

SONGBIRD VOCALIZATION BEHAVIORS AND DENSITY-DEPENDENT SEED
PREDATION REVEAL THE HIDDEN IMPACTS OF LOGGING

By

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To my parents

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Abstract of Dissertation Presented to the Graduate School
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PREDATION REVEAL THE HIDDEN IMPACTS OF LOGGING

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Selective logging is a rapidly expanding and pernicious driver of habitat and species loss in the biodiverse tropics. Little is known about the impacts of logging on ecological processes and animal behavior. In the tropical rainforests of Sabah, Malaysian Borneo, I unraveled the effects of logging on (i) the Janzen-Connell mechanism of negative density-dependence that is crucial for the maintenance of tree community diversity in many tropical ecosystems and (ii) breeding songbird vocalization behaviors, which are critical for mate choice and reproductive success. In logged forest, the fecundity of an endangered tree in the Family Dipterocarpaceae, the dominant tree family in Southeast Asian rainforests, was less than half that in old growth forest. The number of seeds escaping predation increased significantly with density in logged forest, counter to the predictions of the Janzen-Connell mechanism. Furthermore, the relative role of invertebrates and fungi as the primary drivers of negative density dependence was significantly reduced in logged forest while that of vertebrates was elevated. With respect to songbird vocalization behaviors, I found an overall negative trend in per-capita song production rates across 35 species of oscine birds in logged forests. Duets, which are a reliable indicator of pair bond formation, also declined for several species. Species adapted to old growth forest showed declines in song production rates and duetting rates while the converse was true for

species that exploited degraded forests. Species traits, such as habitat breadth and trophic position, explained vocalization behaviors. Modifications to vocalization behaviors suggest potential declines in avian reproductive success may be occurring in logged forests. Furthermore, in the face of enhanced predation risk, breeding songbirds responded by evacuating territories (reduced abundance post-playbacks) and by exhibiting cryptic behavior (reduced per-capita song rates post-playbacks) to avoid detection. These results suggest that the cost of fear can potentially have a negative impact via both population and behavioral responses. In conclusion, examining the impacts of logging through the twin lenses of ecological processes and animal behavior unmasked effects with potentially deleterious consequences for the maintenance and recovery of tree communities and for avian fitness and population viability.

CHAPTER 1
THE IMPACT OF LOGGING ON DENSITY-DEPENDENT PREDATION OF
DIPTEROCARP SEEDS AND SEED PREDATOR COMPOSITION

The Janzen-Connell hypothesis is a leading explanation for the maintenance of tropical plant diversity. It posits that specialized natural enemies reduce seedling survival at high densities near maternal trees, thereby conferring an advantage to locally rare species. The persistence of such ecological processes is critical for tropical rainforest recovery in the wake of pervasive disturbances such as selective logging. I tested the effects of logging on density-dependent seed predation and seedling recruitment of an endemic and endangered tree *Dryobalanops lanceolata* (Dipterocarpaceae) during a recent mast-fruiting event in Sabah, Malaysian Borneo. Seed production in logged forest was less than half that in old growth even during a mast-fruiting year, when most plant recruitment occurs. I found that seed survival did not increase with distance from the maternal tree in logged forest. Seed survival increased with increasing plot-level seed density in logged forest. These results defy both the distance and density predictions of the Janzen-Connell hypothesis. Seed survival in logged forest was similar to that in old growth. However 93% of surviving seedlings in logged forest germinated at locations with canopy cover similar to that in old growth. Stochastic escape from a nomadic large mammalian seed predator further facilitated localized survival in logged forest. The predators responsible for seed mortality differed among old growth and logged forests. Invertebrates and fungal pathogens were the primary drivers of negative density-dependence in old growth. In logged forests, however, rodents significantly increased their role as seed predators. My results suggest that negative density-dependent seed predation, which is vital for the maintenance and recovery of plant diversity in tropical forests and, which may be expected to operate in the reduced seed density conditions of logged forests, may be compromised.

Introduction

Selective logging is expanding rapidly across the tropics (Asner et al. 2009). In the aftermath of such perturbations, the persistence of a range of ecological processes is critical for the maintenance and recovery of biodiversity (Lewis 2009, Morris 2010). Yet, the impact of logging on many ecological processes remains largely unknown (Schleuning et al. 2011, Ewers et al. 2015). Processes that maintain local species diversity are especially vital for tree communities (Gentry 1988, Valencia et al. 1994, Cannon et al. 1998). Of the numerous processes and underlying mechanisms that have been postulated to explain the maintenance of tropical plant diversity (Chesson 2000, Wright 2002), the Janzen-Connell hypothesis (Janzen 1970, Connell 1971) is a leading explanation (Comita et al. 2014).

The Janzen-Connell hypothesis postulates that specialized natural enemies maintain diversity via two interacting mechanisms: (a) by inhibiting regeneration near parent trees where seed and seedling density is high (density effect) and (b) by causing higher mortality of seeds and seedlings near the parent tree than far away (distance effect). This local negative density dependence (NDD), or greater per-capita mortality of seeds and seedlings near conspecific adults of abundant species, confers an advantage to locally rare species and increases the probability of establishment of heterospecifics (Connell et al. 1984, Webb and Peart 1999). The Janzen-Connell hypothesis enjoys substantial empirical support (Augspurger 1984, Clark and Clark 1984, Webb and Peart 1999, Swamy and Terborgh 2010, Matthesius et al. 2011, Swamy et al. 2011, Bagchi et al. 2014, Comita et al. 2014), albeit mostly restricted to the Neotropics (Carson et al. 2008, Bagchi et al. 2011).

Few studies have tested the Janzen-Connell hypothesis in the Asian tropics (Carson et al. 2008). The ecology of Southeast Asian rainforests is notably different from that of other tropical regions worldwide (Janzen 1974). Most importantly, plant reproduction in these dipterocarp-

dominated (Family Dipterocarpaceae) rainforests is characterized by episodic community-wide mast fruiting events (approximately every 3-9 years) (Janzen 1974), during which up to 88% of canopy tree species may fruit synchronously (Curran et al. 1999, Curran and Leighton 2000). . The most plausible explanation for this phenomenon is that it evolved to satiate seed predators (Janzen 1974, Curran and Leighton 2000). During peak fruit fall, many seeds may escape predators and establish thereafter. Predator satiation thus reduces mortality at the highest densities, directly opposing the Janzen-Connell density-dependent mortality predictions (Janzen 1970, 1974). In fact, Janzen (1970) envisioned that his hypothesis might not hold for mast-fruiting Southeast Asian dipterocarps.

Human disturbances can, however, disrupt predator satiation. Selective logging tends to remove the largest and most reproductively active adult trees, leaving smaller individuals behind. The low density of reproductive adult trees left behind may not produce enough seeds to satiate seed predators (Curran et al. 1999, Curran and Webb 2000, Bagchi et al. 2011). Furthermore, the removal of many conspecific adults may cause the remaining reproductive dipterocarps to be spatially isolated from each other in logged forests, potentially reducing cross-pollination and decreasing seed set (Murawski et al. 1994, Ghazoul et al. 1998, Maycock et al. 2005). Consequently, the seed crop in logged forests may be reduced at the scale of the individual tree by high proportions of unpollinated and self-pollinated flowers and at a landscape scale by the reduced number of adult dipterocarps (Bagchi et al. 2011). Despite these issues, the impact of logging on density- and distance-dependent predation and recruitment of dipterocarp seeds and seedlings during mast fruiting years is unknown (Bagchi et al. 2011). Since dipterocarp recruitment primarily occurs during community-wide mast fruiting events (Janzen 1974, Curran

and Leighton 2000), the absence of recruitment in a mast fruiting year would imply deleterious consequences for the recovery of logged forests (Bagchi et al. 2011).

NDD under the Janzen-Connell mechanism was originally envisioned with host-specific pests and pathogens (Janzen 1970, Connell 1971). However, generalist vertebrate seed predators and herbivores cause high seed and seedling mortality for many plant species in tropical forests (Janzen 1974, Asquith et al. 1997, Curran and Leighton 2000, Terborgh et al. 2008, Swamy and Terborgh 2010). Vertebrates forage over relatively large spatial scales and are less likely to cause disproportionately high seed and seedling mortality near conspecific adult trees (Terborgh et al. 1993, Hammond and Brown 1998, Wright 2002, Swamy and Terborgh 2010). Nevertheless, if vertebrates prefer or frequently encounter common species, they may cause frequency-dependent selection (Dyer et al. 2010, Clark et al. 2012) and thus facilitate the establishment of rare species. The role of vertebrates in driving patterns of seed mortality and seedling recruitment, independent of the Janzen-Connell density- and distance-dependent predictions, is poorly known (Clark et al. 2012). This issue is particularly relevant for selective logging, since populations of vertebrate seed predators often increase in logged forests (Cusack et al. 2015, Ewers et al. 2015).

