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

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

Simone Messina[1], David P. Edwards[2], Hamada AbdElgawad[3], Gerrit T. S. Beemster[3], Suzanne Tomassi[2], Suzan Benedick[4], Marcel Eens[1], David Costantini[5]

[1] Behavioural Ecology & Ecophysiology Group, Department of Biology, University of Antwerp, Universiteitsplein 1, 2610 Wilrijk, Belgium

[2] Department of Animal and Plant Sciences, University of Sheffield, Sheffield, S10 2TN, UK

[3] Integrated Molecular Plant Physiology Research (IMPRES), Department of Biology, University of Antwerp, Groenenborgerlaan 171, 2020 Antwerp, Belgium

[4] School of Sustainable Agriculture, Universiti Malaysia Sabah, Malaysia

[5] Unité Physiologie moléculaire et adaptation (PhyMA), Muséum National d'Histoire Naturelle, CNRS; CP32, 57 rue Cuvier 75005 Paris, France

Corresponding author: Simone Messina – Tel. +32 32652285, email: simone.messina@uantwerpen.be

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 understory 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 no long-term effect of logging (last logging rotation occurred ~15 years prior to the study) on the oxidative status of understory 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.

Keywords: oxidative status, antioxidant, canalisation, selective logging, feeding ecology, forest degradation, land-use change

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, Sarre, Poore & Johnson 2011), most of which is being done unsustainably (Edwards, Tobias, Sheil, Meijaard & Laurance 2014; Edwards *et al.* 2019). As a consequence, selectively logged tropical forests are more prevalent than intact old-growth forests in most tropical countries (Laurance, Sayer & Cassman 2014; Lewis, Edwards & Galbraith 2015).

Selectively logged forests are less heterogeneous than old-growth forests (Okuda *et al.* 2003; Senior, Hill, Benedick & Edwards 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 & 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, de Iongh, Kustiawan & de Snoo 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, Baldauf, Mayhew & Hill 2007; Burivalova *et al.* 2015; Costantini, Edwards & Simons 2016; LaManna & Martin 2017) and that can also affect physiological status (Raubenheimer, Simpson & Mayntz 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 understory birds, higher trophic position was found in selectively logged than unlogged forests (Edwards *et al.* 2013), 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, Edwards, Eens & Costantini 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,

98 McGraw & Douglas Robinson 2009). Similarly, omnivorous bats had lower plasma oxidative
99 damage and higher plasma non-enzymatic antioxidant capacity than insectivorous bats
100 (Schneeberger, Czirjak & Voigt 2014).

101 Environmental challenges can affect the oxidative status in different ways. For
102 example, the antioxidant defenses can be weakened by a reduced intake of dietary antioxidants
103 in poor quality habitat or during adverse seasons (Catoni, Peters & Schaefer 2008; Isaksson,
104 Sheldon & Uller 2011). On the other hand, deficiency in dietary antioxidants may be
105 compensated by upregulation of endogenous antioxidants (Vertuani, Angusti & Manfredini
106 2004; Isaksson 2013). Changes in oxidative status may not necessarily translate into fitness
107 costs. For example, an experimental study on free-living jackdaws (*Coloeus monedula*) found
108 that brood size manipulation affected only markers of antioxidant status that were not
109 associated with survival. This finding supported the hypothesis that physiological variables
110 might be robust against changes when related to fitness traits (Boonekamp, Mulder & Verhulst
111 2018).

112 In this correlative, cross-sectional, multi-species study, we have tested for the first time
113 the effects of forest logging on the oxidative status of birds. To this end, we measured multiple
114 blood-based markers to examine the long-term effects of forest logging (last logging rotation
115 occurred ~15 years prior the study) on the oxidative status of 15 understory bird species in
116 Borneo during two years. We also tested if the feeding guild of species explained the effect of
117 logging on their oxidative status, because feeding ecology might also affect oxidative status
118 (e.g., through a different intake of antioxidants; Cohen, McGraw & Douglas Robinson 2009;
119 Costantini 2014) and insectivorous birds show a stronger trophic change in response to logging
120 compared to other feeding guilds (Edwards *et al.* 2013). We tested the following predictions:
121 (i) birds living in logged forests will have higher oxidative damage if the new environmental
122 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 understory 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 understory avifauna of the forest (Ansell, Edwards & Hamer 2011; Edwards *et al.* 2011). Tropical understory 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 (del Hoyo, Elliott, Sargatal, Christie & Kirwan 2019).

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

148 single contiguous lowland rainforest (Fig. 1). Trees of the Family Dipterocarpaceae, which
149 dominate these forests, are valuable timber species. Selective logging in the Ulu Segama-Malua
150 Forest Reserve (4°57042.8″N, 117°56051.7″E) occurred in the late 80's and early 90's at high
151 rate of timber removal (~115 m^3 ha^{-1}), and again about 15 years prior to our study (~31 m^3 ha^{-1}
152 of additional wood extracted) leaving a heavily disturbed forest. After the last logging
153 rotation, the forest was left to recover naturally.

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

165 Every captured bird was marked with an individual numbered ring. Species, ring
166 number, day and time of capture were recorded. Blood samples (≤ 100 µl) were taken from the
167 brachial vein of adult birds only using Microvette CB 300 lithium-heparine tubes (Sarstedt,
168 Numbrecht, Germany), and were stored in ice during the time of mist netting. After transfer to
169 the field laboratory, tubes were centrifuged (10,000 rpm for 5 minutes) to separate plasma from
170 red blood cells which were pipetted in different tubes and stored at cryogenic temperatures in
171 a vapour-shipper (MVE CryoShipper SC 20/12V). In our main laboratory at the University of
172 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).

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 & 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 & Cheeseman 1990; see Supplementary Information); (ii) the non-enzymatic antioxidant capacity in erythrocytes using a ferric ion reducing antioxidant power (FRAE) assay (Benzie & Strain 1996); (iii) the activities of the two antioxidant enzymes superoxide dismutase (SOD) and glutathione peroxidase (GPx) in erythrocytes (Dhindsa, Plumb-Dhindsa & Thorpe 1981; Drotar, Phelps & Fall 1985); (iv) the concentrations of the reduced glutathione (GSH), oxidised glutathione (GSSG) and total glutathione (tGSH) in erythrocytes using reversed-phase high-

