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**Reference:**

Messina Simone, Edwards David P., Marasco Valeria, Canoine Virginie, Cosset Cindy C. P., Tomassi Suzanne, Benedick Suzan, Eens Marcel, Costantini David.- Glucocorticoids link forest type to local abundance in tropical birds  
Functional ecology / British Ecological Society - ISSN 0269-8463 - Hoboken, Wiley, (2020)12 p.  
Full text (Publisher's DOI): <https://doi.org/10.1111/1365-2435.13586>  
To cite this reference: <https://hdl.handle.net/10067/1702100151162165141>

**Glucocorticoids link forest type to local abundance in tropical birds**

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## Abstract

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

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

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

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

**Keywords: macrophysiology, stress physiology, corticosterone, selective logging, forest disturbance, understory bird, tropical rainforest**

## Introduction

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

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

Predicting which species will suffer a decline in population after land-use change is an important but difficult challenge for ecological and conservation scientists. One way to overcome such issues is to quantify the physiological state of individuals under the assumption that individuals' physiological response to changing environmental conditions underlies population viability (Fefferman & Romero 2013; Madliger & Love 2015; Wikelski

& Cooke 2006). The disciplines of macrophysiology and of landscape physiology focus on the variation of physiological traits over time and space with the aim to unravel the causal link between physiological changes and population ecology across different habitats or the same habitats with different degrees of human disturbance (Chown & Gaston 2008; Chown & Gaston 2016; Ellis, McWhorter & Maron 2012). Estimates of local abundance inform us that a given population is at risk only after it has already declined. In contrast, markers of physiological state might (i) have a higher predictive power about the effects of environmental changes on wildlife and (ii) provide a cause-effect relationship between environmental change and fitness outcomes (Cooke *et al.* 2013; Madliger *et al.* 2018).

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

Coping with environmental changes can be energetically expensive for organisms and requires physiological acclimatisation (Messina *et al.* 2018; Vitousek, Jenkins & Safran

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

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

Key unexplored questions are whether variation in fCORT levels is associated with forest type and/or with differences in local abundance of birds between unlogged old-growth

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

## **Material and Methods**

### **Study area**

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



The fieldwork was carried out in three unlogged old-growth forest plots, located within the DVCA (4°57045.2"N, 117°48010.4"E), and in three forest plots that have been logged twice (1987-1991 and 2001-2007) within the US-MFR (4°57042.8"N, 117°56051.7"E; Fig. 1). Logging occurred at high rates of timber removal (145m<sup>3</sup>/ha, Fisher *et al.* 2011), and the last logging rotation occurred about 10 years prior to the study, leaving a heavily disturbed recovering forest.

#### **Data collection and study species**

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

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

Understory birds are highly sedentary residents and forage predominantly in the lower stratum of the forest. All study species are either fully or partially insectivorous (del Hoyo *et al.* 2019; Wilman *et al.* 2014; Supplementary Table S2). The timing of the moult in the differing study species remains to be clarified, but likely occurs throughout the year (Mulyani *et al.* 2017). Reproduction occurs opportunistically throughout wide reproductive windows (del Hoyo *et al.* 2019; more information about seasonal reproductive windows in Supplementary Table S2).

Two tail feathers (outer rectrices) were plucked from each study bird that had completed the moult of juvenile plumage (hereafter adults). Following an aging system for tropical birds based on moult cycles (Johnson *et al.* 2011; Wolfe, Ryder & Pyle 2010), we considered as 'juvenile' birds in active pre-formative moult or in formative (pre-basic) plumage. We did not encounter any birds with known or distinguishable alternate plumage. Feathers were stored in individual paper envelopes at room temperature. Each bird was marked with a unique numbered metal ring to enable individual recognition. Data on body moult were collected at the time of capture; individual birds were assigned scores from 0 to 4

on the base of the moult of contour feathers, following the protocol of DeSante *et al.* (2015) (i.e., 0 = none: no body moult, 4 = heavy: > than 2/3 of all contour feathers are moulting).