I investigated the effects of logging on density-dependent seed predation and seedling recruitment of the endemic and endangered dipterocarp *Dryobalanops lanceolata* (Figure 1-1) during the 2014 mast-fruiting event in Sabah, Malaysian Borneo. After controlling for the density of reproductive adults (maternal trees) between old growth and logged forests by study design, I leveraged natural observations (seedfall traps and unmanipulated seed plots, *Materials and Methods*) and a vertebrate exclosure experiment to test four predictions. First, I expected seed production would be lower in logged forest at the scale of the individual tree and at the landscape scale. Second, during a mast-fruiting event, I expected conditions in logged forests to

be similar to those in old growth forests during partial fruiting episodes, which occur sporadically during non-mast years. During partial events, a limited number of species fruit and the individuals that do so may be spatially isolated from each other (Bagchi et al. 2011). Host-specific pests, pathogens and vertebrate seed predators may be disproportionately attracted to isolated fruiting trees in logged forests, decreasing the per-capita survival of seeds close to parental trees relative to those dispersed far away. Consequently, I predicted NDD would override predator satiation in logged forests during a mast year, facilitating the recovery of plant diversity. Third, I expected seedling recruitment of *D. lanceolata* would be largely restricted to old growth forests even during a mast year. I based this prediction on prior knowledge that large trees with large seed crops are known to have higher seed and seedling survival (Bagchi et al. 2011). Such individuals are usually removed during logging. Furthermore, seeds in logged forests are exposed to increased light penetration and hotter, drier conditions due to the relatively open canopy (Hardwick et al. 2015). All of these factors can negatively affect recruitment (Bruna 1999). Fourth, I predicted that rodents would supplant invertebrates and fungal pathogens as drivers of NDD in logged forests (Clark et al. 2012). Prior research indicates that both native and invasive species of rodents, known predators of dipterocarp seeds (Wells and Bagchi 2005), increase in abundance in logged Bornean forests (Cusack et al. 2015, Ewers et al. 2015). Simultaneously, altered microclimatic conditions in logged forests (Hardwick et al. 2015) can inhibit invertebrate pests and fungi (Ewers et al. 2015), the primary drivers of plant diversity and composition via NDD in undisturbed forests (Bagchi et al. 2014).

Methods

Study Area

I carried out this work in Sabah, Malaysian Borneo at the field sites of the Stability of Altered Forest Ecosystems (SAFE) Project (Ewers et al. 2011) in Kalabakan Forest Reserve and

at old growth sites in the Maliau Basin Conservation Area (MBCA). Kalabakan Forest Reserve lies within the Yayasan Sabah Forest Management Area and has been subject to multiple rounds of selective logging, commencing in 1978 and continuing until the early 2000's. MBCA is a 588.4 km²-protected area designated by the Sabah State Government as a Class I Protection Forest Reserve and comprises undisturbed old growth forest.

Focal Species and Experimental Unit Selection

Dryobalanops lanceolata Burck is a tall emergent tree, reported to grow up to 80 m in height (Soepadmo et al. 2002). Endemic to Borneo, it is widespread in the states of Sabah and Sarawak, growing in mixed-dipterocarp forest on clay-rich soils (Soepadmo and Wong 1995, Soepadmo et al. 2002). The saplings are shade tolerant (Itoh et al. 1995) and can survive many years, expanding horizontally until a canopy gap opens up (Soepadmo et al. 2002). It is a hardwood species valued for its heavy and durable construction timber that is sold under the trade name *Kapur* (Soepadmo et al. 2002). Owing to commercial harvesting and habitat loss, it is threatened outside of protected areas and is classified as Endangered (IUCN Red List v. 2.3) (Ashton 1998). Like other dipterocarps, its winged seeds are dispersed by gyration and, for the most part, fall under and in close proximity to the canopy of the parent tree (Itoh et al. 1997). Fungal pathogens (*pers. obs.*) and invertebrates (Itoh et al. 1995) attack the seeds and seedlings. Vertebrates, such as bearded pigs (*Sus barbatus*) and various species of rodents, also forage on the seeds and can damage small seedlings (*pers. obs.*, Itoh et al. 1995) (Figure 1-1).

During June-July 2014, I located *D. lanceolata* trees along trails in logged and old growth forest. I identified seven individuals for this study in each forest type. For the purpose of this study, each individual tree represents an experimental unit. I selected trees as suitable if they were: (i) fruiting and (ii) separated in space from conspecifics such that seeds from the maternal tree would not be confounded with the seeds of adjacent conspecifics. The closest distance

between two trees that served as experimental units in this study was around 40 m. I make the following assumptions: (i) the seeds of the maternal trees included in this study are not confounded with those from other maternal trees, (ii) since the seeds are wind dispersed, the maximum dispersal distance, as inferred from prior studies (Itoh et al. 1997) and my own observations, is reliable and (iii) the seed shadow declines non-linearly with distance from the maternal tree. Mean DBH, height and crown diameter were all significantly greater for trees in old growth forest than for trees in logged forest (Appendix A). For all data collection and analyses described below, I focused on the seed-to-seedling transition phase over the first three months after seedfall, a demographic bottleneck that can disproportionately influence the structure, dynamics and composition of tree communities (Chambers and MacMahon 1994).

Seedfall Traps

To test whether logging impacts seed production compared to old growth forests, I set up seedfall traps immediately after the initial seedfall was observed (late-July in MBCA and early-August at SAFE). To avoid directional bias, I set up four, 32-m transects from the base of each tree, the first in a random compass direction and each subsequent transect at 90° from the previous (Figure 1-2). I deployed seedfall traps on a log₂ scale at 1, 2, 4, 8, 16 and 32 m along each transect (n = 24 seedfall traps/tree). Traps were 1 × 1 m and constructed from nylon mesh nets suspended at each corner by 1 m PVC pipes. I constrained the furthest distance to 32 m because prior work (Itoh et al. 1997) and my personal observations indicated that the number of seeds landing at and beyond this distance was limited. I collected seeds from the traps at census intervals of around two weeks between 15th July and 22nd October 2014 in MBCA and between 6th August and 7th November 2014 at SAFE.

Unmanipulated Seed Plots

To test whether seed mortality rates were disproportionately high near maternal trees, and how this may be impacted by logging, I set up 1×1 m plots along each transect, 2 m to the left of the seedfall traps at 2, 4, 8, 16 and 32 m distances ($n = 20$ unmanipulated plots/tree) (Figure 1-2). I tagged seeds found naturally dispersed in these plots with numbered plastic tags stapled to the wings (Figure 1-1). At each census interval, I recorded the number of seeds that survived and died in each plot and continuously tagged and monitored new seeds that fell into them. I recorded the status of each seed as one of the following categories: intact (no visible signs of insect, fungal or vertebrate attack), insect predated (with entry/exit holes), fungus infected (with fungal spores), vertebrate predated (gnaw marks on seed and/or partial remains of seed left behind), dead (decomposing or empty), germinating or seedling (Bagchi et al. 2011) (Figure 1-1). I counted seeds that I initially classified as insect or fungus infested as dead only if I determined, on a subsequent census interval, that they had died from the effect of that predator. If vertebrates partially ate or removed a seed that had been attacked by insects or fungi, I classified it as dead based on the original predator (Lewis and Gripenberg 2008). I classified seeds as vertebrate predated only if an intact seed that we tagged during a census interval was found removed at a subsequent interval or if the partial remains of a previously intact, tagged seed were left behind in a plot. Our observations indicate that no seeds survive insect or fungal attack.

Vertebrate Exclosure Treatments

To test the contribution of vertebrate seed predators relative to insects and fungal pathogens to seed survival, I set up exclosure treatments paired with open controls (1×1 m plots) at two seed densities and distances: low (5 seeds/m²) near experimental trees (2 m) and high (50 seeds/m²) far from experimental trees (32 m) (Figure 1-2). Exclosures were $1 \times 1 \times 0.5$

m, made from steel wire with a mesh size of 0.5×0.5 m (Figure 1-1). I set up these treatments along two transects that I chose randomly out of the four emanating from the base of each tree. The low-density treatment was similar to the naturally observed mean seed density in the unmanipulated plots in logged forest (Clark et al. 2007) while the high density treatment was around five times higher than the mean plot-level density naturally dispersed in unmanipulated plots in old growth forest (Clark et al. 2007).