198 performance liquid chromatography with electrochemical detection (Shimadzu, Hai Zhonglu,
199 Shanghai; Sinha *et al.* 2014); and (v) the redox state of the glutathione system GSH/GSSG,
200 which is the ratio between the availability of the antioxidant GSH and the product of its
201 oxidation GSSG, according to Jones (2006). We also measured plasma triglycerides because
202 they are important substrates of lipid oxidative damage, thus higher levels of TBARS might be
203 due to higher amounts of triglycerides in blood (Perez-Rodriguez *et al.* 2015). Mean values
204 (±SD) of markers of oxidative status per each species are shown in Table S3.
205
206 **Statistics**
207 **Forest type and feeding guilds**
208 Linear mixed models (LMMs) were applied to the data for each marker of oxidative status,
209 separately, to test the effects of the main factors forest type and feeding guild. We also included
210 in the model an interaction term between forest type and feeding guild to test for any difference
211 in a given marker between insectivorous and omnivorous species across the two types of forest.
212 In each model, we included a number of potential confounding factors: year of sampling to
213 control for any annual variation in marker values; day and time of blood sampling to control
214 for any seasonal and daily variation in marker values, respectively. In each model, we also
215 included the random factor species to account for conspecific individuals; the factor species
216 was nested within taxonomic family to control for phylogenetic non-independence (as in Koh,
217 Sodhi & Brook 2004; Hamer *et al.* 2015). The random factor plot, necessary to assess possible
218 variability due to local topographic differences within each forest type, was not included in the
219 models because preliminary analyses showed that it did not improve the fitting of any model.
220 The random factor plate, necessary to control for variation in the markers due to unpredictable
221 effects of laboratory analyses, was included in the models for FRAE and GPx only, because

222 only for these two markers it improved the fitting of the models as determined by a decrease
223 of the Akaike Information Criterion over a value of 2.
224
225 The concentration of TRIG was not included in the model for TBARS because a preliminary
226 model including the fixed effect TBARS, the covariate TRIG and the species as random factor,
227 did not detect any significant covariation between the two variables (LMM: $F = 0.05$, $P = 0.81$).
228 The factor individual was also not included in the models because we only had repeated
229 measurements for 14 birds within a same year and 12 birds between years (or fewer depending
230 on the marker). For these individuals, we calculated the coefficient of variation for each marker
231 of oxidative status (Table S4 and S5). Significance threshold of our models was set at $P < 0.05$
232 and non-significant interaction terms were removed only if the fitting of the model improved
233 as estimated by a decrease of the Akaike Information Criterion over a value of 2. Distribution
234 of model residuals was checked using the Shapiro-Wilk test. When model residuals did not
235 meet the assumption of normal distribution, data were square-root or log-transformed ($\log_{10} +$
236 1) and normality was tested again. Heteroscedasticity was assessed by plotting residuals vs.
237 fitted values.
238 Analyses of outliers were implemented for every model by measuring the Cook's
239 distance with fixed cut-off at 4/n (n = sample size). Detected outliers were removed from the
240 database and the respective models were run again. Results were generally similar between
241 models with or without outliers except in two cases. We reported models including all
242 individuals, specifying if removal of outliers affected the outcomes. Given the low number of
243 samples in some species (Table S2), we re-ran the models excluding from the database those
244 species with less than five samples for type of forest, for any given marker. Results are shown
245 in Table S8. All statistical analyses were performed using R (R Core Team 2013).
246

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.* 2020). 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, $P = <0.01$; 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.

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.

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 understory 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 genetic selection (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, Kanerva, Salminen, Nikinmaa & Eeva 2011; Bodey *et al.* 2020), 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 & 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, Marion, Yvon le, Jean-Patrice & Criscuolo 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, Watson, Nord & Isaksson 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 & Sieving 2016; Williamson & 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, Gale, Pierce, Khamcha & Sankamethawee 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, Crowther, Brodie & Bernard 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, Rainio, Ruuskanen & Korpimaki 2018). However, Ruuskanen, Morosinotto, Thomson, Ratnayake and Korpimäki (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 & Gutteridge 2015). Thus, the higher GSH/GSSG values might indicate an upregulation of the glutathione system to counteract accumulation of hydrogen peroxide (Ault & 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, Örnborg, Stephensen

& Andersson 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, Komdeur, Burke & Richardson 2011; Giordano, Costantini, Pick & Tschirren 2015). Elevated trophic flexibility of our study species in selectively logged forest compared to unlogged (Edwards *et al.* 2013; Hamer *et al.* 2015; Corlett 2017; Mansor, Abdullah, Halim, Nor & Ramli 2018), and a large abundance of invertebrates in both old-growth and naturally regenerating selectively logged forests (Edwards, Backhouse, Wheeler, Khen & Hamer 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, Sheldon & Uller 2011; Sikalidis *et al.* 2014). Animal proteins generally contain larger quantities of cysteine and methionine than plant proteins (Wiesenborn 2012; Brede, Wecke & Liebert 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, Kim, Harris & Williams 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 & Dell'Omo 2006; Cohen, McGraw & Douglas Robinson 2009; Isaksson 2013; North, Kinniburgh & Smits 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, Coto-Montes & Poeggeler 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, De Vos, Decuypere & Buyse 2008; Angilletta 2009). If such increased metabolism results in higher production of the superoxide anion, birds would need

445 to upregulate SOD to control its pro-oxidant effects. An increase of glutathione and non-
446 enzymatic antioxidant capacity might also be needed to reduce increased levels of hydrogen
447 peroxide produced by SOD reaction with superoxide anion (Fig. S1). Lower level of TBARS
448 in 2018 compared to 2017 could actually be an effect of the higher antioxidant defences.
449 Although we do not have information about different production and access to food sources
450 between 2017 and 2018, annual variation in abiotic conditions might be another important
451 factor involved in the regulation of antioxidants to investigate further.
452
453 **Population abundance and antioxidants**
454 Although we found significant changes between unlogged and logged forest for two out of
455 eight markers, effect size estimates enabled us to detect several small to large differences
456 among forest types, indicating that the effects of logging varied among markers. Small changes
457 in physiological traits may be biologically important (Møller & Jennions 2002; Garamszegi
458 2006). We found correlative evidence that variation in four markers (FRAE, GSH, tGSH, and
459 GPx) between forest types was significantly associated with differences in local abundance of
460 birds between forests. Specifically, species with higher levels of these four antioxidant markers
461 in a given type of forest were less abundant there than in the other forest type. This result may
462 suggest that a higher investment in certain antioxidant mechanisms (e.g. glutathione cycle)
463 might be part of a trade-off between self-maintenance and fitness traits (e.g., reproduction),
464 which translates into population effects. For example, energetic constraints might rise from
465 increased consumption of molecules of ATP for the synthesis of both GSH and GPx (Halliwell
466 & Gutteridge 2015). However, we expect that other physiological mechanisms were also
467 involved in the response of birds to selectively logged forests (e.g., the regulation of the
468 hypothalamic-pituitary-adrenal axis), concurring to the trade-off between self-maintenance and
469 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, Sadre-Marandi, Best & Reed 2017; Boonekamp, Mulder & Verhulst 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 more resilient to forest logging (Costantini, Edwards & Simons 2016). Srinivasan and Quader (2019) also reported that changes in demographic vital rates of sub-tropical understory 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 understory 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 genetic selection) 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