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

### **Feather corticosterone measurements**

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

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

### **Statistical analysis**

To assess relationships between fCORT, forest type and year of sampling, we ran linear mixed models (LMMs) for each species (Table 1), separately, using SPSS Statistics 23. We chose to run LMMs separately by species because it is still unclear the extent to which fCORT levels are comparable among different species (Romero & Fairhurst 2016). Models included Forest type (2 levels) and Year (3 levels) as fixed factors. Plot was included as a random factor to control for possible variability due to local topographic/environmental differences within each forest type. Transect nested within Plot was removed from the models due to overfitting. The factor individual was not included in the models because we only had seven or fewer birds with more than one measurement between years per species. The

inclusion of individual identity as random factor in preliminary tests did not change the outcomes because it had a residual variance ranging from  $1.09 \pm 0.22$  (estimate  $\pm$  SE) to close to zero. For these recaptured individuals, the coefficient of variation of fCORT across years was actually large (46.45% on average), showing low individual consistency across seasons (Supplementary Table S7). Significance threshold of LMMs was set at  $P < 0.05$  (results in Table 1). For each model, Shapiro-Wilk test of residuals were performed to check normality; heteroscedasticity was assessed by plotting residuals vs. fitted values (Zuur, Ieno & Elphick 2010). Data were log-transformed ( $\log_{10} + 1$ ) when model residuals did not meet the normal distribution, then normality was tested again. We also tested for potential differences in body moult state between unlogged and logged forest through Mann-Whitney Test and we found no differences (Supplementary Table S8).

Then, two different linear mixed models were performed to test whether the differences in fCORT between co-specific populations were related to their difference in abundance between unlogged and logged forests. To do so, first, we used means, standard deviations and sample sizes to calculate annual Hedges'  $g$  effect sizes for each comparison of fCORT between co-specific populations living in unlogged and logged forests. Standardized effect sizes are analytical tools helpful to compare magnitude and direction of biological patterns and to assess the relevance of weak, but biologically important effects (Garamszegi 2006). Effect sizes were calculated using the *compute.es* package (Del Re 2013) in R (R Core Team 2013). The Hedges'  $g$  effect size measures how much one group differs from another, accounting for small sample sizes (Cooper, Hedges & Valentine 2009). Following Cohen (1988), effect sizes can be considered small (Hedges  $g = 0.2$ , explaining 1% of the variance), intermediate (Hedges  $g = 0.5$ , explaining 9% of the variance) or large (Hedges  $g = 0.8$ , explaining 25% of the variance). In our case, positive effect size estimates indicate that fCORT in a given species is higher in logged than in unlogged forest. Second, annual

species' capture numbers for each type of forest were combined to estimate the Relative Population Abundance (RPA) Index as follows:  $[(\text{abundance in logged forest} - \text{abundance in unlogged forest}) / (\text{abundance in logged forest} + \text{abundance in unlogged forest})]$  (Supplementary Table S4). The RPA Index is positive for species with higher abundance in logged forest and negative for species with higher abundances in unlogged forest. Abundance data were corrected for sampling effort  $[\text{Number of captures} / (\text{Expected Effort (nets*hours)})]$ . Recaptured individuals were included in the abundance counts because recapture rates were low (mean recapture rate across species: 0.16 individuals) and similar between unlogged and logged forests (mean frequencies difference: 0.01). Moreover, preliminary models showed that outcomes were unchanged if recaptured individuals were included or not.

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

Given that interspecies data analysis may require accounting for phenotypic similarities due to common ancestry (Hansen & Martins 1996), we tested for a phylogenetic

signal of the species-specific RPA Index to assess whether a phylogenetically based statistical method was needed for our linear mixed models (Supplementary Material; Revell, Harmon & Collar 2008). The phylogenetic signals of the RPA Index measured as overall between years, and separately for each year were low and not statistically different from 0 (Supplementary Table S9). Thus, in accordance with previous studies (Blomberg & Garland 2003; Rheindt, Grafe & Abouheif 2004), we did not include phylogeny in our multispecies model.