To set up these treatments, I collected intact (*i.e.* no visible evidence of predator attack), mature seeds of *D. lanceolata* from around 20 trees, all in MBCA and none of which were the maternal trees in this study. I thoroughly mixed these seeds together and added 5 or 50 seeds to each plot as appropriate. I placed the seeds on the soil in a regular grid, mimicking the natural conditions when dipterocarp seeds gyrate from the parent tree and land on the ground. I tagged and monitored the status of each seed in an identical manner as the seeds in the unmanipulated plots. Since *D. lanceolata* seeds do not fly very far from the maternal tree (Itoh et al. 1997), I did not observe any untagged seeds from the maternal tree in any of the 32 m open controls and thus did not have to remove any. I removed seeds that fell into the low-density open controls on a continuous basis. I added seeds approximately one month after commencement of seedfall at MBCA and continued monitoring until the end of the study. To test whether varying light penetration in old growth and logged forests influences seed survival, I measured proportion canopy cover as a proxy for light availability with a type-A spherical densiometer (Lemmon 1956). I averaged four readings at each edge of the 1×1 m plots and repeated this for all unmanipulated plots, exclosures and open controls along all transects of each tree.

Statistical Analyses

I used generalized linear mixed models for all analyses described below. I parameterized models with the *glmer* function in package ‘lme4’ (Bates et al. 2015) in R (v. 3.2.1) (R Development Core Team 2015).

Seedfall

I modeled seedfall as additive and interactive effects of forest type and distance from the maternal tree and of forest type and the traits of individual trees (DBH, height and crown diameter). I assumed a Poisson error distribution and specified random intercepts for the effect of individual trees. I also allowed the effect of distance and traits to vary between trees as normally distributed random effects (*i.e.* random intercept and slope model).

Seed survival

I modeled seed survival to seedling stage at the end of three months as a function of forest type, distance to the maternal tree, conspecific density at the start of the monitoring and all interactions between these predictors. I included total seedfall at each tree as a measure of fecundity and canopy cover at each plot as a measure of light availability. I assumed a binomial error distribution and included intercept terms for each census in the model as random effects, thereby allowing overall survival rate to change over time. This analysis is similar to the Cox proportional hazards model (Egli and Schmid 2001). I included the interaction between census and forest type as a random effect to account for the fact that the relationship between survival and time may vary between old growth and logged forest. I also included intercept terms for plots and trees as random effects and allowed the relationship between survival and census to vary between plots as a random effect (random intercept and slope model).

Seed survival in exclosure treatments

I modeled seed survival in the exclosures and open controls as a function of forest type, exclosure treatment, initial seed densities and all interactions between these predictors. I added distance from the experimental tree and canopy cover at each experimental plot and controls as additional fixed effects. Again, I assumed a binomial error distribution and included intercept terms for each census in the model as random effects, thereby allowing overall survival rate to change over time. I also included intercept terms for plots and trees as random effects and allowed the relationship between survival and census to vary between forest type as a random effect.

Results

Seedfall

Seed production declined significantly in logged forest: I collected 2327 seeds (13.85 seeds/m², SE = ± 1.07) from seedfall traps in old growth forest compared to 1025 (6.10 seeds/m², SE = ± 0.57) in logged forest. Crown diameter had a significant positive effect on seed production. However, I did not observe a significant interaction between logging and crown diameter on seed production (Table 1-1). Seedfall declined significantly with distance from the maternal tree and this was stronger in logged forest (Figure 1-3). Thus, less seeds were falling into each distance category in logged forest and the seed shadow spanned a shorter distance as well. Only 13 seeds reached six, 32-m plots in old growth while none did so in logged forest (Figure 1-3).

Seed Survival

Unmanipulated seed plots

I observed 1533 seeds (10.95 seeds/m², SE = ± 1.01) naturally dispersed in unmanipulated seed plots in old growth forest compared to 787 (5.62 seeds/m², SE = ± 0.67) in

logged forest. In old growth forest, 91 seedlings (12.46% of the seeds that naturally dispersed into the unmanipulated plots) survived to the end of three months compared to 104 seedlings (13.21%) in logged forest. Defying predictions, per-capita seed survival marginally increased in logged forest (Figure 1-4). Against expectations, seed survival did not vary with total seedfall. Seed survival increased with canopy cover. In logged forest, 98 seedlings (93.33%) germinated where prior logging had been less intense (canopy cover was greater) (Ewers et al. 2011). Only seven seeds (6.67%) survived to seedling stage under sparse canopy cover where microclimatic conditions are hostile (Hardwick et al. 2015). Seed survival increased with increasing plot-level seed density in logged forest, against the density prediction of the Janzen-Connell hypothesis (Table 1-1). In both forest types, seed survival did not vary with distance from the maternal tree (Table 1-1, Figure 1-5).

Vertebrate exclosure treatments

I added 1540 seeds to 56 vertebrate exclosures and paired open controls, spread equally between the maternal trees old growth and logged forest. At the tail end of the seedfall, between October 1-19, bearded pigs depredated much of the fallen seeds and seedlings at my old growth site. They also destroyed the exclosures at four out of the seven trees. However, pigs did not visit my logged site in similar numbers (Curran et al. 2004) or damage any exclosures. To enable comparison of seed survival from exclosure treatments, I truncated the data from logged forest to the last census at old growth before depredation by pigs (~ 41-47 days after seed addition). In old growth I found no exclosure effect (Figure 1-5). 305 seeds survived to seedlings (79.22% out of 385 added) in open controls compared to 295 (76.62%) in exclosures. Invertebrates and fungal pathogens caused all mortalities. In logged forest, consistent with my predictions, seed survival increased in exclosures. In the exclosures, 227 seeds (58.96%) survived compared to 86 in open controls (22.34%). Rodents predated 238 seeds (61.82%) in the open controls while invertebrates

and fungal pathogens predated 61 (15.84%). Overall, seed survival declined in logged forest. Seed survival also declined with plot-level seed density, consistent with the density effect of the Janzen-Connell hypothesis. Again, seed survival increased with canopy cover. In the unmanipulated plots in old growth forest, rodents predated only 17 seeds (1.20% out of 1413) (Curran and Leighton 2000). In contrast, invertebrates and fungi predated 799 (56.55%). During the same period in logged forest, vertebrates (mostly rodents) predated 287 seeds (36.61% out of 784) while invertebrates and fungi predated 377 (48.09%). At the end of the monitoring (after depredation by pigs), mortality due to all vertebrates in old growth forest rose to 376 (24.53% out of 1533). However, mortality due to invertebrates and fungi remained significantly higher at 967 (63.08%) (Figure 1-5). In logged forest, at the end of the monitoring, all vertebrates predated 302 seeds (38.37% out of 787) while invertebrates and fungi predated 380 (48.28%) (Figure 1-6).

Discussion

Janzen (1970) envisioned that the Janzen-Connell mechanism might not operate in mast-fruited dipterocarp-dominated rainforests due to predator satiation. In logged forests, however, most large adult trees in prime reproductive condition are removed. The resulting lower seed densities may cause NDD to override predator satiation in logged forests during a mast year. My results, on the basis of the distance prediction of the Janzen-Connell hypothesis, suggest that predator satiation may be occurring in old growth forest but not in logged forest (Table 1-1). Had predator satiation occurred in logged forest, few seeds, if any, would have escaped predation especially since mean seed production rate is less than half that in old growth during a mast year (Figure 1-3) (Curran and Webb 2000). Furthermore, I expected seed survival to increase with distance from the maternal tree in logged forest, given that the lower seed production rates are likely conducive for NDD to operate. However, there was no significant interaction between

logging and distance from the maternal tree (Table 1-1, Figure 1-5). Against the classic prediction, the number of seeds escaping predation also increased with seed density in logged forests (Table 1-1). These results together suggest that negative density-dependence, which may be expected to operate in the reduced seed density conditions of logged forests (Bagchi et al. 2011), may actually be compromised.

