

# Understory avifauna exhibits altered mobbing behavior in tropical forest degraded by selective logging

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**Abstract** In understanding the impacts of selective logging on biodiversity, relatively little is known about the critical behavioral link between altered forest conditions and population persistence. Predator-mobbing is a widespread anti-predator behavior in birds that expresses a well-known trade-off influencing prey survival under predation risk. Here, we ask whether the predator-mobbing behavior of understory forest birds is altered by selective logging and associated forest structural changes in the highly endangered lowland rainforest of Sumatra. At four study sites spanning a gradient of logging-induced forest degradation, we used standardized mobbing and owl call playbacks with predator model presentation to elicit the predator-mobbing behavior of understory prey birds, compared birds' mobbing intensity across sites, and related variation in this intensity to forest vegetation structure. We found that selective logging altered birds' predator-mobbing intensity (measured by behavioral conspicuousness and propensity to approach the predator) as well as forest structure, and

that vegetative changes to canopy and understory were correlated with contrasting responses by the two major bird foraging guilds, gleaning versus flycatching birds. We additionally discuss the implications of our findings for further hypothesis testing pertaining to the impacts of selective logging on the ecological processes underlying prey-mobbing behavior, particularly with regards to predator-prey interactions and prey accrual of energy reserves.

**Keywords** Birds · Foraging guild · Habitat change · Playback · Sumatra · Understory

## Introduction

As a major form of forest use worldwide and particularly in the tropics, selective logging causes structural and biological alterations to forest habitat on a vast scale (Burivalova et al. 2014; Edwards et al. 2014). Understanding the impacts of selective logging on tropical forest biodiversity is of critical importance to informing conservation strategies (Putz et al. 2001; Edwards et al. 2011). While the patterns of how species richness and community composition respond to selective logging are relatively well understood (for reviews, see Barlow et al. 2007; Gibson et al. 2011; Burivalova et al. 2014; Edwards et al. 2014), we are yet to obtain a good understanding of how ecological processes that underlie these patterns are altered in selectively logged forests (Morris 2010). Limited evidence suggests that selective logging can influence a number of ecological processes important to biodiversity persistence across levels of biological organization, from reproductive rates at the species level (Srinivasan et al. 2015) to various forms of species interactions involving diet (Woodcock et al. 2013; Edwards et al. 2013), predation rates (Ewers et al. 2015),

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seed dispersal (Schleuning et al. 2011; Slade et al. 2011; Ewers et al. 2015), and pollination (Carneiro et al. 2011; Schleuning et al. 2011). However, empirical evidence generally remains scarce, particularly considering the breadth of ecological processes that are important to biodiversity persistence. Filling this knowledge gap is of high scientific and applied significance because it holds the key to identifying the mechanisms of logging-induced biodiversity changes.

Behavior is a key translational link between habitat conditions and the persistence of animal individuals and populations; it is, therefore, an important category of ecological process for which the impacts of selective logging warrant better understanding (e.g., Lonsdorf 2007; Castro-Arellano et al. 2009). Mobbing is a widespread behavior across multiple animal taxa, particularly fish, birds and mammals (Altmann 1956; Curio et al. 1978; Pitcher et al. 1986). In its typical form, it happens under risk-related situations, and involves the joint inspection, and often assault, by prey on predators or nest parasites (Altmann 1956; Curio et al. 1978; Krams et al. 2006). In forest birds, a common form of mobbing is a multi-species congregation of excitedly vocalizing individuals with conspicuous visual displays directed at a focal predator, and is elicited by cues pointing to the predator's presence and/or activity status (Hurd 1996; Sieving et al. 2004). At the individual level, predator-mobbing behavior of forest birds can depend on multiple factors related to the predator (e.g., identity, abundance and activity status; Gehlbach and Leverett 1995; Sandoval and Wilson 2012), prey (e.g., identity and breeding status; Hurd 1996; Berziņš et al. 2010) and local habitat (e.g., vegetation structure; Hendrichsen et al. 2006). Considering that selective logging can change the profiles of the predator and prey communities (Jullien and Thiollay 1996; Dunn 2004; Barlow et al. 2007; Carrete et al. 2009) and habitat conditions (Thiollay 1992; Hardus et al. 2012) in tropical forests, it is likely that avian predator-mobbing behaviors are sensitive to the impacts of selective logging. However, empirical evidence of such impacts remains nonexistent.

Understanding the impacts of selective logging on predator-mobbing behavior can potentially inform the mechanisms of biodiversity change caused by selective logging. Predator-mobbing behavior is the expression of an underlying cost–benefit trade-off for prey survival under predation risk. It is thought to reduce prey vulnerability to predation risk by harassing, harming or driving predators away and/or reducing the efficacy of predators' future hunting success through improved information about predator location and status (Dugatkin and Godin 1992; Caro 2005; Graw and Manser 2007). Mobbing may have other benefits such as teaching offspring about predators (Graw and Manser 2007) and/or advertising participants' social status (Arnold 2000). On the other hand, predator-mobbing can incur

costs in the form of energy expenditure (Collias and Collias 1978), foregone time spent on fitness-enhancing activities such as foraging (Dugatkin and Godin 1992), and possible predation from the target predator (Denson 1979; Curio and Regelmann 1985; Sordahl 1990) or other predators foraging nearby (referred to as “ambient predators” in this study; Sordahl 1990; Ostrow 2006). Therefore, alterations in predator-mobbing behavior should signal alterations in one or more of the various aspects of this cost–benefit trade-off, all of which are known to be related to prey fitness. For this reason, understanding how and to what extent prey birds' mobbing behavior is altered by selective logging may illuminate fertile avenues for hypothesis testing regarding these underlying, fitness-related ecological processes (e.g., energetic reserves, predator–prey encounter patterns, habitat-mediated risk perception; reviewed above) that could aid in understanding and mitigating biodiversity changes in logged forest.