520 determine the extent to which variation in oxidative status markers translates into fitness
521 outcomes to determine the role of oxidative status in explaining among-species variation in
522 persistence in logged forests.
523
524 **Acknowledgements**
525 We thank the University of Antwerp, FWO (PhD fellowship 1140117N) and the King Leopold
526 III Fund for Nature Exploration and Conservation for supporting and funding S.M. Further
527 funding was provided by MNHN (ATM 2018) and CNRS to DC. We thank Tanith Hackney,
528 Jessey Chai Yee Wei, Ezron Gerald, Chong Yi Yao, Tan Chen Hong, Rayzigerson Rodney
529 Chai, Amy Donnison, Sylwia Zbijewska, Rose Fogliano, Patrick Cannon, Mike Kaputa, Cheoh
530 Chuan Ong and in particular Cindy P. Cosset for their valuable assistance with fieldwork. We
531 thank Danny Huybrecht for his help with laboratory analyses and Josie Meaney-Ward for
532 administrative support. We thank the Associate Editor, Dominic Cram and two anonymous
533 reviewers for providing comments that helped us to improve presentation and interpretation of
534 results.
535
536 **Authors' contributions**

537 • SM, DC, DE conceived the ideas and designed methodology;
538 • DC, DE, ME, GB, SB coordinated different phases of the study;
539 • SM, ST, DC collected samples;
540 • SM, HA performed laboratory analyses;
541 • SM analysed the data;
542 • SM led the writing of the manuscript;
543 • All authors contributed critically to the drafts and gave final approval for publication.

544
545 **References**

546 Angilletta, M.J. (2009) Thermal adaptation: A theoretical and empirical synthesis. Oxford, UK: Oxford
547 University Press. https://doi:10.1093/acprof:oso/9780198570875.001.1

548 Ansell, F.A., Edwards, D.P., & Hamer, K.C. (2011) Rehabilitation of Logged Rain Forests: Avifaunal
549 Composition, Habitat Structure, and Implications for Biodiversity-Friendly REDD+. *Biotropica,*
550 **43,** 504-511. https://doi:10.1111/j.1744-7429.2010.00725.x
551 Arbainsyah, de Iongh, H.H., Kustiawan, W., & de Snoo, G.R. (2014) Structure, composition and diversity
552 of plant communities in FSC-certified, selectively logged forests of different ages compared to
553 primary rain forest. *Biodiversity and Conservation,* **23,** 2445-2472.
554 https://doi:10.1007/s10531-014-0732-4
555 Ault, J.G., & Lawrence, D.A. (2003) Glutathione distribution in normal and oxidatively stressed cells.
556 *Experimental Cell Research,* **285,** 9-14. https://doi:10.1016/s0014-4827(03)00012-0
557 Benzie, F.I., & Strain, J.J. (1996) The ferric reducing ability of plasma (FRAP) as a measure of
558 ‘‘antioxidant power’’: The FRAP assay. *Analytical Biochemistry,* **239,** 70-76.
559 https://doi:10.1006/abio.1996.0292
560 Blaser, J., Sarre, A., Poore, D., & Johnson, S. (2011) Status of tropical forest management 2011. ITTO
561 Technical Series No 38. International Tropical Timber Organization, Yokohama, JP.
562 Bodey, T.W., Cleasby, I.R., Blount, J.D., McElwaine, G., Vigfusdottir, F., & Bearhop, S. (2020) Consistent
563 measures of oxidative balance predict survival but not reproduction in a long-distance
564 migrant. *J Anim Ecol*. https://doi:10.1111/1365-2656.13237
565 Boonekamp, J.J., Mulder, E., & Verhulst, S. (2018) Canalisation in the wild: effects of developmental
566 conditions on physiological traits are inversely linked to their association with fitness. *Ecology*
567 *Letters,* **21,** 857-864. https://doi:10.1111/ele.12953
568 Brede, A., Wecke, C., & Liebert, F. (2018) Does the Optimal Dietary Methionine to Cysteine Ratio in
569 Diets for Growing Chickens Respond to High Inclusion Rates of Insect Meal from Hermetia
570 illucens? *Animals (Basel),* **8**. https://doi:10.3390/ani8110187
571 Burivalova, Z., Lee, T.M., Giam, X., Sekercioglu, C.H., Wilcove, D.S., & Koh, L.P. (2015) Avian responses
572 to selective logging shaped by species traits and logging practices. *Proceedings of the Royal*
573 *Society B: Biological Sciences,* **282,** 20150164. https://doi:10.1098/rspb.2015.0164
574 Catoni, C., Peters, A., & Schaefer, M.H. (2008) Life history trade-offs are influenced by the diversity,
575 availability and interactions of dietary antioxidants. *Animal Behaviour,* **76,** 1107-1119.
576 https://doi:10.1016/j.anbehav.2008.05.027
577 Cerullo, G.R., & Edwards, D.P. (2019) Actively restoring resilience in selectively logged tropical forests.
578 *Journal of Applied Ecology,* **56,** 107-118. https://doi:10.1111/1365-2664.13262
579 Cohen, A., McGraw, K.J., Wiersma, P., Williams, J.B., Robinson, W.D., Robinson, T.R., . . . Ricklefs, R.E.
580 (2008) Interspecific Associations between Circulating Antioxidant Levels and Life-History
581 Variation in Birds. *The American Naturalist,* **172,** 178-193. https://doi:10.1086/589456
582 Cohen, A.A., McGraw, K.J., & Douglas Robinson, W. (2009) Serum antioxidant levels in wild birds vary
583 in relation to diet, season, life history strategy, and species. *Oecologia,* **161,** 673-683.
584 https://doi:10.1007/s00442-009-1423-9
585 Cohen, J. (1988) Statistical power analysis for the behavioral sciences, (2nd edn). Hillsdale: Lawrence
586 Earlbaum Associates
587 Corlett, R.T. (2017) Frugivory and seed dispersal by vertebrates in tropical and subtropical Asia: An
588 update. *Global Ecology and Conservation,* **11,** 1-22. https://doi:10.1016/j.gecco.2017.04.007
589 Costantini, D. (2014) Oxidative Stress and Hormesis in Evolutionary Ecology and Physiology—A
590 Marriage Between Mechanistic and Evolutionary Approaches. Berlin, Heidelberg: Springer-
591 Verlag. https://doi:10.1007/978-3-642-54663-1
592 Costantini, D. (2019) Understanding diversity in oxidative status and oxidative stress: the
593 opportunities and challenges ahead. *Journal of Experimental Biology,* **222**.
594 https://doi:10.1242/jeb.194688
595 Costantini, D., & Dell'Omo, G. (2006) Environmental and genetic components of oxidative stress in
596 wild kestrel nestlings (Falco tinnunculus). *Journal of Comparative Physiology B,* **176,** 575-579.
597 https://doi:10.1007/s00360-006-0080-0