In the experimental exclosures and open controls, seed densities were similar to (low – 5 seeds/m²) or greater than (high – 50 seeds/m²) the mean natural plot-level densities in logged and old growth forests respectively (Clark et al. 2007). The negative effect of plot-level density on seed survival that we subsequently observed in these experimental plots (as expected under the Janzen-Connell mechanism) indicate that *D. lanceolata* populations in logged forests are likely seed limited *i.e.* seeds fail to arrive at saturating densities at all potential recruitment sites (Eriksson and Erhén 1992, Turnbull et al. 2000, Nathan and Muller-Landau 2000, Schupp et al. 2002). The observed seed limitation was likely due to two processes. The first is source limitation (Nathan and Muller-Landau 2000, Schupp et al. 2002, Clark et al. 2007). Large trees in prime reproductive condition in old growth produce large seed crops (Figure 1-3, Appendix A). In logged forests, most large trees are removed during the first round of logging (Fisher et al. 2011, Struebig et al. 2013). Experimental trees were variable in terms of DBH, height and crown diameter both old growth and logged sites (Table 1-2). However, the lack of a significant interaction between logging and crown diameter on seed production suggests that seed production may not simply be driven by tree size. Other factors such as the relative isolation of conspecific adults in logged forests and the potential reduction in cross-pollination may also contribute to low seed production (Murawski et al. 1994, Ghazoul et al. 1998, Maycock et al. 2005). The second is dispersal limitation (Nathan and Muller-Landau 2000, Schupp et al. 2002,

Clark et al. 2007). The distance covered by seeds is greater in old growth than in logged forest likely because of the greater crown diameter of the trees in the former. I observed similar patterns of seed limitation across the wider dipterocarp community in logged forests (Appendix B). My experimental results, if generalizable to the wider plant community, imply that selective logging destabilizes an ecological process critical for the maintenance and recovery of plant diversity in tropical forests. My findings therefore have major implications for the viability of logged forests in biodiversity hotspots of Southeast Asia.

Seed survival rates were similar between old growth and logged forest. There are several potential explanations for this result. First, there was high variation in seedfall among the trees at the logged site. Second, > 93% of surviving seedlings in logged forest germinated in locations with canopy cover similar to that in old growth forest. Dense canopies can prevent 95% of the visible light from penetrating through to the earth's surface (Hardwick et al. 2015). This canopy cover keeps the air and soil beneath the canopy relatively cool during daylight hours. Prior research in these old growth and logged sites shows that microclimatic conditions are indeed significantly altered due to changes in the vegetation cover (Hardwick et al. 2015). The availability of suitable microsites or establishment limitation (Eriksson and Erhén 1992, Clark et al. 1998, Nathan and Muller-Landau 2000) therefore strongly influences the recruitment of *D. lanceolata* in concert with seed limitation. In logged forest, such suitable microsites for germination may be sparse, especially in intensively logged locations with low surrounding forest cover (Ewers et al. 2011). This raises potential concerns about the successful transition from seed to seedling in logged forests, a key phase of establishment limitation in plants (Clark et al. 2007). The third explanation is the regional escape hypothesis proposed by Curran and Leighton (2000). This hypothesis posits that a tree community, at a local scale, may either

completely escape seed predation by nomadic vertebrates or may incur substantial seed destruction and predator satiation. Bearded pigs are largely nomadic in nature, moving over large-spatial scales in search of food (Curran and Leighton 2000). In the months prior to the mast (February-June 2014), I observed solitary bearded pigs in both logged and old growth sites. During the mast, in the old growth site, I observed several healthy sows, each with up to 12 piglets. I also observed large groups of pigs (Curran and Leighton 2000). However, in the logged site, I did not observe such gatherings during the mast. It is likely that nomadic groups of pigs missed the logged forest completely or avoided it altogether due to the paucity of nutritious seeds (Curran and Leighton 2000). This enabled the regional escape of the local seeds. Should pigs have visited my logged site in large groups as in old growth, seedling survival rates would likely have been lower than observed.

I provide strong experimental evidence that logging diminishes the functional role of invertebrates and fungal pathogens (Ewers et al. 2015), with respect to density-dependent seed predation and seedling recruitment of a native endangered tree (Figure 1-6). A likely reason for this result is that the altered microclimatic conditions in logged forests (Hardwick et al. 2015) may inhibit certain species of invertebrates and fungi (Ewers et al. 2015). Despite extensive predation by bearded pigs towards the tail end of the seedfall in old growth forest (Curran and Webb 2000), invertebrates and fungi remained the primary drivers of NDD in my unmanipulated plots. The contribution to seed mortality by resident small mammals in old growth prior to the advent of pigs was a mere 1.2%, similar to the rates observed by Curran and Leighton (2000) in their seminal work on predator satiation. I demonstrate that vertebrate seed predation can impact seedling recruitment more than establishment limitation (Clark et al. 2012) when forests are subjected to logging.

My results suggest an anthropogenic shift in the operation of a critical ecological process in tropical forests. I demonstrate that understanding the influence of disturbances such as selective logging on ecological processes can unravel hidden impacts that may otherwise be masked.

Table 1-1. Model results showing effects of various factors and treatments (over controls) on various response variables.

Response Variable	Factor	β	SE	Z	p
Seed Production					
	Logging	-0.83	0.31	-2.68	0.007
	Crown diameter	1.35	0.61	2.24	0.03
	Logging \times Crown diameter	-0.91	0.84	-1.08	0.28
	Distance	-0.10	0.02	-6.41	< 0.001
	Logging \times Distance	-0.05	0.02	-1.89	0.06
Seed Survival in Unmanipulated Plots					
	Logging	2.53	1.45	1.74	0.08
	Total seed production	0.08	0.42	0.18	0.86
	Canopy cover	0.63	0.32	1.95	0.05
	Seed density	-0.15	0.11	-1.35	0.18
	Logging \times Seed density	1.14	0.48	2.40	0.02
	Distance	-0.03	0.02	-1.51	0.13
	Logging \times Distance	-0.11	0.08	-1.45	0.15
Seed Survival in Vertebrate Exclosures and Open Controls					
	Logging	-12.67	6.21	-2.02	0.04
	Exclosure	1.44	2.55	0.56	0.57
	Logging \times Exclosure	10.36	4.44	2.22	0.02
	Seed Density	-7.57	2.53	-2.99	0.003
	Canopy Cover	3.68	1.38	2.66	0.008

Definition of factors as parameterized in generalized linear mixed models above: Logging = effect of forest type (old growth v logged) on seed production or seed survival as appropriate to the model being considered, Crown diameter = effect of tree crown diameter on seed production, Logging \times Crown diameter = interactive effect of forest type (old growth v logged) and crown diameter on seedfall, Distance = effect of distance from the maternal tree on seed production or survival as per the model, Logging \times Distance = interactive effect of forest type (old growth v logged) and distance from maternal tree in each forest type on seedfall, Total Seed Production = effect of fecundity of experimental trees on seed survival, Canopy cover = effect of 1 \times 1 m plot-level canopy cover on seed survival, Seed density = effect of plot-level seed density on seed survival, Logging \times Seed density = interactive effect of forest type and plot-level seed density on seed survival, Logging \times Distance = interactive effect of forest type and distance from the maternal tree on seed survival, Exclosure = effect of vertebrate exclosures and paired open controls on seed survival, Logging \times Exclosure = effect of forest type and vertebrate exclosures and paired open controls on seed survival.

Table 1-2. Size measurements of individual *D. lanceolata* trees in old growth and logged forest.

Tree ID	DBH (cm)	Height (m)	Crown Diameter (m)
Old Growth			
DL7	114.00	46.67	19.10
DL5	71.20	39.30	16.00
DL9	67.10	41.17	11.90
DL6	67.80	47.05	11.15
DL4	67.20	51.05	9.10
DL10	82.30	48.17	7.20
DL8	61.90	50.55	5.85
Logged			
DL13	71.00	38.17	11.90
DL12	56.80	35.17	9.10
DL14	51.00	37.17	8.95
DL3	42.10	23.17	6.00
DL2	36.50	22.42	5.80
DL11	38.90	22.17	5.60
DL1	46.00	24.42	4.75

Figure 1-1. *Dryobalanops lanceolata* is an Endangered dipterocarp endemic to Borneo. Clockwise from top left: A) A mature seed germinates in old growth forest. *D. lanceolata* seeds are characterized by five wings. Seeds are green when they fall from the tree and germinate within 5-7 days of touching the soil. They turn bright pink upon germination. B) Seeds are susceptible to predation by invertebrates (exit holes). Insect larvae have consumed these seeds from within, C) Fungal pathogens and, D) Vertebrates (seed consumed and only wings remaining) (See Methods – Unmanipulated seed plots for details on classification of seed predators). E) Seedlings germinating within a vertebrate exclosure in logged forest. Rodents predated most seeds in open controls in logged forest. Most seedlings in our experimental plots and exclosures in old growth forest germinated to seedling stage before bearded pigs (*Sus barbatus*) depredated them. F) Naturally dispersed tagged seedlings germinating in one of our unmanipulated plots. G) *D. lanceolata* saplings from a previous fruiting event in old growth forest. We observed only two saplings in logged forest, both growing under canopy cover conditions similar to those in old growth forest. (All photographs courtesy of author).