Here, we ask whether the predator-mobbing behavior of understory forest birds is altered by selective logging and associated forest structural changes in the lowland rainforest of Sumatra, a critically endangered component of the species-rich Sundaland lowland rainforest ecosystem threatened by selective logging and land conversion (Lambert and Collar 2002; Hua et al. 2011; Edwards et al. 2011). At four study sites spanning a gradient of logging-induced forest degradation in Sumatra, we used standardized playback methods to elicit the predator-mobbing behavior of understory forest birds. We measured prey birds' mobbing intensity at the community level to compare across sites, distinguishing between the guilds of gleaning and flycatching species, and related variation in this intensity to forest vegetation structure. We additionally discuss the implications of our findings for further hypothesis testing.

## Materials and methods

### Study site

Our study involved one primary forest site and three degraded, post-logging forest sites (“DEG1, 2, 3” hereafter). The primary forest site was located in the Way Canguk Biological Station inside the Bukit Barisan Selatan National Park in Lampung Province (5°39'S, 104°24'E, 30–60 m a.s.l.). The 900-ha Way Canguk Biological Station is the last sizable patch of primary lowland rainforest in Sumatra; a big part of its dipterocarp-dominated forest remains in generally intact condition (O'Brien and Kinnaid 1996). DEG1-3 were within the Harapan Rainforest Ecosystem Restoration Project in Jambi Province (2°08'S, 103°22'E, 50–80 m a.s.l.), which at the time of the study covered 98,554 ha of post-selective logging, secondary

lowland rainforest in varying stages of regeneration (Hua et al. 2011). Judging from canopy height, DEG1 was the least degraded with medium-to-high canopy while DEG3 the most degraded with mostly low canopy; the three sites were spaced  $\geq 2$  km apart. The Way Canguk Biological Station was not the ideal baseline to compare with the Harapan Rainforest because it is  $\sim 600$  km away, but it was the only candidate for the study because of the near-complete absence of intact lowland forest remaining in Sumatra. Additionally, we tried to maximize the validity of our cross-site behavioral comparisons by conducting them within species occurring across all study sites (see below).

### Study design

At each study site, we delineated a 125 ha ( $1000 \times 1250$  m) plot with 30 sampling points spaced 250 m apart at which we conducted standardized playbacks to elicit the predator-mobbing behavior from understory forest birds. For each playback, we used visual and auditory cues to simultaneously mimic the presence of (1) a perched Sunda Scops-owl *Otus lempiji*, a major predator for small-bodied forest birds in lowland Sundaland (MacKinnon and Phillips 1993) and a known target of avian mobbing (F.H. pers. obs.) and (2) an ongoing mobbing event targeted at this predator. We recorded two measures of the intensity of mobbing behavior during playback, and measured two aspects of vegetation structure that we considered most influential on birds' mobbing intensity. We conducted all mobbing playbacks between 08:30 and 13:00 on days without rain or strong wind. To disentangle the relationship between avian mobbing intensity and logging-induced habitat change, we controlled for the effects of other confounding factors in three ways. (1) We conducted fieldwork in a short time span to avoid potential effects of seasonality: mid-late June and early-mid July of 2011 for Harapan Rainforest and Way Canguk Biological Station, respectively. (2) We set up playbacks at standardized microenvironments to minimize the influence of immediate vegetation structure on avian mobbing behavior (see below). (3) We accounted for the effects of several remaining nuisance factors (e.g., time of day) in statistical analyses (see below).

To mimic the presence of the Sunda Scops-owl, we used a wooden model of the owl in perched posture (Online Resource Appendix 1 Fig. A1) and a 74-s recording of the species' territorial vocalization; these cues provided the focal point toward which prey birds directed their mobbing behaviors (Chandler and Rose 1988). To mimic an ongoing mobbing event targeted at this predator, we used a 28-s recording of simultaneous mobbing vocalizations of five small-bodied understory bird species present at all of our study sites. Adding this stimulus, which was recorded at a naturally occurring mobbing event in the general region,

was important because it represented redundant social information about the predator being mobbed and served to strengthen prey birds' behavioral responses (Sandoval and Wilson 2012). We put both recordings on 10-min loops (see Online Resource Appendix 1 for more details on the recordings).