598 Costantini, D., Edwards, D.P., & Simons, M.J.P. (2016) Life after logging in tropical forests of Borneo: A
599 meta-analysis. *Biological Conservation,* **196,** 182-188.
600 https://doi:10.1016/j.biocon.2016.02.020
601 Costantini, D., Marasco, V., & Moller, A.P. (2011) A meta-analysis of glucocorticoids as modulators of
602 oxidative stress in vertebrates. *Journal of Comparative Physiology B,* **181,** 447-456.
603 https://doi:10.1007/s00360-011-0566-2)
604 del Hoyo, J., Elliott, A., Sargatal, J., Christie, D.A., & Kirwan, G. (2019) Handbook of the birds of the
605 worlds alive. Barcelona, ES: Lynx Edictions
606 Del Re, A.C. (2013) compute.es: compute effect sizes. R package version 0.2-2. *Available at:*
607 *http://cran.r-project.org/web/packages/compute.es,*
608 Dhindsa, R.S., Plumb-Dhindsa, P., & Thorpe, T.A. (1981) Leaf senescence: Correlated with increased
609 levels of membrane permeability and lipid peroxidation, and decreased levels of superoxide
610 dismutase and catalase. *Journal of Experimental Botany,* **32,** 93-101.
611 https://doi:10.1093/jxb/32.1.93
612 Drotar, A., Phelps, P., & Fall, R. (1985) Evidence for glutathione peroxidase activities in cultured plant
613 cells. *Plant Science,* **42,** 35-40. https://doi:10.1016/0168-9452(85)90025-1
614 Edwards, D.P., Backhouse, A.R., Wheeler, C., Khen, C.V., & Hamer, K.C. (2012) Impacts of logging and
615 rehabilitation on invertebrate communities in tropical rainforests of northern Borneo. *Journal*
616 *of Insect Conservation,* **16,** 591-599. https://doi:10.1007/s10841-011-9444-1
617 Edwards, D.P., Larsen, T.H., Docherty, T.D., Ansell, F.A., Hsu, W.W., Derhe, M.A., . . . Wilcove, D.S.
618 (2011) Degraded lands worth protecting: the biological importance of Southeast Asia's
619 repeatedly logged forests. *Proceedings of the Royal Society B: Biological Sciences,* **278,** 82-90.
620 https://doi:10.1098/rspb.2010.1062
621 Edwards, D.P., Socolar, J.B., Mills, S.C., Burivalova, Z., Koh, L.P., & Wilcove, D.S. (2019) Conservation of
622 Tropical Forests in the Anthropocene. *Current Biology,* **29,** R1008-R1020.
623 https://doi:10.1016/j.cub.2019.08.026
624 Edwards, D.P., Tobias, J.A., Sheil, D., Meijaard, E., & Laurance, W.F. (2014) Maintaining ecosystem
625 function and services in logged tropical forests. *Trends in Ecology & Evolution,* **29,** 511-520.
626 https://doi:10.1016/j.tree.2014.07.003
627 Edwards, D.P., Woodcock, P., Newton, R.J., Edwards, F.A., Andrews, D.J.R., Docherty, T.D.S., . . . Hamer,
628 K.C. (2013) Trophic flexibility and the persistence of understory birds in intensively logged
629 rainforest. *Conservation Biology,* **27,** 1079-1086. https://doi:10.1111/cobi.12059
630 El-Shafey, N.M., & AbdElgawad, H. (2012) Luteolin, a bioactive flavone compound extracted from
631 Cichorium endivia L. subsp. divaricatum alleviates the harmful effect of salinity on maize. *Acta*
632 *Physiologiae Plantarum,* **34,** 2165-2177. https://doi:10.1007/s11738-012-1017-8
633 Esterbauer, H., & Cheeseman, K.H. (1990) Determination of aldehydic lipid peroxidation products:
634 malonaldehyde and 4-hydroxynonenal. *Methods in enzymology,* **186,** 407-421.
635 https://doi:10.1016/0076-6879(90)86134-h
636 Ewers, R.M., Boyle, M.J., Gleave, R.A., Plowman, N.S., Benedick, S., Bernard, H., . . . Turner, E.C. (2015)
637 Logging cuts the functional importance of invertebrates in tropical rainforest. *Nature*
638 *Communication,* **6,** 6836. https://doi:10.1038/ncomms7836
639 Garamszegi, L.Z. (2006) Comparing effect sizes across variables: generalization without the need for
640 Bonferroni correction. *Behavioral Ecology,* **17,** 682-687. https://doi:10.1093/beheco/ark005
641 Gibson, L., Lee, T.M., Koh, L.P., Brook, B.W., Gardner, T.A., Barlow, J., . . . Sodhi, N.S. (2011) Primary
642 forests are irreplaceable for sustaining tropical biodiversity. *Nature,* **478,** 378-381.
643 https://doi:10.1038/nature10425
644 Giordano, M., Costantini, D., Pick, J.L., & Tschirren, B. (2015) Female oxidative status, egg antioxidant
645 protection and eggshell pigmentation: a supplemental feeding experiment in great tits.
646 *Behavioral Ecology and Sociobiology,* **69,** 777-785. https://doi:10.1007/s00265-015-1893-1

Granados, A., Crowther, K., Brodie, J.F., & Bernard, H. (2016) Persistence of mammals in a selectively logged forest in Malaysian Borneo. *Mammalian Biology - Zeitschrift für Säugetierkunde,* **81,** 268-273. https://doi:10.1016/j.mambio.2016.02.011

Gray, M.A., Baldauf, S.L., Mayhew, P.J., & Hill, J.K. (2007) The response of avian feeding guilds to tropical forest disturbance. *Conservation Biology,* **21,** 133-141. https://doi:10.1111/j.1523-1739.2006.00557.x

Halliwell, B., & Gutteridge, J.M.C. (2015) Free radicals in biology and medicine, (Fifth edn). Oxford, UK: Oxford University Press. https://doi:10.1107/S2059798317004533

Hambly, C., Pinshow, B., Wiersma, P., Verhulst, S., Piertney, S.B., Harper, E.J., & Speakman, J.R. (2004) Comparison of the cost of short flights in a nectarivorous and a non-nectarivorous bird. *Journal of Experimental Biology,* **207,** 3959-3968. https://doi:10.1242/jeb.01233

Hamer, K.C., Newton, R.J., Edwards, F.A., Benedick, S., Bottrell, S.H., & Edwards, D.P. (2015) Impacts of selective logging on insectivorous birds in Borneo: The importance of trophic position, body size and foraging height. *Biological Conservation,* **188,** 82-88. https://doi:10.1016/j.biocon.2014.09.026

Hardeland, R., Coto-Montes, A., & Poeggeler, B. (2003) Circadian rhythms, oxidative stress, and antioxidative defense mechanisms. *Chronobiology International,* **20,** 921-962. https://doi:10.1081/cbi-120025245

Hardwick, S.R., Toumi, R., Pfeifer, M., Turner, E.C., Nilus, R., & Ewers, R.M. (2015) The relationship between leaf area index and microclimate in tropical forest and oil palm plantation: Forest disturbance drives changes in microclimate. *Agricultural and Forest Meteorology,* **201,** 187-195. https://doi:10.1016/j.agrformet.2014.11.010

Hill, J.K., & Hamer, K.C. (2004) Determining impacts of habitat modification on diversity of tropical forest fauna: the importance of spatial scale. *Journal of Applied Ecology,* **41,** 744-754. https://doi:10.1111/j.0021-8901.2004.00926.x