A



B



G



C



F



D



E

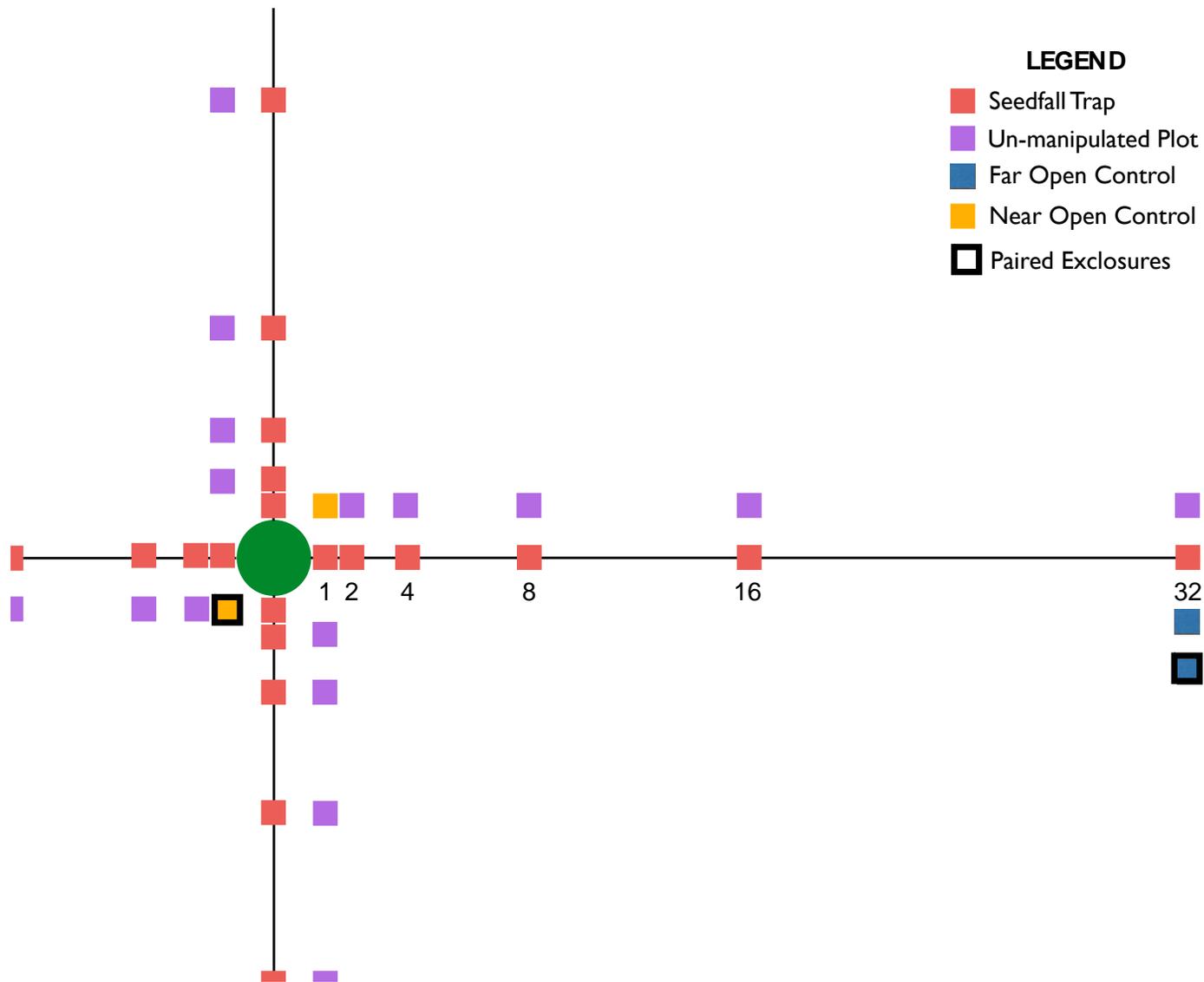


Figure 1-2. Study design showing seedfall traps, un-manipulated plots, paired vertebrate exclosures and open controls along four-32m transects from the base of experimental *D. lanceolata* trees (green circle). I set up the first transect in a random compass direction and the remaining at 90° to the previous.

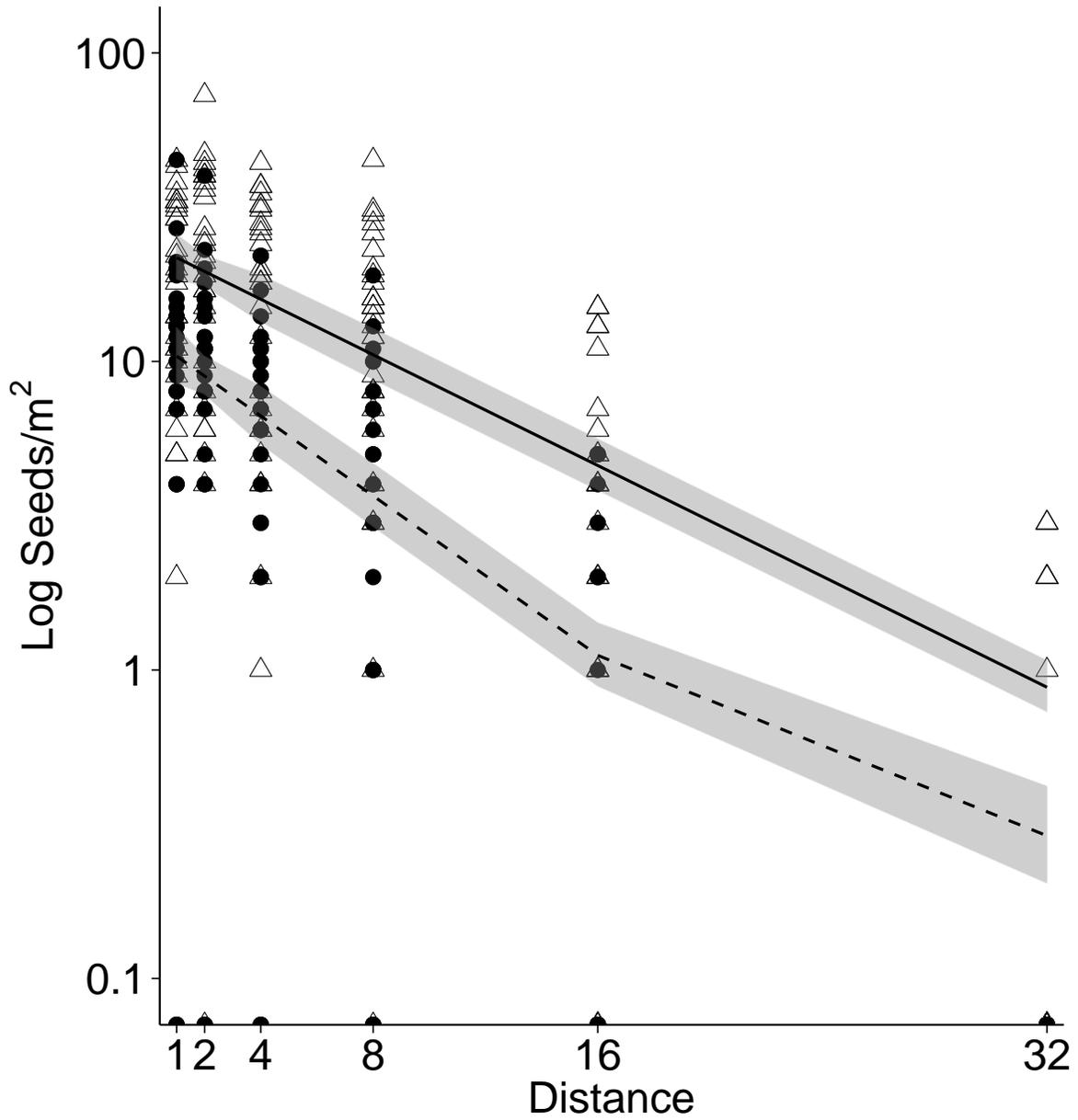


Figure 1-3. The relationship between *D. lanceolata* seedfall and distance from the maternal trees in each forest type. Open triangles are the total number of seeds falling into each 1 m² seedfall trap at 1, 2, 4, 8, 16 and 32 m in old growth forest. Closed circles represent the same in logged forest. The continuous line is the number of seeds predicted to fall at each distance in old growth forest by the generalized linear mixed model fitted to the data. The dashed line represents the same in logged forest.