## Results

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

The linear mixed model performed to explore the within-year relationship between fCORT and RPA Index showed a significant increase of negative RPA Index in 2018 compared to 2016 (LMM: estimate $\pm$ SE = -0.32 $\pm$ 0.11,  $P < 0.01$ ), indicating that certain species switched their relatively higher population abundance from selectively logged forest (positive RPA Index) to unlogged forest (negative RPA Index). The interaction between fCORT and year was also significant (Table 2); in 2016 and 2018, species with relatively higher fCORT in unlogged forest (negative effect size) were relatively more abundant in logged forest (positive RPA Index) in the same year; in 2017, species with relatively higher

fCORT in logged forest (positive effect size) were also relatively more abundant in logged forest (positive RPA Index; Fig. 3).

Finally, in the linear mixed model performed to explore if fCORT at year ( $x$ ) predicted RPA Index of the following year ( $x+1$ ), we found a significant negative relationship between fCORT and RPA Index (LMM: estimate $\pm$ SE =  $-0.21\pm0.07$ ,  $P = 0.01$ ; random factor species: variance $\pm$ SE =  $0.002\pm0.05$ ; Fig. 4). Specifically, higher concentrations of fCORT for the species within a given forest type, as compared to the other type of forest, at year ( $x$ ), were associated with lower population abundance of that same species the following year ( $x+1$ ), within the same forest type. The opposite trend was found for relatively lower concentrations of fCORT.

## Discussion

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



biomarker to assess and predict the population responses of tropical non-migratory understory birds to environmental changes.

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

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

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

Population dynamics can be affected by changes in survival, reproductive success and immigration/emigration. Carry-over effects of higher fCORT concentrations are negatively correlated with survival and reproduction. For example, harlequin ducks (*Histrionicus histrionicus*) show negative correlation between CORT levels in back feathers moulted pre-breeding and reproductive decision (Hansen *et al.* 2016). Similarly, in northern common eiders (*Somateria mollissima borealis*) an increase in fCORT following a disease outbreak had indirect negative effects on reproduction and survival the following breeding season, which occurred approximately nine months later (Harms *et al.* 2015). Although we did not

find any study investigating the link between CORT, dispersion and habitat quality, it is probable that particularly stressed individuals are more prone to emigrate in search of better conditions (Massot & Aragon 2013). In our study, bird species are resident and opportunistic breeders (del Hoyo *et al.* 2019; Mulyani *et al.* 2017). Thus, a reduced local abundance might indicate lower survival or reproductive success of low-quality individuals (possibly having higher fCORT) rather than dispersion toward habitats of higher quality.

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

Seasons prior to fieldwork in 2016 and 2017 were affected by El Niño-Southern Oscillation (ENSO) events. ENSO events are composed by the El Niño warming phase and La Niña cooling counterpart. Compared to 2018 and to the average values in the last thirty years, the weather conditions (mean temperatures and total rainfalls) in the study area were substantially warmer and drier in 2016 and less warm but rainier in 2017 (climate data of DVCA provided by South East Asia Rainforest Research Partnership). Such extreme changes in weather conditions affect CORT production in vertebrates (Romero & Wikelski 2001;

Wingfield *et al.* 2018). We found that fCORT levels for 2016 and 2017 were significantly lower than in 2018 for seven bird species out of ten (Fig. 2). It is possible that the prolonged situation of stress due to unpredictable climatic events induced a dampened HPA-axis activity, with consequent decrease in CORT production, probably because too energetically demanding to sustain (Angelier & Wingfield 2013; Hau *et al.* 2010; Wingfield & Sapolsky 2003). Further studies are needed to clarify the link between CORT production and direct (e.g., rainfall, temperature, or wind) and indirect (e.g., food availability) effects of weather conditions.

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

The RPA Index in our study can be considered indicative for relative population density, with some limitations. For example, we have no information on factors that may affect species density estimation based on mist-netting data, such as species' home ranges and patterns of movement (Efford *et al.* 2016) in logged forest compared to unlogged. We found significant within-year relationships between fCORT and RPA Index, indicating that production of CORT might also reflect the current conditions in the forests. The cause of these relationships between fCORT and RPA Index is currently unknown, but it might be that

annual variation in local relative densities of birds affected the HPA axis activity. Future studies will need to estimate the local density of species to test the extent to which this could be one route through which CORT production affects population size.