Hua, F., & Sieving, K.E. (2016) Understory avifauna exhibits altered mobbing behavior in tropical forest degraded by selective logging. *Oecologia,* **182,** 743-754. https://doi:10.1007/s00442-016-3695-1

Isaksson, C. (2013) Opposing effects on glutathione and reactive oxygen metabolites of sex, habitat, and spring date, but no effect of increased breeding density in great tits (Parus major). *Ecology and Evolution,* **3,** 2730-2738. https://doi:10.1002/ece3.663

Isaksson, C., Örnborg, J., Stephensen, E., & Andersson, S. (2005) Plasma Glutathione and Carotenoid Coloration as Potential Biomarkers of Environmental Stress in Great Tits. *Ecohealth,* **2,** 138-146. https://doi:10.1007/s10393-005-3869-5

Isaksson, C., Sheldon, B.C., & Uller, T. (2011) The Challenges of Integrating Oxidative Stress into Life-history Biology. *BioScience,* **61,** 194-202. https://doi:10.1525/bio.2011.61.3.5

Jones, P.D. (2006) Redefining oxidative stress. *Antioxidants & Redox Signaling,* **8,** 1865-1879. https://doi:10.1089/ars.2006.8.1865

Koh, L.P., Sodhi, N.S., & Brook, B.W. (2004) Ecological correlates of extinction proneness in tropical butterflies. *Conservation Biology,* **18,** 1571-1578. https://doi:10.1111/j.1523-1739.2004.00468.x

Koivula, M.J., Kanerva, M., Salminen, J.P., Nikinmaa, M., & Eeva, T. (2011) Metal pollution indirectly increases oxidative stress in great tit (Parus major) nestlings. *Environmental Research,* **111,** 362-370. https://doi:10.1016/j.envres.2011.01.005

LaManna, J.A., & Martin, T.E. (2017) Logging impacts on avian species richness and composition differ across latitudes and foraging and breeding habitat preferences. *Biological Reviews,* **92,** 1657-1674. https://doi:10.1111/brv.12300

Laurance, W.F., Sayer, J., & Cassman, K.G. (2014) Agricultural expansion and its impacts on tropical nature. *Trends in Ecology and Evolution,* **29,** 107-116. https://doi:10.1016/j.tree.2013.12.001

Lewis, S.L., Edwards, D.P., & Galbraith, D. (2015) Increasing human dominance of tropical forests. *Science,* **349,** 827-832. https://doi:10.1126/science.aaa9932

Lin, H., De Vos, D., Decuypere, E., & Buyse, J. (2008) Dynamic changes in parameters of redox balance after mild heat stress in aged laying hens (Gallus gallus domesticus). *Comparative Biochemistry and Physiology Part C: Toxicology & Pharmacology,* **147,** 30-35. https://doi:10.1016/j.cbpc.2007.07.005

Mansor, M.S., Abdullah, N.A., Halim, M.R.A., Nor, S.M., & Ramli, R. (2018) Diet of tropical insectivorous birds in lowland Malaysian rainforest. *Journal of Natural History,* **52,** 2301-2316. https://doi:10.1080/00222933.2018.1534015

McNab, B.K. (1988) Food habits and the basal rate of metabolism in birds. *Oecologia,* **77,** 343-349. https://doi:10.1007/BF00378040

Messina, S., Edwards, D.P., Eens, M., & Costantini, D. (2018) Physiological and immunological responses of birds and mammals to forest degradation: A meta-analysis. *Biological Conservation,* **224,** 223-229. https://doi:10.1016/j.biocon.2018.06.002

Messina, S., Edwards, D.P., Marasco, V., Canoine, V., Cosset, C.C.P., Tomassi, S., . . . Costantini, D. (2020) Glucocorticoids link forest type to local abundance in tropical birds. *Functional Ecology***,** in press. https://doi:10.1111/1365-2435.13586

Møller, A.P., & Jennions, M.D. (2002) How much variance can be explained by ecologists and evolutionary biologists? *Oecologia,* **132,** 492-500. https://doi:10.1007/s00442-002-0952-2

Morosinotto, C., Rainio, M., Ruuskanen, S., & Korpimaki, E. (2018) Antioxidant Enzyme Activities Vary with Predation Risk and Environmental Conditions in Free-Living Passerine Birds. *Physiological and Biochemical Zoology,* **91,** 837-848. https://doi:10.1086/697087

Nijhout, H.F., Sadre-Marandi, F., Best, J., & Reed, M.C. (2017) Systems Biology of Phenotypic Robustness and Plasticity. *Integrative and Comparative Biology,* **57,** 171-184. https://doi:10.1093/icb/icx076

North, M.A., Kinniburgh, D.W., & Smits, J.E.G. (2017) European Starlings (Sturnus vulgaris) As Sentinels of Urban Air Pollution: A Comprehensive Approach from Noninvasive to Post Mortem Investigation. *Environ Sci Technol,* **51,** 8746-8756. https://doi:10.1021/acs.est.7b01861

Okuda, T., Suzuki, M., Adachi, N., Quah, E.S., Hussein, N.A., & Manokaran, N. (2003) Effect of selective logging on canopy and stand structure and tree species composition in a lowland dipterocarp forest in peninsular Malaysia. *Forest Ecology and Management,* **175,** 297-320. https://doi:10.1016/S0378-1127(02)00137-8

Perez-Rodriguez, L., Romero-Haro, A.A., Sternalski, A., Muriel, J., Mougeot, F., Gil, D., & Alonso-Alvarez, C. (2015) Measuring oxidative stress: the confounding effect of lipid concentration in measures of lipid peroxidation. *Physiological and Biochemical Zoology,* **88,** 345-351. https://doi:10.1086/680688

Putz, F.E., Zuidema, P.A., Synnott, T., Peña-Claros, M., Pinard, M.A., Sheil, D., . . . Zagt, R. (2012) Sustaining conservation values in selectively logged tropical forests: the attained and the attainable. *Conservation Letters,* **5,** 296-303. https://doi:10.1111/j.1755-263X.2012.00242.x

R Core Team (2013) R: a language and environment for statistical computing. *R Foundation for Statistical Computing, Vienna, Austria. Available at: http://www.rproject.org/*,

Raubenheimer, D., Simpson, S.J., & Mayntz, D. (2009) Nutrition, ecology and nutritional ecology: toward an integrated framework. *Functional Ecology,* **23,** 4-16. https://doi:10.1111/j.1365-2435.2009.01522.x

Ruuskanen, S., Morosinotto, C., Thomson, R.L., Ratnayake, C.P., & Korpimäki, E. (2017) Food supplementation, but not predation risk, alters female antioxidant status during breeding. *Behavioral Ecology and Sociobiology,* **71**. https://doi:10.1007/s00265-017-2299-z

Salmon, P., Watson, H., Nord, A., & Isaksson, C. (2018) Effects of the Urban Environment on Oxidative Stress in Early Life: Insights from a Cross-fostering Experiment. *Integr Comp Biol,* **58,** 986-994. https://doi:10.1093/icb/icy099