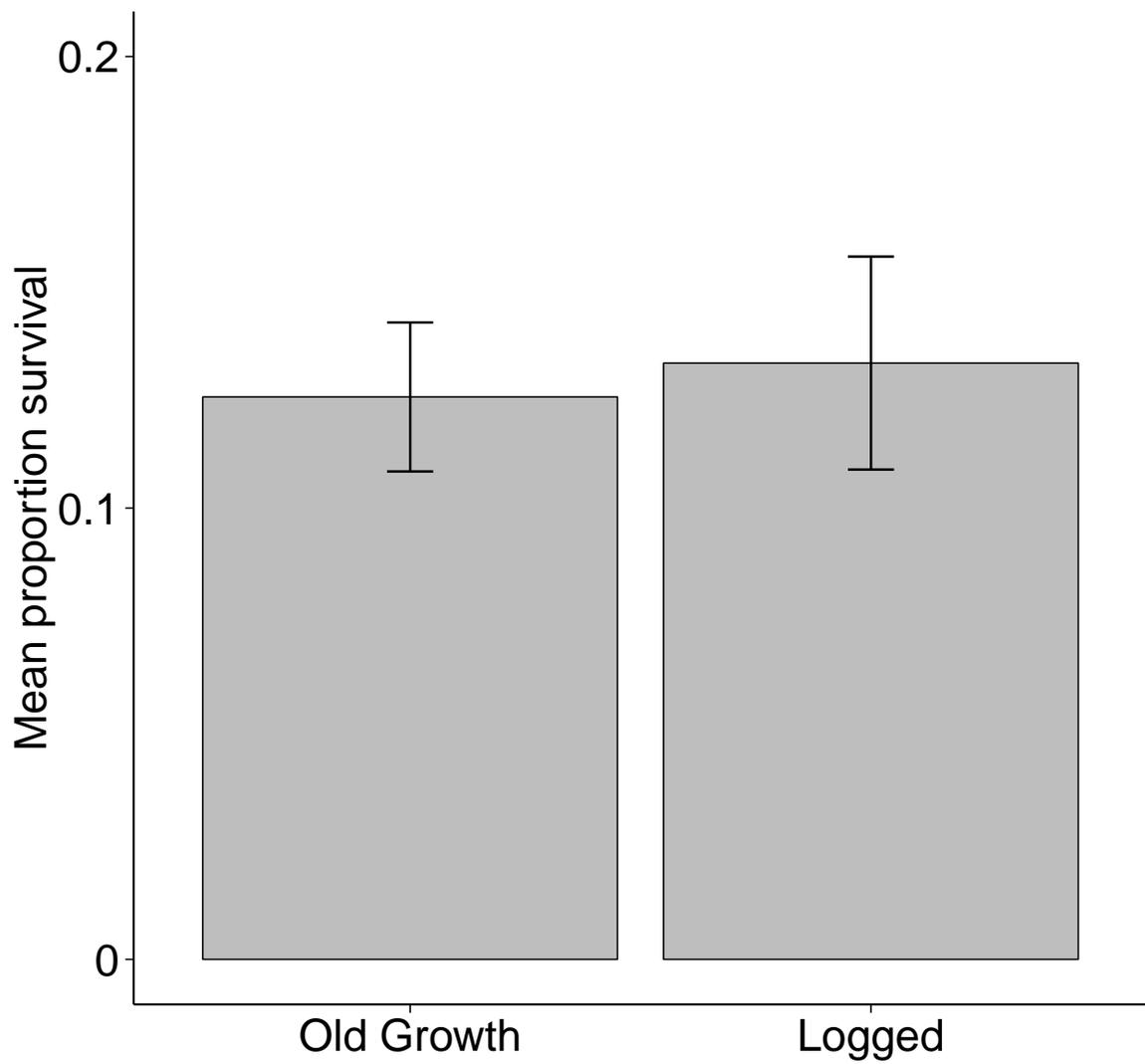


Figure 1-4. Mean proportion survival of *D. lanceolata* seedlings in old growth and logged forest.

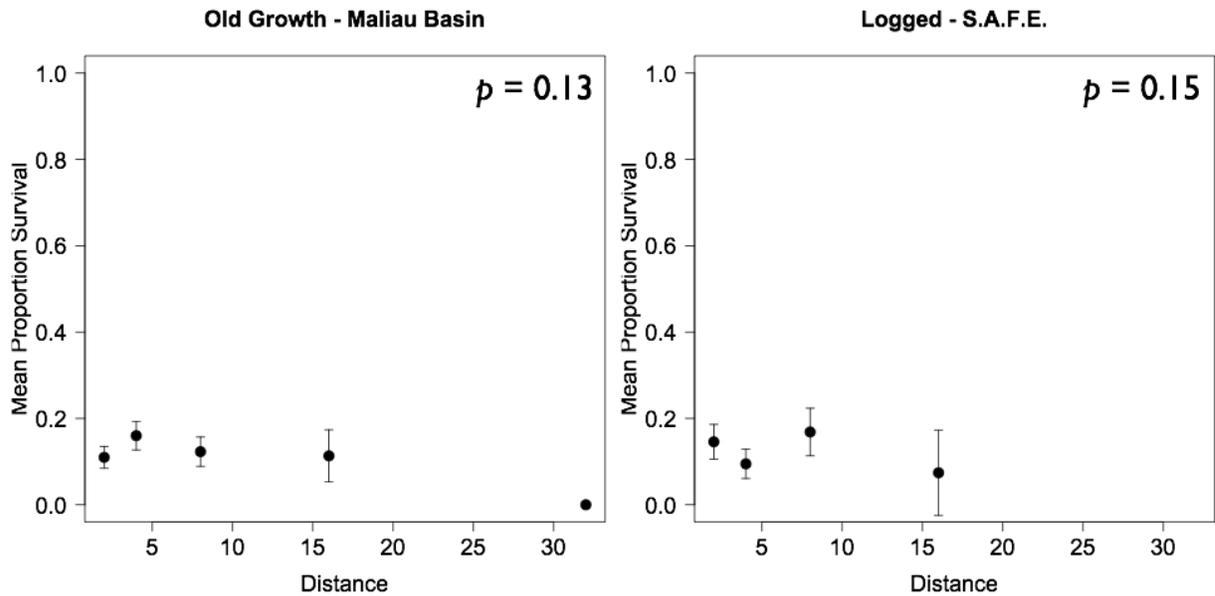


Figure 1-5. The relationship of seed survival with distance from the maternal tree. Seed survival did not increase with distance in old growth forest (left). This is expected during a mast fruiting year when there is a high density of seeds everywhere and distance does not matter for seed survival (Janzen, 1970). However, I observed a similar pattern in logged forest (right) despite the fact that seed densities in the same were less than half that in old growth. Low seed densities may make it conducive for NDD to operate, potentially leading to higher seed survival at greater distances from the maternal tree. Yet, this was not observed.