We expected that the way in which selective logging influenced birds' predator-mobbing intensity should depend on birds' foraging technique, which determines birds' general activity patterns and in part defines vigilance rates and other aspects of predation avoidance (Lima 1993; Martínez and Zenil 2012). The two dominant foraging techniques exhibited by understory birds are gleaning (picking food off nearby substrates) and flycatching (making short flights to capture moving/distant prey). Gleaning birds rely on intensive search of substrates for food that compromises their ability to scan for predators (visual vigilance), putting them at a disadvantage in early detection of threats; they also typically rely on escape into obstructive cover as their primary anti-predator strategy (Lima 1993). In contrast, flycatching birds rely on frequent scans of surrounding space for prey which simultaneously allows scan-based vigilance; they thus typically rely on pre-emptive predator detection and when escape is needed, utilize aerial maneuvers rather than obstructive cover (Lima 1993). The predation aspect in prey birds' cost-benefit trade-off during mobbing (i.e., the benefit of avoiding future predation from the focal predator, and the cost of immediate predation from the focal and ambient predators), particularly in relation to changed forest structure caused by selective logging, may thus take different forms for gleaning versus flycatching birds. For this reason, we analyzed birds' mobbing intensity on the level of ecological guilds defined by the gleaning versus flycatching foraging technique.

### Playback protocol

Within 10 m of each sampling point, we first chose a location that met three qualitative criteria for vegetation structure to set up the playback system: (1) canopy within a 15-m radius was generally closed, (2) there was perching substrate within a 3-m radius in the understory (1–5 m above ground), and (3) vegetation within a 10-m radius was not too dense and thus allowed for field observation. We then set up the owl model and a camouflaged speaker for the owl vocalization on top of a 3-m pole, making sure the model was not covered by vegetation. We set up another camouflaged speaker for mobbing vocalizations in vegetation 1–2 m away from the pole at  $\sim 2$  m above ground facing the owl model. We connected each speaker via extension cords to an iPod player and controlled them remotely. We demarcated 3- and 15-m distance bands from the owl model in four ordinal directions with color ribbons to

**Table 1** Aspects of mobbing behavior scored during focal sampling to quantify mobbing conspicuousness

| Behavioral measure                   | Aspect of scoring           | Definition   | Score range                    |
|--------------------------------------|-----------------------------|--|--------------------------------|
| Mobbing conspicuousness <sup>†</sup> | Movement                    | Frequency of body movement (perch changes and flights)                           | 0, 1, 2, or 3                  |
|                                      | Flicking                    | Frequency of wing- and tail-flicking   | 0, 1, 2, or 3                  |
|                                      | Vocalization                | Frequency of vocalization (all types)  | 0, 1, 2, or 3, +1 <sup>§</sup> |
|                                      | Other activity <sup>¶</sup> | Frequency of other behaviors (preening and foraging)                             | 0, 1, 2, or 3                  |
|                                      | Overall score               | Tallied score across all five measures, assuming equal weight of scoring aspects | 0–15                           |
| Approach propensity <sup>‡</sup>     | Proximity                   | Whether focal individual approached to within 3 m of the model                   | 0 or 1                         |

<sup>†</sup> Scores for each conspicuousness aspect involve integers between 0 and 3 representing zero frequency (i.e., behavior did not occur), low frequency (i.e., behavior occurred occasionally), medium frequency (i.e., behavior occurred relatively frequently), and high frequency (i.e., behavior occurred incessantly), respectively

<sup>§</sup> An additional score was added to the Vocalization score if the focal individual produced harsh scolding calls during the focal sampling, as we assumed this would enhance the conspicuousness of the scolding individual

<sup>¶</sup> Behaviors under this category are not typical mobbing behaviors, but involved body movements that should increase individual's conspicuousness

<sup>‡</sup> Score for approach propensity involves integers of 0 and 1, representing birds' approach distance to playback center as >3 m (0) and ≤3 m (1)

provide visual aid for behavioral data collection, and designated the spherical space within 3 m of the owl model and the cylindrical space within a 15-m radius of the owl model as the 3- and 15-m scales, respectively. After setting up the playback system, we retreated to 10 m away from the owl model, waited for 2 min, and conducted playbacks for 10 min. We fixed the playbacks at natural and undistorted volumes to our ears at a 10-m distance.

### Measuring mobbing intensity

We focused on understory forest birds, defined in our study as non-raptorial bird species whose activities are predominantly below the forest canopy, according to field guides of the region (Smythies 1981; MacKinnon and Phillips 1993; Jeyarajasingam and Pearson 1999). We considered birds attracted to within the 15-m scale as exhibiting mobbing behavior, on which we quantified mobbing conspicuousness and approach propensity as the two measures of mobbing intensity. To measure mobbing conspicuousness, we conducted focal sampling of opportunistically chosen individuals for 2 min or until they were lost from view, trying our best to avoid double observing the same individuals. We scored five aspects of behavioral conspicuousness including frequency of movement and vocalization (Table 1; Chandler and Rose 1988), and tallied scores across all aspects to form a composite conspicuousness score. Although the length of focal spans differed among birds due to the opportunistic nature of focal sampling, we expected no systematic bias in scores across study sites. F.H. took all conspicuousness scores. We quantified individual birds' approach propensity as their likelihood of approaching the owl model to within the 3-m scale given that they participated in mobbing. To do this, for each

species at each sampling point, we counted the largest number of individuals that at any time during the playback came within the 15-m (denoted as  $n_{15}$ ) and 3-m (denoted as  $n_3$ ) scales, respectively. For the purpose of using individual birds as the unit of statistical analysis (see below), for each species at each sampling point, we assigned  $n_3$  individuals to the status of having entered the 3-m scale. Two different field assistants with comparable ornithological skills assisted F.H. in conducting these counts at Way Canguk Biological Station and Harapan Rainforest, respectively; independent counts made by F.H. and assistants were discussed and cross-checked for inconsistencies immediately after each playback (see Online Resource Appendix 2 for more details on mobbing intensity measurement).