Schneeberger, K., Czirjak, G.A., & Voigt, C.C. (2014) Frugivory is associated with low measures of plasma oxidative stress and high antioxidant concentration in free-ranging bats. *Naturwissenschaften,* **101,** 285-290. https://doi:10.1007/s00114-014-1155-5

Senior, R.A., Hill, J.K., Benedick, S., & Edwards, D.P. (2018) Tropical forests are thermally buffered despite intensive selective logging. *Global Change Biology,* **24,** 1267-1278. https://doi:10.1111/gcb.13914

Sikalidis, A.K., Mazor, K.M., Lee, J.I., Roman, H.B., Hirschberger, L.L., & Stipanuk, M.H. (2014) Upregulation of capacity for glutathione synthesis in response to amino acid deprivation: regulation of glutamate-cysteine ligase subunits. *Amino Acids,* **46,** 1285-1296. https://doi:10.1007/s00726-014-1687-1

Sinha, A.K., AbdElgawad, H., Giblen, T., Zinta, G., De Rop, M., Asard, H., . . . De Boeck, G. (2014) Anti-oxidative defences are modulated differentially in three freshwater teleosts in response to ammonia-induced oxidative stress. *PLoS One,* **9,** e95319. https://doi:10.1371/journal.pone.0095319

Sodhi, N.S., Koh, L.P., Clements, R., Wanger, T.C., Hill, J.K., Hamer, K.C., . . . Lee, T.M. (2010) Conserving Southeast Asian forest biodiversity in human-modified landscapes. *Biological Conservation,* **143,** 2375-2384. https://doi:10.1016/j.biocon.2009.12.029

Somsiri, K., Gale, G.A., Pierce, A.J., Khamcha, D., & Sankamethawee, W. (2019) Habitat structure affects nest predation of the Scaly-crowned Babbler (Malacopteron cinereum) by macaques and snakes in a Thai-seasonal evergreen forest. *Journal of Ornithology*. https://doi:10.1007/s10336-019-01724-0

Srinivasan, U., & Quader, S. (2019) Size–logging interactions and population dynamics in tropical understorey birds. *Current Science,* **116,** 795-801. https://doi:10.18520/cs/v116/i5/795-801

Sylvie, G., Marion, K., Yvon le, M., Jean-Patrice, R., & Criscuolo, F. (2012) Of the importance of metabolic phases in the understanding of oxidative stress in prolonged fasting and refeeding. *Physiol Biochem Zool,* **85,** 415-420. https://doi:10.1086/666364

Tilman, D., Clark, M., Williams, D.R., Kimmel, K., Polasky, S., & Packer, C. (2017) Future threats to biodiversity and pathways to their prevention. *Nature,* **546,** 73-81. https://doi:10.1038/nature22900

van de Crommenacker, J., Komdeur, J., Burke, T., & Richardson, D.S. (2011) Spatio-temporal variation in territory quality and oxidative status: a natural experiment in the Seychelles warbler (Acrocephalus sechellensis). *Journal of Animal Ecology,* **80,** 668-680. https://doi:10.1111/j.1365-2656.2010.01792.x

Vertuani, S., Angusti, A., & Manfredini, S. (2004) The Antioxidants and Pro-Antioxidants Network: An Overview. *Current Pharmaceutical Design,* **10,** 1677-1694. https://doi:10.2174/1381612043384655

Wiesenborn, W.D. (2012) Sulfur Contents of Spiders and Insects in Desert Riparian Habitat. *Florida Entomologist,* **95,** 952-960. https://doi:10.1653/024.095.0420

Williamson, J.L., & Fagan, M.E. (2017) Predator playback, foraging height, and phylogeny affect gap crossing behavior in tropical forest birds. *Ornitologia Neotropical,* **28,** 163-174.

Wilman, H., Belmaker, J., Simpson, J., De La Rosa, C., Rivadeneira, M.M., & Jetz, W. (2014) EltonTraits 1.0: Species-level foraging attributes of the world's birds and mammals. *Ecology,* **95,** 20-27. https://doi:10.1890/13-1917.1

Yap, K.N., Kim, O.R., Harris, K.C., & Williams, T.D. (2017) Physiological effects of increased foraging effort in a small passerine. *Journal of Experimental Biology,* **220,** 4282-4291. https://doi:10.1242/jeb.160812

Table 1 – 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
	Forest	1,328.05	0.173	0.677
	Guild	1,3.85	8.301	0.047*

tGSH	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

Figure Captions

Figure 1 – (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.

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 ($P < 0.05$).

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 understory bird species for the years 2017 and 2018. Circles = insectivores; triangles = omnivores.