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

## **Acknowledgements**

We thank the University of Antwerp, the FWO (Fonds Wetenschappelijk Onderzoek, PhD fellowship 1140117N; Travel grant V409218N), the EMBO (Short-Term Fellowship 7470) and the Leopold III (Fonds voor Natuuronderzoek en Natuurbehoud) for supporting and funding S.M. VM was supported by a Marie Skłodowska-Curie Individual Fellowship (704582). Further funding was provided by MNHN (ATM 2018) and CNRS to DC. We thank Tanith Hackney, Jessey Chai Yee Wei, Ezron Gerald, Chong Yi Yao, Tan Chen Hong, Rayzigerson Rodney Chai, Amy Donnison, Sylwia Zbijewska, Rose Fogliano, Patrick Cannon, Mike Kaputa, Cheoh Chuan Ong, Luke Nelson, Anna Lello-Smith, Lucas Pavan and Beth King for their valuable assistance with fieldwork. We thank Berry Maletzky for

assistance with laboratory analysis. We thank Michael O'Brien (SEARRP) for providing us climate data of DVCA and Raoul Van Damme for his personal explanations about phylogenetic analysis.

#### Authors' contributions

- SM, DC, DE conceived the ideas and designed methodology;
- DC, DE, ME, VC, SB coordinated different phases of the study;
- SM, CC, ST, DC, DE collected samples;
- SM, VM, VC performed laboratory analyses;
- SM analysed the data;
- SM led the writing of the manuscript;

All authors contributed critically to the drafts and gave final approval for publication.

#### Data Accessibility

Data are deposited in the Dryad Digital Repository: <https://doi.org/10.5061/dryad.w3r2280n3> (Messina et al. 2020).

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

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

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

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

## Figure Captions

Figure 1 – (a) Danum Valley Conservation Area in the Malaysian state of Sabah, Borneo (b) The green area corresponds to the Yayasan Sabah logging concession, and the yellow area corresponds to the Danum Valley Conservation Area and Palum Tambun watershed reserve. (c) Distribution of study plots between unlogged forest (square symbols) and selectively logged forest (triangular symbols); grey areas are plantations.

Figure 2 – Seven out of 10 understory bird species showed significant among year variation in fCORT. Least square means  $\pm$  standard error of the mean fCORT levels of each sampling year are shown. Different superscripts (a and b) represent significant differences ( $P < .05$ ). Note that only those cases where post-hoc tests were run are shown.