### Measuring vegetation structure

We measured two aspects of forest structure that are likely to be influential on understory birds' mobbing behavior: canopy cover and understory density. A more open canopy may render birds more susceptible to aerial attacks from ambient predators (Carrascal and Alonso 2006; Castro-Arellano et al. 2009), while a denser understory may increase obstructive cover with contrasting consequences for prey detection of or escape from the focal and ambient predators (Lazarus and Symonds 1992; Sieving et al. 2004). These two aspects of forest structure could thus influence birds' mobbing intensity by potentially changing the predation aspect in birds' cost–benefit trade-off during mobbing (Dugatkin and Godin 1992), and may likely influence gleaning and flycatching birds differentially because of the different anti-predator strategies of these two guilds. At each sampling point, we set up two concentric circular plots with a 5- and 10-m radius, respectively.

We measured percentage canopy cover at plot centers with a type-A densiometer, and measured understory density at heights relevant to avian mobbing activities (3, 4, and 5 m above ground) using a  $1 \times 1$  m “density” board divided equally into 36 cells (after Nudds 1977). Further details on vegetation structure measurement are provided in Online Resource Appendix 3.

### Statistical analysis

We assigned mobbing species to gleaning versus flycatching guilds based on field guides for the region (Smythies 1981; MacKinnon and Phillips 1993; Jeyarajasingam and Pearson 1999) and our field experiences (see Online Resource Appendix 4 for further details of guild assignment), and conducted all analyses on the guild level. The identity and number of mobbing birds differed across study sites (see Results), and this could confound the interpretation of the potential difference in mobbing intensity when the analyses were conducted on the guild level. We thus constructed a standard pool of individuals for each guild that had identical species composition across study sites, and only included individuals in these pools for analyses. To construct the standard pools, we identified, for each species, the lowest number of individuals across the four study sites denoted as “ $n_L$ ”, and drew  $n_L$  individuals randomly without replacement from each site to include in the pool.

We used generalized linear mixed models (GLMMs) to analyze the variation of mobbing conspicuousness and approach propensity across the four study sites for the gleaning guild (Zuur et al. 2009). We considered individual birds in the species pools as the unit of analysis, with their conspicuousness score and approach propensity (measured as whether or not each individual entered the 3-m scale) as the response variables. For the mobbing conspicuousness score, we used Poisson error distribution and a log link function; for approach propensity, we used binomial error distribution and a logit link function. For fixed effects, the global models included the identity of study sites, and two nuisance covariates to statistically account for confounding factors of mobbing behavior: (1) the time of playback represented as the number of minutes since sunrise (centered and scaled), and (2) the number of bird individuals that entered the 3-m scale excluding the individual in question, as a proxy of the intensity of social information (Sandoval and Wilson 2012). For random effects, we included the identities of (1) study locations (Way Canguk Biological Station versus Harapan Rainforest), (2) sampling points, and (3) species because individuals sharing these factors likely behaved more similarly. For the flycatching guild, because of low sample size ( $N = 6$  and 9 per site for mobbing conspicuousness and approach propensity, respectively), we discarded the random effects and instead used

generalized linear models (GLMs) of the same fixed effects structure, with the recognition that this likely biased our analysis toward more significant results (see “Discussion”).

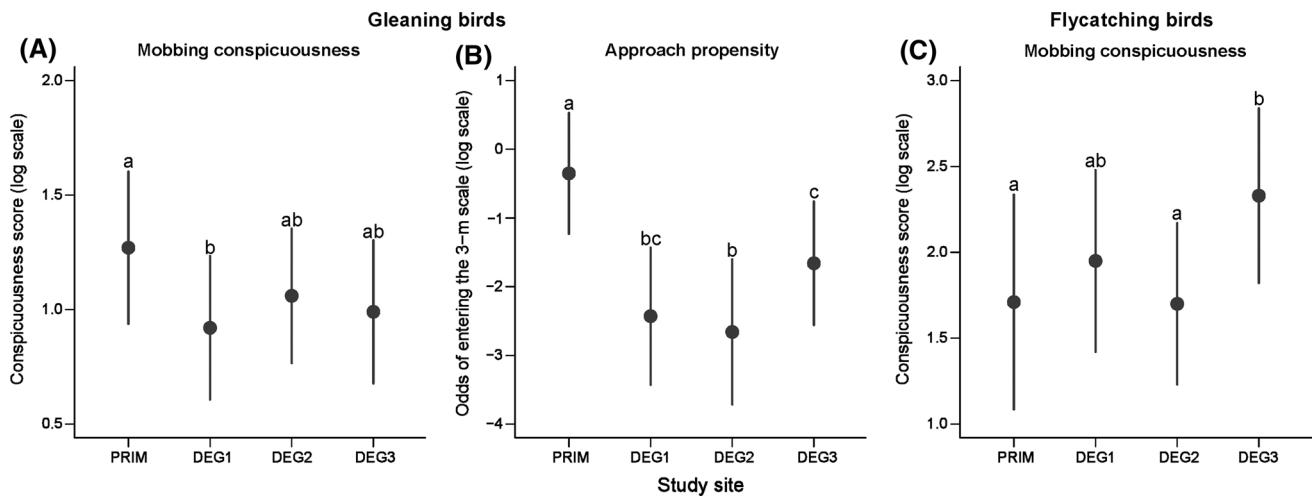
We used analysis of variance (ANOVA) to analyze the difference of canopy cover and understory density (both centered and scaled) across the four study sites. We further used GLMMs and GLMs, respectively, for the gleaning and flycatching guilds to analyze the relationship between avian mobbing intensity and vegetation structure, again using individual birds in the species pools as the unit of analysis and its conspicuousness score and approach propensity as response variables. For GLMMs and GLMs, we averaged vegetation measures across the eight adjacent neighboring points surrounding each sampling point (points at plot edges had fewer neighboring points) to characterize vegetation structure at a spatial scale more relevant to prey birds’ daily environment, as opposed to the exact sampling point where we conducted mobbing playbacks. We used the same global model structures for GLMMs and GLMs as above, but replaced the identity of study sites with the two measures of vegetation structure, after confirming the lack of strong collinearity between canopy cover and understory density ( $r_{\text{Pearson}} = 0.36$ ,  $df = 114$ ,  $P < 0.01$ ).