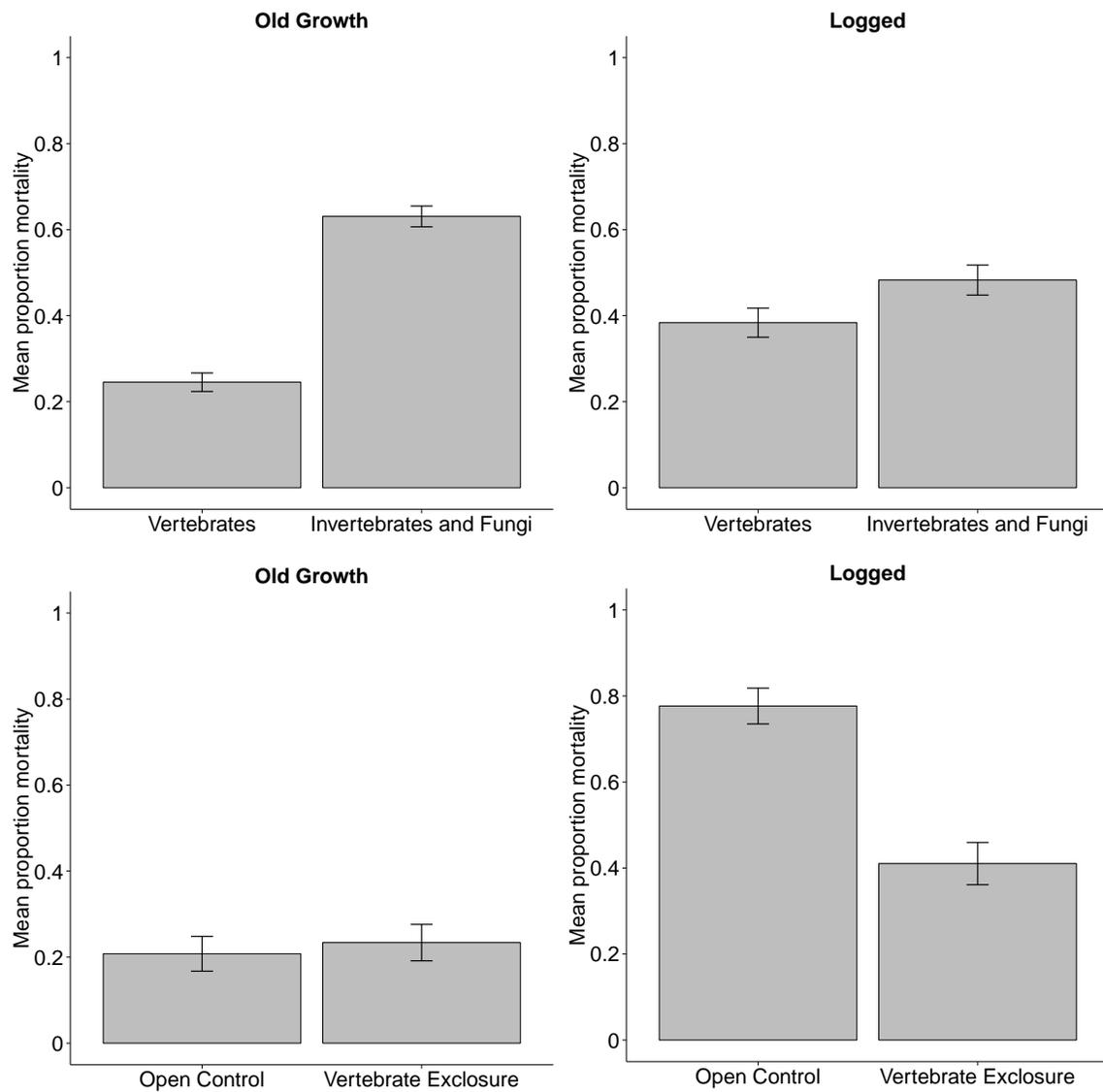


Figure 1-6. Contribution of vertebrates and invertebrates and fungal pathogens to *D. lanceolata* seed mortality in unmanipulated seed plots in old growth and logged forest. Invertebrates and fungal pathogens were the dominant drivers of negative density-dependence in old growth forest even though bearded pigs predated a large proportion of the seeds and seedlings (A). The role of invertebrates and fungal pathogens as seed predators was significantly reduced in logged forest (B). We found no effect of exclusion in old growth (C). All mortalities in exclusions were due to invertebrates and fungal pathogens. In logged forest, we found a significant exclusion effect (D). Rodents predated most seeds in open controls.

CHAPTER 2

DECODING SONGBIRD VOCALIZATIONS REVEALS THE HIDDEN IMPACTS OF LOGGING

Selective logging is a widespread driver of landscape change and biodiversity loss in the tropics. The effects of logging on biodiversity have been primarily evaluated with population and community metrics. The behavioral responses of taxa, however, have received less attention. Birdsong is a fundamental behavioral trait in mate choice, pairing success and in the establishment and defense of territories. Alterations to singing behavior may have ramifications for fitness and population dynamics. I contrasted two behavioral traits important for pairing success in breeding oscines, the rate of male song production and duetting rates of songbirds, against the widely used population metrics of occupancy and abundance. Focusing on a community of 35 species of oscine birds in old growth and logged forests in Sabah, Malaysian Borneo, I asked: (i) Do changes in behavior (singing and duetting rates) reveal the same patterns, in terms of species-level responses, as changes in occurrence and abundance? (ii) Are there effects on vocalization behaviors in addition to the effect of abundance? and, (iii) Can variation among species in changes in population and behavioral responses to logging be predicted by vegetation covariates and species traits? I leveraged a novel bioacoustic sampling design to estimate occupancy and abundance for each species in old growth and logged forests. I then estimated per-capita singing rates for each species and per-pair duetting rates for a subset of eight babbler species (Families Pellorneidae and Timaliidae). My results indicate that vocalization behaviors reveal similar patterns as occurrence and abundance, in terms of overall species-level responses to logging. However, I found that many forest interior species are showing declining per-capita singing rates and per-pair duetting rates in logged forests in addition to the effects of logging on abundance. I observed the opposite for habitat generalists. Species traits such as habitat breadth and trophic position predicted changes in occurrence,

abundance and vocalization behaviors. Behavioral metrics reveal similar patterns as population measures. However, altered vocalization rates in addition to the effect on abundance for many species suggest that logging may impact a behavior that is important for mate choice.

Bioacoustic and signal processing technologies facilitate cost-effective monitoring of animal behavior in response to global change and can serve as valuable tools for biodiversity conservation and management.

Introduction

Selective logging is a rapidly expanding threat to tropical forests and biodiversity (Asner et al. 2009). The ecological impact of logging, however, has been the subject of debate (Didham 2011, Edwards and Laurance 2013, Michalski and Peres 2013), especially in the light of investigations that indicate minimal impacts to the majority of species in certain taxonomic groups (Berry et al. 2010, Edwards et al. 2011, Woodcock et al. 2011, Wearn et al. 2013). Inferences made primarily on the basis of population and community metrics have been criticized as potentially misleading (Didham 2011, Michalski and Peres 2013). Such interpretations rely on the assumption that the presence of a species (Edwards and Laurance 2013) is correlated with the absence of an impact (van Horne 1983, Bock and Jones 2004). However, this may not necessarily be the case (Ware et al. 2015). Logging may have hidden impacts on aspects of animal behavior (Caro 1999, Anthony and Blumstein 2000), such as changes in pairing success (Lampila et al. 2005) or the creation of ecological traps (Battin 2004, Fletcher et al. 2012). Such impacts, ultimately, may have significant adverse effects on fitness and population dynamics (Lima 1998, Werner and Peacor 2003, Cresswell 2008). Yet potential behavioral effects remain poorly understood (Johns 1986).

In breeding oscines, singing is a fundamental behavioral trait in mate choice, pairing success and in the establishment and defense of territories (Catchpole and Slater 1995, Grant and

Grant 1997, Slabbekoorn and Smith 2002, Slabbekoorn and Ripmeester 2008), ultimately influencing sexual selection (Gil and Gahr 2002) and individual fitness (Catchpole and Slater 1995). Song characteristics such as the rate of song production by males, song frequencies and temporal modulations have a major impact on pairing success (Catchpole and Slater 1995, Gil and Gahr 2002). In particular, male song production rate is known to be vital for pairing success (Gottlander 1987, Radesater et al. 1987, Gil and Gahr 2002). Singing rate is a behavioral trait that is often limited by food availability (Gottlander 1987). When it comes to mate selection by females, it has been suggested that the quality of the territory may matter above male characteristics (*e.g.* age, body size, plumage color, etc.) or even song repertoire (Alatalo et al. 1986). Overall, the rate of song production by a male songbird may reflect territory quality (Hoi-Leitner et al. 1995). For instance, in high quality territories with abundance food resources, males may need to spend less time foraging relative to singing. The opposite may be true for males in poor quality territories (Hoi-Leitner et al. 1995, Gil and Gahr 2002). Females may therefore use singing rate as a proximate cue indicating the quality of the territory held by a male (Yasukawa 1981, Hoi-Leitner et al. 1995).

Furthermore, some species duet, which can provide key insights into reproductive status. Duets occur when two birds, usually a breeding pair, synchronize their songs by overlapping or alternating them (Farabaugh 1982). Duets serve multiple functions (Mennill and Vehrencamp 2008). They are important in the successful formation (Hall 2004, Slater and Mann 2004) and maintenance (Wiley and Wiley 1977) of pair-bonds. A breeding pair may duet to remain in acoustic contact (Thorpe 1963), especially in densely forested habitats where direct visual contact is often obscured (Mennill and Vehrencamp 2008). A high rate of duetting is also important for territory defense and in mate guarding by the individuals of a breeding pair

(Mennill and Vehrencamp 2008). It is unknown whether logging causes songbirds to adjust these vocalization behaviours (Catchpole and Slater 1995, Mennill and Vehrencamp 2008).