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

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

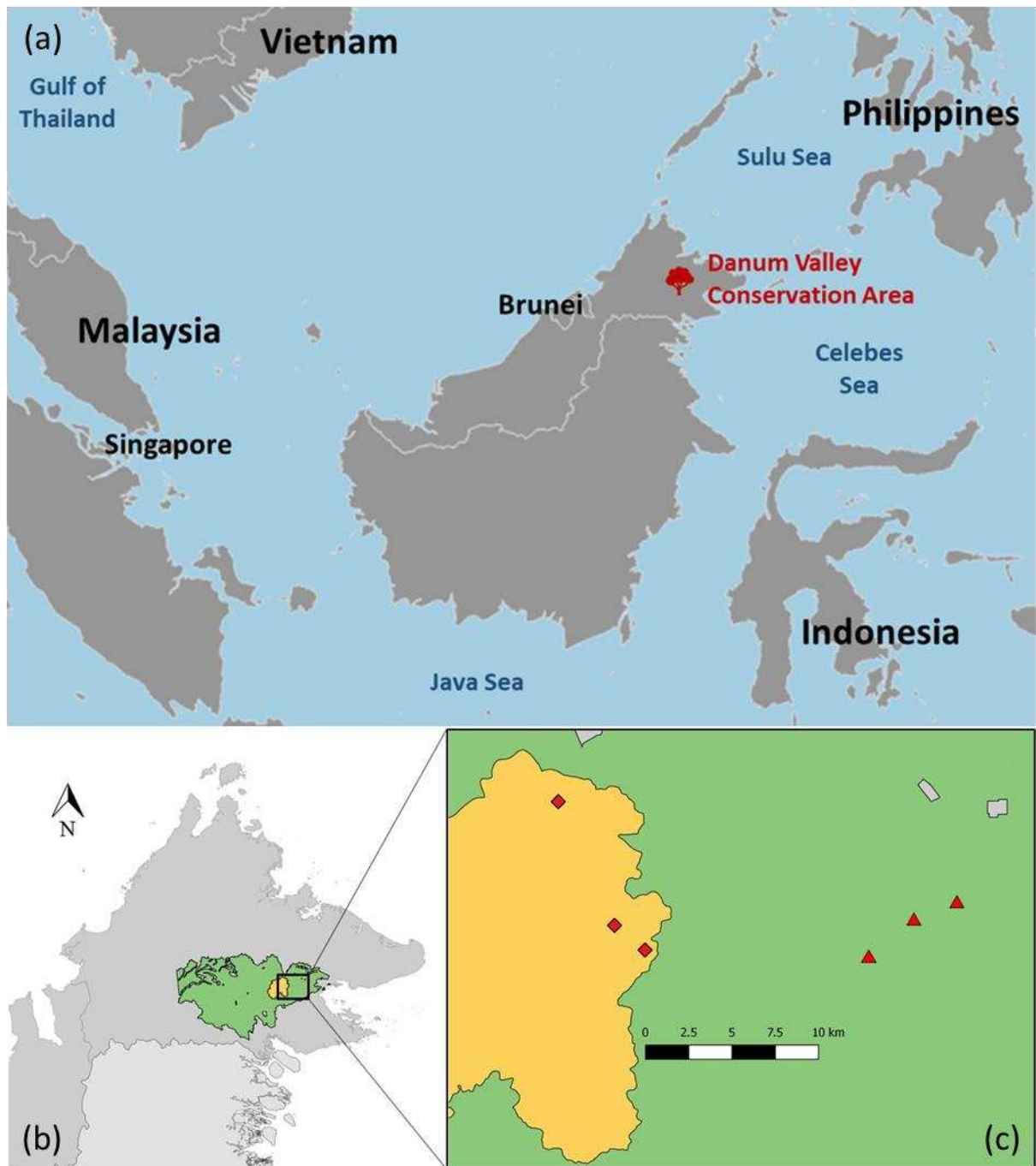


Figure 1

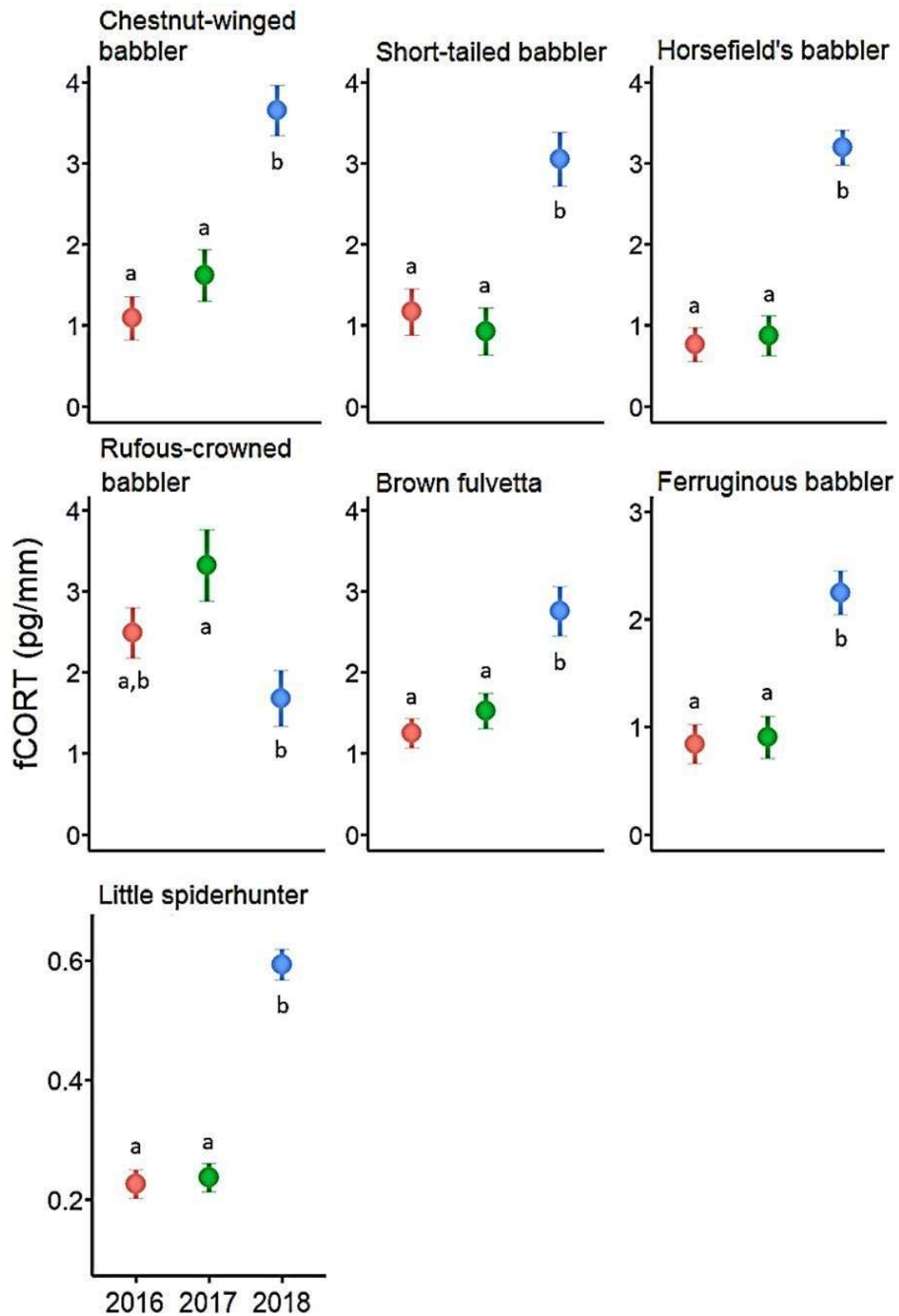
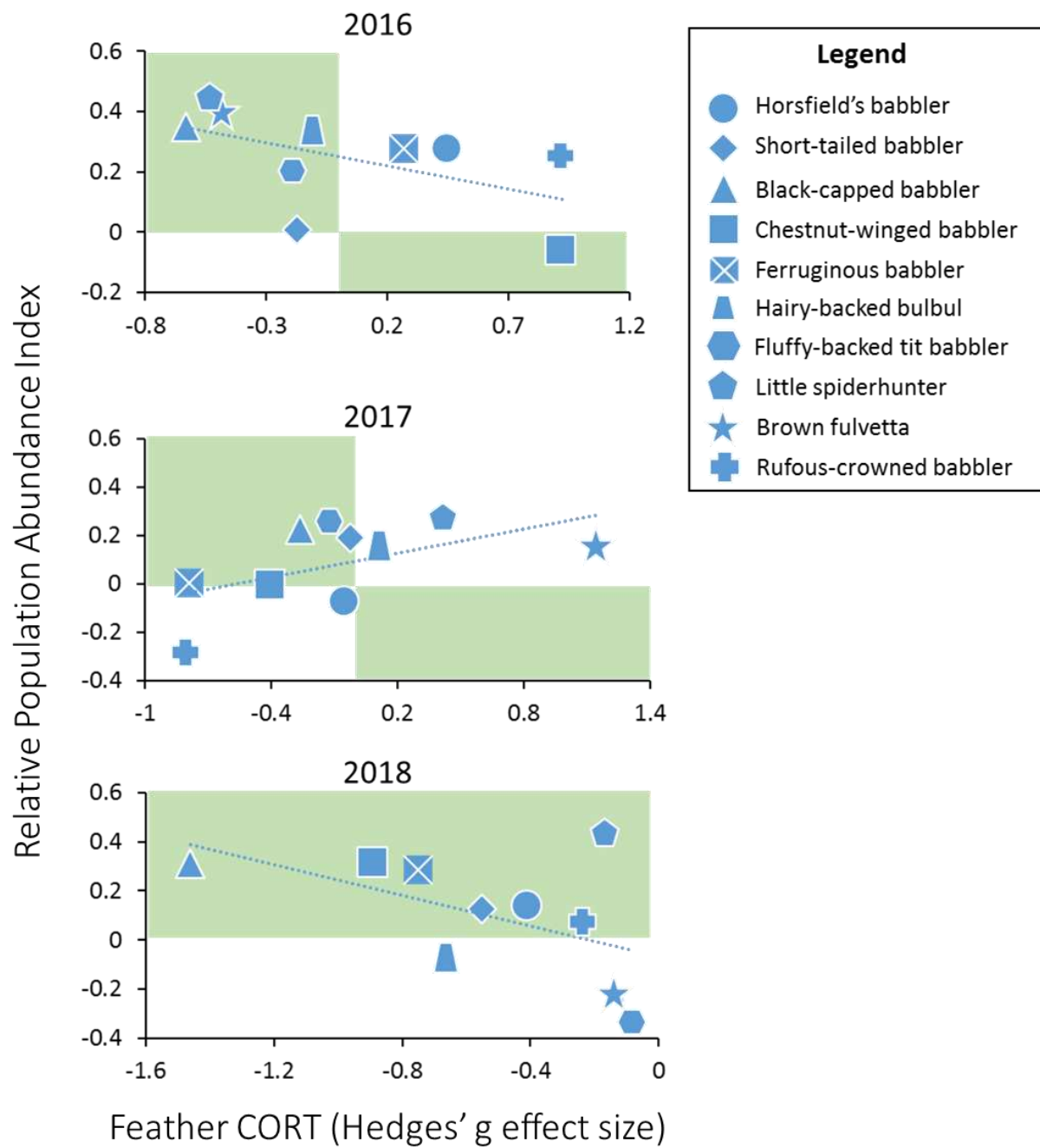