For each analysis involving GLMMs/GLMs, we built a full set of sub-models based on the global model (i.e., using all combinations of candidate covariates), and used Akaike’s information criterion corrected for small sample size (AICc) to rank the models (Burnham and Anderson 2002). We accepted models from the lowest AICc until the cumulative model weight exceeded 0.95, and used this 95 % confidence model set as the basis for statistical inference using the “natural averaging” approach (Burnham and Anderson 2002). We conducted all analyses in R.3.0.2 (R Core Team 2013), with the packages “lme4” (version 1.0-4; Bates et al. 2015) for GLMM and “AICcmodavg” (version 1.33; Mazerolle 2015) for model selection and model averaging.

## Results

### Overall community response to mobbing playbacks

We elicited mobbing behavior from a total of 992 understory bird individuals belonging to 45 species at 101 sampling points ( $N = 30, 22, 24$ , and 25 for the primary forest site and DEG1-3, respectively; Online Resource Appendix 5 Table A5.1), and conducted focal sampling on 565 individuals belonging to 42 species. We were able to include 156 individuals belonging to 15 species in the analysis of mobbing conspicuousness, and 324 individuals belonging to 18 species in the analysis of approach propensity (Online Resource Appendix 5 Table A5.1).



**Fig. 1** Differences in the mobbing behavior of understory birds among study sites with different degrees of habitat degradation. “PRIM” refers to the primary forest site. **a** Behavioral conspicuousness ( $N = 33$  birds per site); **b** approach propensity ( $N = 72$  birds per site) of gleaning birds; **c** behavioral conspicuousness ( $N = 6$  birds

per site) of flycatching birds. Sites with statistically different intensities (the 95 % confidence interval of one site not overlapping with the mean of the site in comparison) are represented by different letters. Error bars represent 95 % confidence intervals

### Differences in birds’ mobbing intensity across study sites

Under standardized mobbing stimuli, gleaning birds exhibited weaker predator-mobbing behaviors in selectively logged forest compared with primary forest. Their mobbing conspicuousness was significantly lower at site DEG1 than at the primary forest site (Fig. 1a;  $N = 33$  per site, belonging to 11 species), and their approach propensity was significantly lower at all degraded forest sites (Fig. 1b;  $N = 72$  per site, belonging to 13 species) than at the primary forest site. We did not detect significant differences in gleaning birds’ mobbing conspicuousness or approach propensity among the selectively logged forest sites.

The evidence for flycatching birds exhibiting differential mobbing intensity between selectively logged and primary forests was weaker than in the case of gleaning birds. We found that birds’ mobbing conspicuousness was significantly higher at site DEG3, the most degraded of the selectively logged sites, than at the primary forest site and site DEG2 (Fig. 1c;  $N = 6$  per site, belonging to four species). We detected no significant difference in birds’ approach propensity among study sites ( $N = 9$  per site, belonging to five species). Information on model performance for both guilds is provided in Online Resource Appendix 6 Table A6.1.