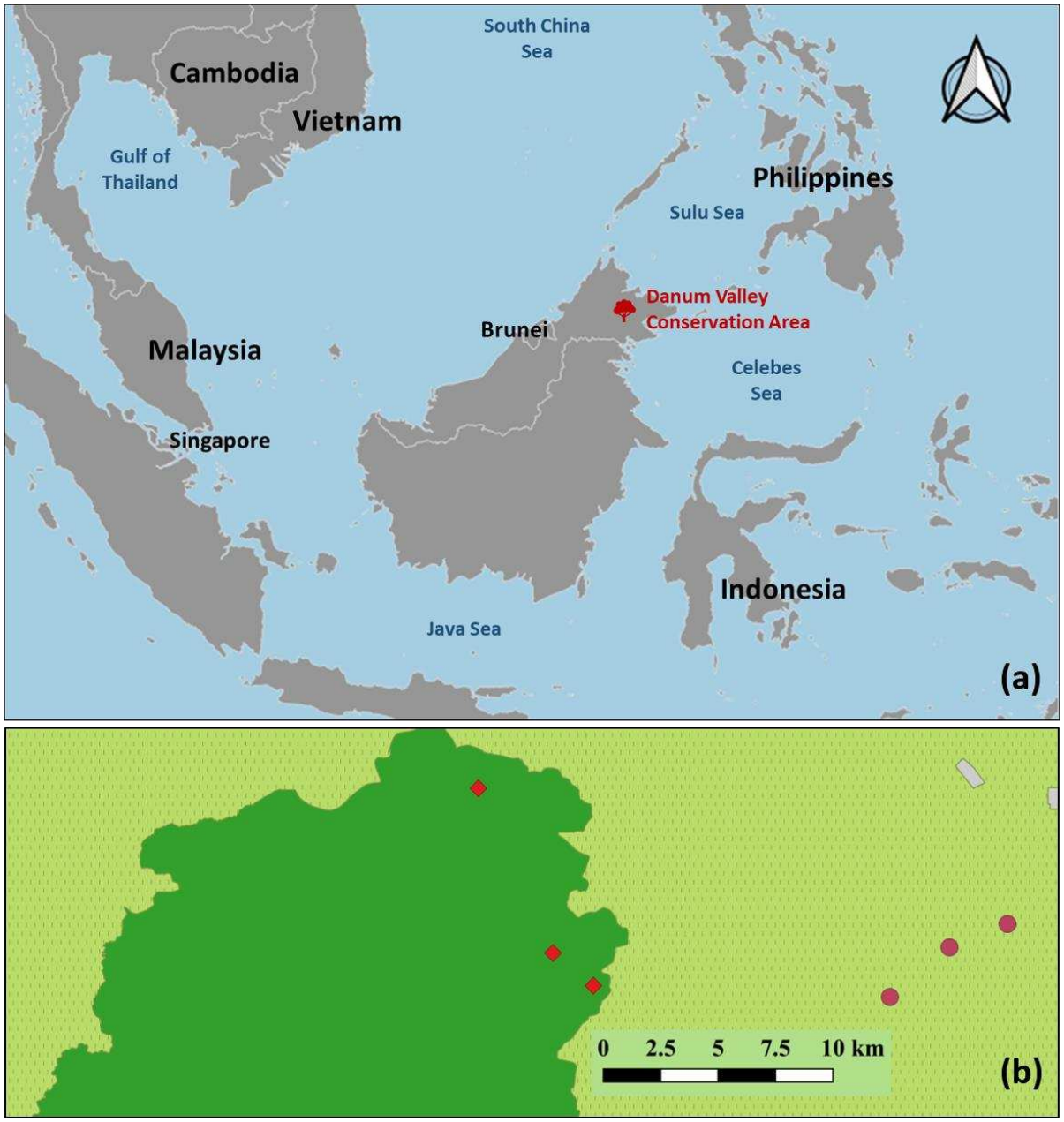

South China Sea
Cambodia
Vietnam
Gulf of Thailand
Philippines
Sulu Sea
Danum Valley Conservation Area
Brunei
Malaysia
Celebes Sea
Singapore
Indonesia
Java Sea
(a)
0 2.5 5 7.5 10 km
(b)

Figure 1

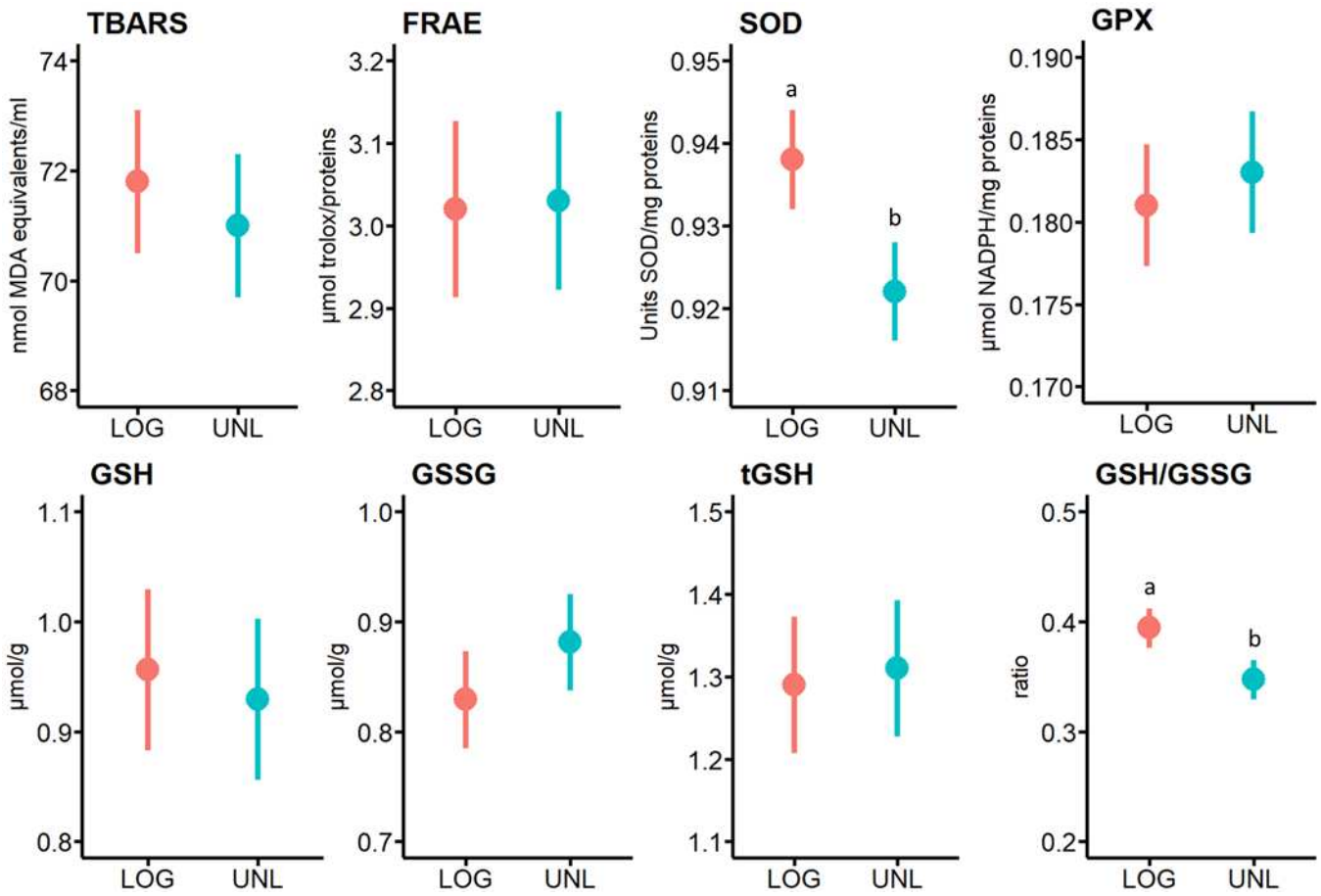

TBARS
nmol MDA equivalents/ml
74
72
70
68
LOG
UNL
FRAE
µmol trolox/proteins
3.2
3.1
3.0
2.9
2.8
LOG
UNL
SOD
Units SOD/mg proteins
0.95
0.94
0.93
0.92
0.91
a
b
LOG
UNL
GPX
µmol NADPH/mg proteins
0.190
0.185
0.180
0.175
0.170
LOG
UNL
GSH
µmol/g
1.1
1.0
0.9
0.8
LOG
UNL
GSSG
µmol/g
1.0
0.9
0.8
0.7
LOG
UNL
tGSH
µmol/g
1.5
1.4
1.3
1.2
1.1
LOG
UNL
GSH/GSSG
ratio
0.5
0.4
0.3
0.2
a
b
LOG
UNL