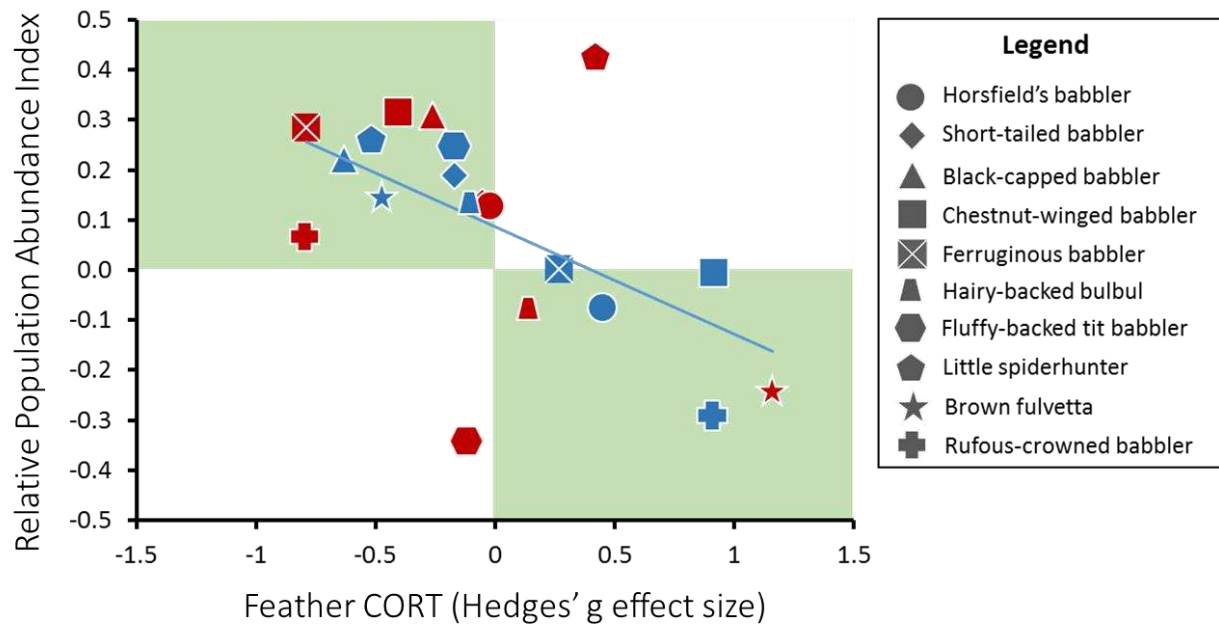
Figure 2



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775 Figure 3





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777 Figure 4