### Relationship between birds’ mobbing intensity and vegetation structure

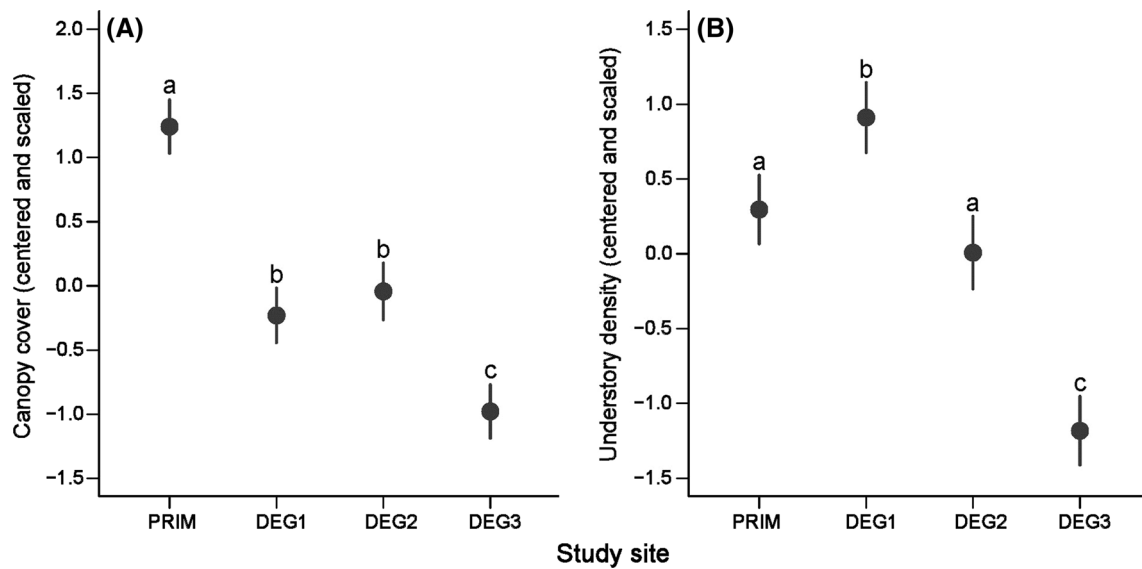
Forest structure significantly differed among sites of different degradation status. More degraded forests had

significantly lower canopy cover (Fig. 2a). While more degraded forest among the selectively logged forest sites had significantly lower understory density, the primary forest site had an intermediate understory density between DEG1 and DEG3 (Fig. 2b).

For both gleaning and flycatching birds, forest structure at least partially mediated the differences in birds’ mobbing intensity among study sites: we found strong relationships between vegetation structure and the mobbing intensity of both guilds (Table 2). Gleaning birds’ mobbing conspicuousness was positively related to canopy cover ( $N = 33$  per site, belonging to 11 species), while their approach propensity was negatively related to understory density ( $N = 72$  per site, belonging to 13 species). Flycatching birds’ mobbing conspicuousness was negatively related to canopy cover ( $N = 6$  per site, belonging to four species). Information on model performance for both guilds is provided in Online Resource Appendix 6 Table A6.2.

## Discussion

We found that in the lowland rainforest of Sumatra, understory birds exhibited altered predator-mobbing behavior in selectively logged forest compared with primary forest (Fig. 1). The two guilds distinguished by different foraging techniques, gleaning versus flycatching species, exhibited such behavioral alteration in contrasting ways (Fig. 1). Moreover, forest structure at least partially mediated the observed behavioral alteration, through its influence on birds’ mobbing behavior that again took contrasting forms



**Fig. 2** Differences in vegetation structure among study sites with different degrees of habitat degradation. “PRIM” refers to the primary forest site. **a** Canopy cover. **b** Understory density.  $N = 30, 22, 24,$  and  $25$  for PRIM, DEG1, DEG2, and DEG3, respectively. Sites with sta-

tistically different vegetation measures (the 95 % confidence interval of one site not overlapping with the mean of the site in comparison) are represented by different letters. Error bars represent 95 % confidence intervals

**Table 2** Model-averaged results of the relationship between avian mobbing behavior and vegetation structure

| Foraging guild | Mobbing measure     | $N$ per site <sup>†</sup> | Time                        | Group size                  | Canopy cover                | Understory density          |
|----------------|---------------------|---------------------------|-----------------------------|-----------------------------|-----------------------------|-----------------------------|
| Gleaning       | Conspicuousness     | 33                        | -0.01 (-0.13, 0.1)          | 0.03 (-0.02, 0.08)          | <b>0.15 (0.02, 0.29)</b>    | -0.09 (-0.22, 0.03)         |
|                | Approach propensity | 72                        | -0.11 (-0.48, 0.27)         | 0.01 (-0.17, 0.19)          | -0.08 (-0.66, 0.5)          | <b>-0.63 (-1.05, -0.21)</b> |
| Flycatching    | Conspicuousness     | 6                         | <b>-0.25 (-0.49, -0.01)</b> | <b>-0.22 (-0.35, -0.08)</b> | <b>-0.27 (-0.53, -0.01)</b> | -0.15 (-0.43, 0.12)         |
|                | Approach propensity | 9                         | -0.01 (-0.81, 0.79)         | -0.03 (-0.43, 0.37)         | -0.26 (-1, 0.47)            | -0.32 (-1.16, 0.51)         |

Table lists the slopes of covariates that according to multi-model inference predicted birds’ mobbing behavior, with their 95 % confidence intervals based on unconditional standard error shown in parenthesis. In bold are covariates with a significant effect (i.e., 95 % confidence interval not spanning zero)

<sup>†</sup>  $N$  per site refers to the number of bird individuals in the pools for each guild at each site

for gleaning versus flycatching guilds (Table 2). Predator-mobbing is a widespread behavior among forest birds that is induced by predation risk and fundamentally of an anti-predator nature (Altmann 1956; Curio et al. 1978). Its ubiquitous occurrence despite its myriad of potential costs (Dugatkin and Godin 1992) suggests that it is of considerable fitness value to prey. The finding that such a behavior is affected by selective logging thus highlights the impacts that selective logging could have on important animal behaviors and in general, ecological processes that may underlie the persistence of biodiversity in selectively logged forests (e.g., Castro-Arellano et al. 2009; see more below). Such impacts, unlikely to be captured by numerical measures of species richness and community composition,

remain an understudied yet potentially profound aspect of the ecological impacts of selective logging.