Figure 2

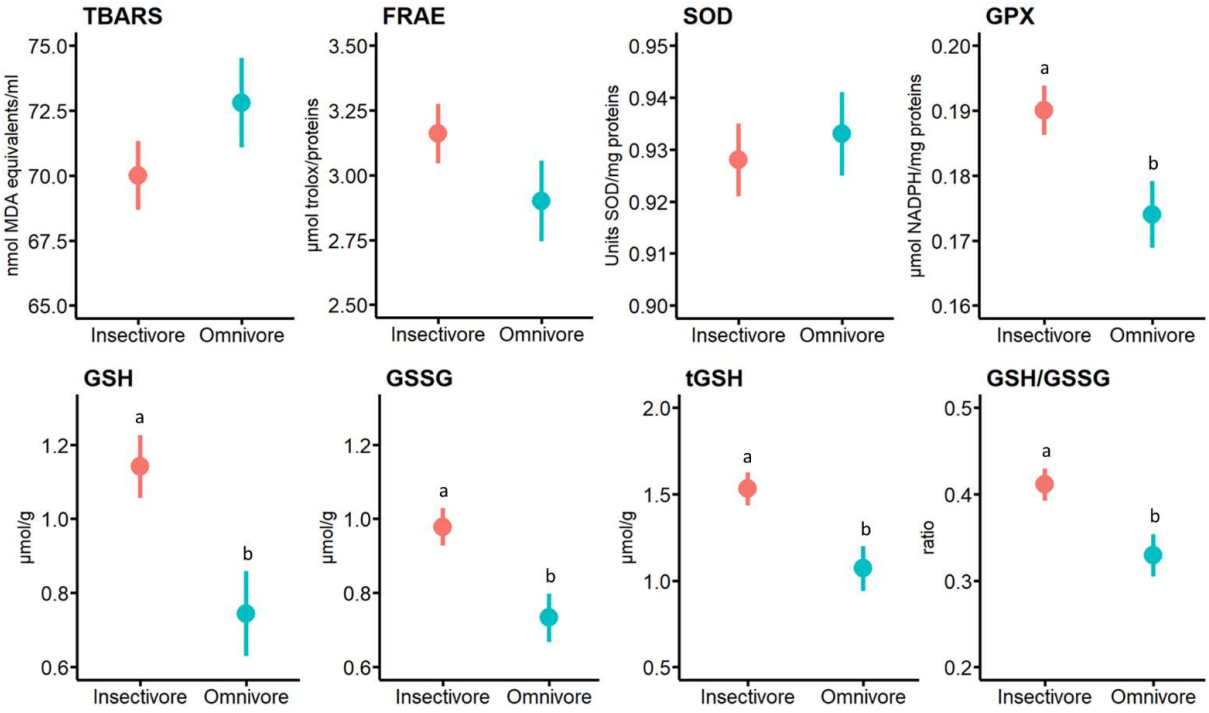
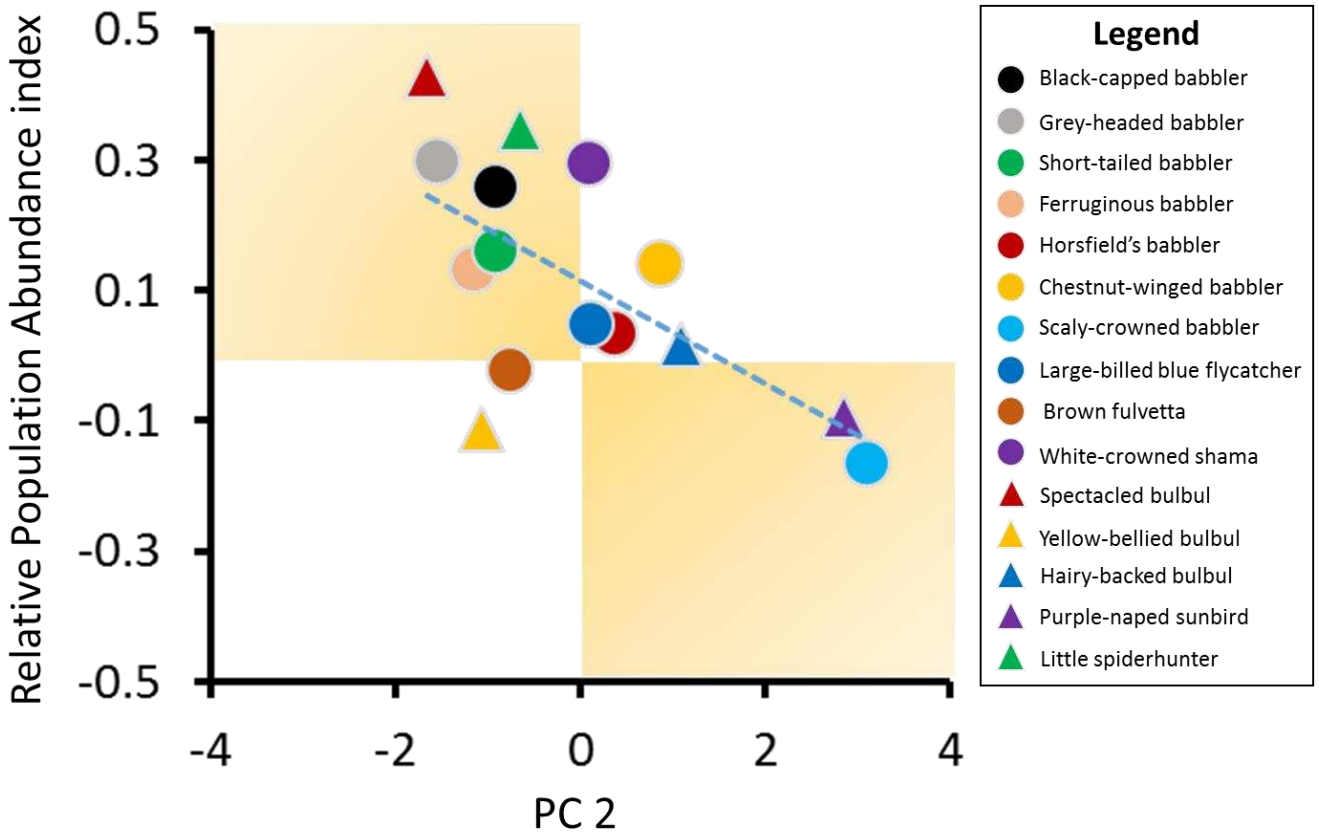

TBARS
nmol MDA equivalents/ml
75.0
72.5
70.0
67.5
65.0
Insectivore
Omnivore
FRAE
µmol trolox/proteins
3.50
3.25
3.00
2.75
2.50
Insectivore
Omnivore
SOD
Units SOD/mg proteins
0.95
0.94
0.93
0.92
0.91
0.90
Insectivore
Omnivore
GPX
µmol NADPH/mg proteins
0.20
0.19
0.18
0.17
0.16
a
b
Insectivore
Omnivore
GSH
µmol/g
1.2
1.0
0.8
0.6
a
b
Insectivore
Omnivore
GSSG
µmol/g
1.2
1.0
0.8
0.6
a
b
Insectivore
Omnivore
tGSH
µmol/g
2.0
1.5
1.0
0.5
a
b
Insectivore
Omnivore
GSH/GSSG
ratio
0.5
0.4
0.3
0.2
a
b
Insectivore
Omnivore

Figure 3



851
852 Figure 4