cinereum
Malacopteron magnirostre
Malacocincla malaccensis
Macronous ptilosus
Malacopteron affine
Enicurus leschenaulti
Alcippe brunneicauda
Copsychus stricklandii
Pitta ussheri
Trichastoma bicolor
Stachyris erythroptera
Kenopia striata
Blythipicus rubiginosus
Rhipidura perlata
Anthreptes simplex
Malacopteron magnum
Pellorneum capistratum
Pomatorhinus montanus
Malacocincla sepiaria
Pitta baudii
Zoothera interpres
Pycnonotus eutilotus
Alophoixus phaeocephalus
Hypogramma hypogrammicum
Chalcophaps indica
Arachnothera longirostra
Pycnonotus brunneus
Tricholestes criniger
Alophoixus tephrogenys
Pycnonotus erythropthalmos
Pycnonotus atriceps
Dicaeum trigonostigma
Prionochilus xanthopygius
Prionochilus maculatus
Pycnonotus melanoleucos
Insectivores
Omnivores
Frugivores
-2
0
2
4
Response to Logging

Figure 2

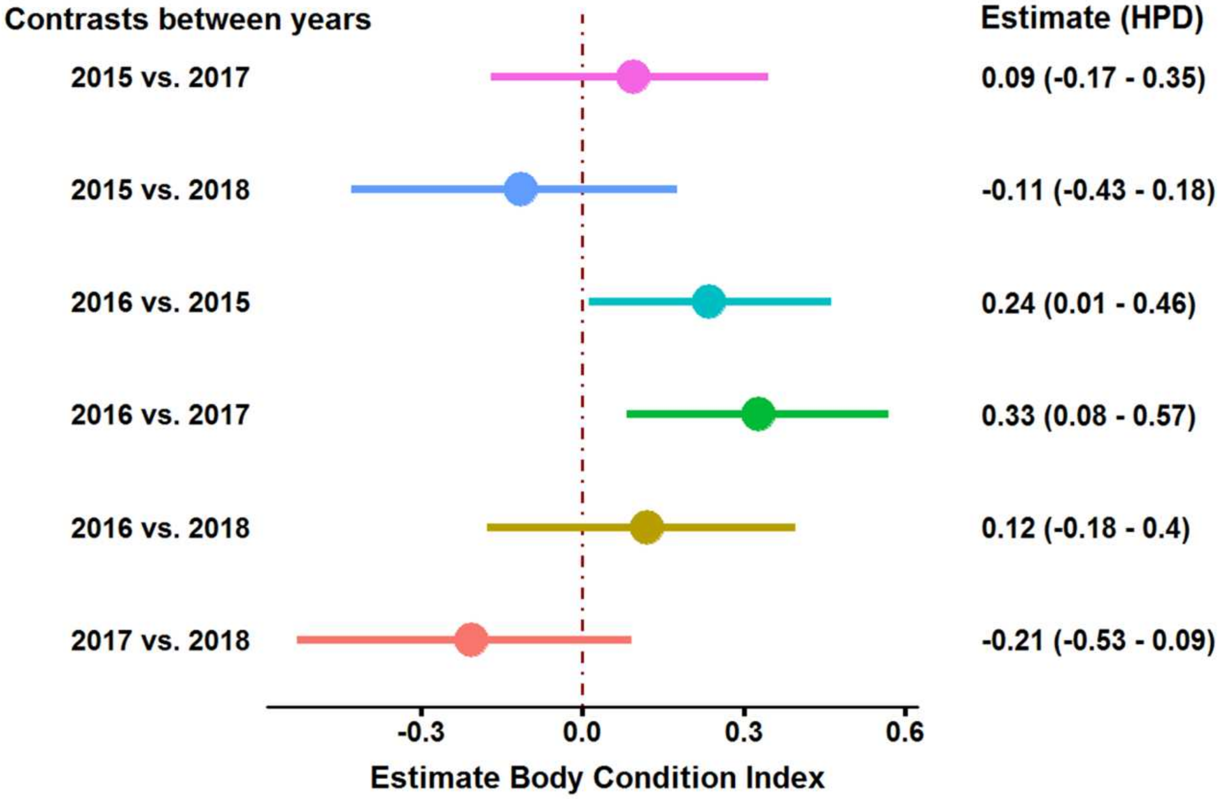
Contrasts between years
Estimate (HPD)
2015 vs. 2017
0.09 (-0.17 - 0.35)
2015 vs. 2018
-0.11 (-0.43 - 0.18)
2016 vs. 2015
0.24 (0.01 - 0.46)
2016 vs. 2017
0.33 (0.08 - 0.57)
2016 vs. 2018
0.12 (-0.18 - 0.4)
2017 vs. 2018
-0.21 (-0.53 - 0.09)
-0.3
0.0
0.3
0.6
Estimate Body Condition Index

Figure 3