Predator-mobbing behavior is the expression of a cost-benefit trade-off for prey (Dugatkin and Godin 1992); the impact that it sustains from selective logging could thus be mediated through and suggests the impacts of selective logging on one or more of the underlying aspects for this trade-off. According to current understanding, predator-mobbing behavior is primarily driven by the need to reduce future predation from the predator targeted by mobbing, but is also constrained by its potential costs of energy expenditure, foregone fitness-enhancing activities, and risk of predation from the target and ambient predators (Curio and Regelmann 1985; Sordahl 1990; Dugatkin and Godin

1992; Caro 2005). Having accounted for a number of confounding factors, our finding of altered mobbing behavior in selectively logged forest suggests that one or more of the following aspects pertaining to the cost–benefit trade-off for mobbing prey may have been influenced by selective logging. As we discuss below, these aspects are all closely related to prey fitness and population persistence. The possibility that they are influenced by selective logging thus illuminates fertile avenues for further hypothesis testing that could more directly explore the mechanisms of logging impacts on biodiversity.

### Predation risk from the Sunda Scops-owl and ambient predators during mobbing

The potential predation during mobbing by the target predator (Sunda Scops-owl in our study) and other ambient predators represents a large potential cost for mobbing birds: their vulnerability to such predation risk is accentuated by the attention-focusing and conspicuous nature of their mobbing behaviors (Denson 1979; Curio and Regelman 1985; Sordahl 1990; Ostrow 2006). Altered avian mobbing intensity between selectively logged and primary forests may thus suggest altered predation risk as perceived by prey birds during mobbing. With respect to predation risk from the Sunda Scops-owl, although we standardized our playback conditions, the ease with which prey birds could pinpoint the owl (in the form of the owl model) may be different in selectively logged versus primary forests because of different vegetation structure (Hendrichsen et al. 2006). This could result in different predation risk from the owl as perceived by mobbing birds. On the other hand, variation in mobbing intensity between selective logged and primary forests may suggest associated variation among habitats in the ambient predation risk as perceived by mobbing birds during mobbing and in general, on a daily basis. Although direct empirical evidence is virtually nonexistent, there are good theoretical reasons to expect prey perception of ambient predation risk to be vulnerable to the impacts of selective logging. For one thing, as discussed above, the abundance and behavior of predators and prey could be different between selectively logged and primary forests, thus changing the level of actual and perceived predation risk for prey (Gehlbach and Leverett 1995). In addition, habitat structure, which tends to be drastically altered by selective logging (Johns 1988), determines the rates and outcomes of predator–prey encounters (Crowder and Cooper 1982; Whittingham and Evans 2004; Andruskiw et al. 2008; Chalfoun and Martin 2009) and, in turn, influences prey risk perception, as suggested by alterations in prey foraging (Mandelik et al. 2003; Verdolin 2006; Whittingham et al. 2006) and grouping (Boinski et al. 2003; Orpwood et al. 2008) behaviors. There is yet to be a direct test of how prey

perception of ambient predation risk is impacted by selective logging, but our findings corroborate the above theoretical reasoning to suggest that altered prey risk perception is a likely aspect of the ecological impacts of selective logging.

### General predation risk from the Sunda Scops-owl

In our study, the key benefit of predator-mobbing is likely to reduce the future predation risk prey face on a daily basis from the target predator, the Sunda Scops-owl (Dugatkin and Godin 1992; Caro 2005; Graw and Manser 2007). Differences in avian mobbing intensity between selectively logged and primary forests thus may suggest differences in the general predation risk posed by the owl as perceived by the prey. This possibility is supported by two lines of evidence from previous studies. (1) Increased mobbing intensity of forest birds can be related to increased abundance of and/or risk from the predator species that is the target of mobbing (Krams et al. 2010; Sandoval and Wilson 2012; Tilgar and Moks 2015). (2) Selective logging is known to change the abundance (Thiollay 1992; Burivalova et al. 2014), activity patterns (Castro-Arellano et al. 2009), and dietary/prey preference (Edwards et al. 2013; Ewers et al. 2015) of animal populations. The dynamics between prey birds and the Sunda Scops-owl may thus differ between selective logged and primary forests, which in turn may lead to altered levels of predation risk posed by the owl and, in turn, perceived by prey birds (Gehlbach and Leverett 1995) in selectively logged forest.

### Accrue ment of energy reserves

Mobbing entails energy costs through the spending of energy reserves and forfeiture of foraging time (Dugatkin and Godin 1992). Indeed, adequate and accessible internal and external energy reserves of prey must support the energetic costs of a given intensity of mobbing, a behavior that is both nonessential for immediate survival and risky to perform (Cuthill and Houston 1997). Alterations in mobbing intensity in selectively logged forests may, therefore, reflect alterations in the body energy reserve or environmental food availability for mobbing birds. This possibility is supported by previous studies showing changes in the body condition of animals (e.g., Olupot 2000; Bernard 2002) or the availability of their environmental food resources (e.g., Heiduck 2002; Simard and Fryxell 2003; Hardus et al. 2012; but see Knop et al. 2004, Yap et al. 2007) in selectively logged forest compared with primary forest.

Gleaning and flycatching birds contrasted in the way their mobbing intensity responded to selective logging (Fig. 1); this contrast corresponded to the contrasting



relationship of mobbing intensity and vegetation structure between the two guilds (Table 2). In light of the different anti-predator strategy between gleaning and flycatching birds, these findings are best interpretable if the observed alterations in birds' mobbing behavior between selectively logged and primary forests were primarily driven by predation risk-related aspects that underlie the cost–benefit trade-off of mobbing, as discussed above. In general, in terms of anti-predator strategy, gleaning birds rely on protective cover for predator escape, while flycatching birds rely on pre-emptive predator detection and aerial maneuvers for predator escape (Lima 1993). Considering that in forest habitats, protective cover for gleaning birds can be obstructive cover for flycatching birds (Lazarus and Symonds 1992), logging-induced forest structural changes can influence gleaning versus flycatching species in contrasting ways with regard to their interactions with predators. In our study, the relationship between canopy cover and mobbing intensity was positive for gleaning birds but negative for flycatching birds. This may be because a more open canopy can render gleaning birds more exposed to potential aerial attacks from ambient predators cruising above forest canopy (Castro-Arellano et al. 2009), but can allow flycatching birds to better detect these ambient predators, thus influencing their mobbing behavior differentially through birds' perception of ambient predation risk. The contrasting responses of mobbing intensity to selective logging between gleaning and flycatching species may also have been mediated through birds' perception of the predation risk posed by the Sunda Scops-owl during mobbing and in general: forest structural changes in protective or obstructive cover may influence this perceived risk in different ways for the two guilds, and flycatching birds may in general be less sensitive to selective logging in their risk perception because of their more efficient predator detection strategy. Overall, the contrasting findings between gleaning versus flycatching species suggest that altered predator–prey interactions likely underlay the observed alterations in birds' mobbing behavior in selectively logged forest compared with primary forest.

Three caveats to our findings warrant discussion. First, the study site for primary forest was of considerable distance (~600 km) to the study sites for selectively logged forest. Despite our effort to maximize the validity of their comparison by conducting analysis within species using standardized species pools, regional differences in environmental conditions between these sites could potentially have confounded the effects of selective logging on avian mobbing behavior. However, because forest structure (an ecological aspect known to be sensitive to logging effects; Johns 1988) was found to predict birds' mobbing intensity, we believe that this potential issue is unlikely to have driven

our major findings. Second, our study was based on a relatively small sample size (22–30 playback trials for each study site) in relatively compact research plots (125 ha for each study site), which could limit the ability of our findings to broadly represent the effects of selective logging. Our findings should thus be taken with this caveat in mind, and more robust understanding of the effects of selective logging on avian mobbing behavior can benefit from studies based on larger sample sizes. Finally, for analysis of data on the flycatching guild, we used GLMs as opposed to GLMMs because of limited sample size, thus did not account for potential non-independence in data structure. This likely increased the risk of type I errors, biasing our conclusions for the flycatching guild toward more significant results (Legendre 1993; Zuur et al. 2009). Thus, the relatively weak evidence we found for the flycatching guild may in fact have been even weaker.

When they occur, intensifications of perceived and actual predation risk and shortages in energy reserves can have strong fitness impacts on prey population dynamics and community assembly over time because these factors all figure heavily into prey fitness. Predation risk has long been recognized as a key force structuring ecological and evolutionary dynamics (Lima and Dill 1990). More recently, the nature of fitness responses to variable risk landscapes has been traced through to measurable impacts on both population and community vital rates such as reproductive effort and settlement patterns of breeding birds, respectively (e.g., Zanette et al. 2011; Hua et al. 2013, 2014). On the other hand, the importance of energy reserves in allowing organisms to engage in activities crucial for realizing fitness is even more self-evident. It is thus likely that the ecological consequences of one or more of the above factors being impacted by selective logging will continue to shape the persistence of prey communities in selectively logged forests over time.

Our study adds to an increasing body of evidence for the impacts (Carneiro et al. 2011; Schleuning et al. 2011; Slade et al. 2011; Edwards et al. 2013; Woodcock et al. 2013; Ewers et al. 2015; Srinivasan et al. 2015), or lack thereof (Cloutier et al. 2007; Ewers et al. 2015; Fayle et al. 2015) of selective logging on ecological processes. Compared with patterns of biodiversity numerical change in selectively logged forests, the understanding of how ecological processes are affected by selective logging is much less well established. Many ecological processes either directly underlie biodiversity persistence (e.g., seed dispersal and population vital rates), or reveal important information about other ecological processes that underlie biodiversity persistence (e.g., mobbing behavior in our study). How these potentially important ecological processes are impacted by selective logging is, therefore, indispensable

in correctly and fully understanding the patterns and processes of biodiversity persistence in selectively logged forests, and warrant more research attention.

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**Author contribution statement** F.H. and K.E.S. conceived and designed the experiments. F.H. performed the experiments and analyzed the data. F.H. and K.E.S. wrote the manuscript.

#### Compliance with ethical standards

**Ethical approval** All applicable institutional and/or national guidelines for the care and use of animals were followed.

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