I hypothesize that avian vocalization behaviors in response to logging may be influenced by the structure of the surrounding vegetation (Lima et al. 1987, Lima 1990) and by the ecological and life-history traits of different species of songbirds (Cleary et al. 2007, Newbold et al. 2013, Burivalova et al. 2015, Hamer et al. 2015). Vegetation cover affords protection from predation when singing (Niemi and Hanowski 1984, Lima et al. 1987, Lima 1990, 2009, Lima and Dill 1990). Birds singing at more exposed perches take fewer risks, upon perceiving a threat, than birds singing at perches protected by cover (Duncan and Bednekoff 2006, Moller et al. 2008). Selective logging eliminates much of the tall, contiguous canopy cover and, over time, transforms the relatively open understory into a dense tangle of secondary growth (Johns 1988, Edwards et al. 2011). Such drastic changes to vegetation structure may influence risk perception (Rodríguez et al. 2001), potentially causing different species to variably modify their vocalization behaviors. The variations in behavioral responses among species are then likely to be an interactive effect of ecological traits such as preference of foraging stratum and foraging strategy. For instance, species that primarily forage in the mid-story are likely to perceive heightened risk in the open canopy of logged forests. Species that forage by gleaning may perceive greater risk (Thiollay 1999) than species that forage by sallying or hawking, a foraging strategy that may be associated with enhanced vigilance.

I contrasted two behavioral traits important during pairing in breeding songbirds, the rate of male song production and duetting rates, against the widely used population metrics of occupancy and abundance. I focused on 35 species of oscines (six families) (Table 2-1) in old growth and logged forests in Sabah, Malaysian Borneo. The species within these families share

several traits, yet prior research indicates that these species vary in their population responses to logging (Lambert 1992, Lambert and Collar 2002, Cleary et al. 2007, Edwards et al. 2011). Specifically, I asked: (i) Do changes in behavior (singing and duetting rates) reveal the same patterns, in terms of species-level responses, as changes in population measures (occurrence and abundance)? (ii) Are there effects on vocalization behaviors in addition to the effect of abundance? and, (iii) Can variation among species in changes in population and behavioral responses to logging be predicted by vegetation covariates and species traits? I used a bioacoustic sampling design to estimate occupancy and abundance in old growth and logged forests. I then estimated per-capita song production rates per minute per unit area (song density hereafter) by breeding males of each species and per-pair duet production rates per minute per unit area (duet density hereafter) for a subset of eight duetting babbler species (Families Pellorneidae and Timaliidae) (del Hoyo et al. 2007). On the basis of prior research (Cleary et al. 2007, Newbold et al. 2013, Burivalova et al. 2015, Hamer et al. 2015), I expected that the species most likely to exhibit declines in population and behavioral measures would be those with large body size, high trophic position and low dietary breadth. I also predicted that declines in population and behavioral metrics would be greater among forest interior sallying insectivores and midstory gleaning insectivores due to potential differences in predation risk perception in these two groups (Lambert and Collar 2002, Cleary et al. 2007). I conclude by highlighting the implications of my findings for breeding songbirds in the context of selective logging, the applications of bioacoustic sampling for behavioral studies, conservation and management and, future research priorities.

Methods

Study Area

I carried out this study in Sabah, Malaysian Borneo in logged forest at the experimental site of the Stability of Altered Forest Ecosystems (SAFE) Project (Ewers et al. 2011) and in nearby old growth controls in the Maliau Basin Conservation Area (MBCA) (Figure 2-1). SAFE is located in the Kalabakan Forest Reserve, a logging concession comprised of hill dipterocarp forest within the Yayasan Sabah Forest Management Area. As part of SAFE, experimental forest fragments are being created of different sizes (1 ha, 10 ha, 100 ha) and landscape context, with fragment creation initiating in 2014. Prior to this experiment, this area was subjected to multiple rotations of logging, the first of which began in the 1970's (Chong 2005, Fisher et al. 2011). Commercially valuable trees > 60 cm DBH were extracted and $112.96 \text{ m}^3 \text{ ha}^{-1}$ of timber was removed (Fisher et al. 2011). The second rotation, commencing in the 2000's (Chong 2005, Fisher et al. 2011), encompassed three rounds (Struebig et al. 2013). Trees > 40 cm DBH were targeted (Fisher et al. 2011). 25.87, 22.32 and $18.16 \text{ m}^3 \text{ ha}^{-1}$ of timber was extracted during each round respectively (Yayasan Sabah, unpublished data). Logging ended in 2007-08 (Fisher et al. 2011), by which time $179 \text{ m}^3 \text{ ha}^{-1}$ of timber had been cumulatively removed (Struebig et al. 2013). Extensive collateral damage to forest structure also occurred due to the establishment of a grid of skid trails, access roads and log-landing areas (Wearn et al. 2013). The six experimental blocks (A-F) at SAFE (Ewers et al. 2011) have therefore been subjected to varying intensities and timings of timber extraction and comprise a heterogeneous landscape. Forest quality is highly variable and ranges from grassy open areas and low scrub vegetation, to nearly intact remnants on steep inclines and in rocky sections. The third rotation of logging to clear the concession for plantation, while leaving the experimental fragments, commenced in April 2013 and is currently ongoing.

The study site at MBCA (~ 70 km from the SAFE experimental site) mostly comprises old growth hill dipterocarp forest. Two of the SAFE control sites in MBCA (OG1, OG2) have never been logged, while OG3 was lightly logged in the 1970's and 1990's (Ewers et al. 2011).

Avian Acoustic Surveys

I used Song Meter SM2+ GPS (Wildlife Acoustics Inc., Concord, MA, U.S.A.) automated recording units (ARU's) to record avian vocalizations during April-July 2014. My sampling window coincides with the major part of the breeding season for most of my focal species, which can stretch from March-September in Sabah (del Hoyo et al. 2005, 2006, 2007, Phillipps and Phillipps 2011). Forest clearing at the SAFE experimental site was ongoing during our field sampling and the fragments had not yet been created. Therefore, my data represents responses of birds to prior logging at SAFE, rather than fragmentation (Chong 2005, Fisher et al. 2011, Struebig et al. 2013), in relation to unlogged old growth controls in the Maliau Basin. I sampled 32 logged plots in Blocks B, D, E and F at SAFE and 18 old growth plots in OG1 and OG2 at Maliau (Fig. 1). For the purpose of my study, a plot refers to a 1 ha circular fragment, the smallest experimental unit at SAFE (Ewers et al. 2011). I set up microphone arrays at a subset of my plots (16 SAFE, 12 Maliau) and single ARU's at the remaining plots (16 SAFE, 6 Maliau). I used measuring tape, a compass (Suunto KB-20, Suunto Oy, Finland) and a GPS receiver (Garmin GPSMAP 60CSx, Garmin Ltd., Switzerland) to configure arrays that covered the entire 1 ha plot: I placed one ARU at the center of each plot and the remaining five at radii of 50 m from the center and adjacent to the plot boundary (the radius of a 1 ha fragment is ~ 56 m) (Figure 2-1). I sampled the 1 and 100 ha fragments (prior to fragment creation) in each of the abovementioned blocks at SAFE. In the 1 ha fragments, I deployed arrays in the fragments closest to and furthest away from the adjacent 100 ha fragment and single ARU's in the two fragments in between (Figure 2-1). In the 100 ha fragments, I deployed arrays at the core and

edge and single ARU's in the two plots in between, thus mirroring the design in the 1 ha fragments. In old growth controls, I deployed arrays and single ARU's in identical fashion at plots in OG1 and OG2. I sampled each plot for five days, and programmed the ARU's to record bird vocalizations continuously for six hours each day, commencing with the dawn chorus at 6:00 AM and ending at 12:00 PM.

Vegetation Sampling

To test whether population and behavioral responses to logging are a function of alterations in vegetation structure, I quantified vegetation cover in the foraging strata used by understory and midstory songbirds. I first defined ground birds as those that forage primarily on and within 1 m of the ground, understory birds as those that forage between 4-5 m of the ground and midstory birds as those that forage above 5 m but below the canopy (del Hoyo et al. 2005, 2006, 2007, Wunderle Jr. et al. 2006, Hamer et al. 2015). To quantify vegetation cover in the foraging stratum used by ground and understory birds, I measured proportion understory density within each of our plots. In plots with microphone arrays, I set up six concentric circular vegetation plots, each with inner radius 5 m and outer radius 10 m respectively. I centered the first concentric plot in the middle of a 1 ha plot and equally spaced the remaining five at distances of 35 m from the central ARU, along the radii of the array. I measured proportion understory density with a 1 × 1 m density-board divided into 36 equal checkerboard squares (modified from Nudds 1977), at five height levels above the ground (0-1, 1-2, 2-3, 3-4 and 4-5 m), at 5 m and 10 m radii, in four compass directions, the first being at random (40 measurements/plot). In plots with a single ARU, I set up one concentric plot, centered on the ARU. My measurements thus encompassed the entire understory, as defined above, from ground level up to 5 m. To quantify vegetation cover in the foraging stratum used by midstory birds, I

measured proportion canopy cover at the center of each concentric plot with a type-A spherical densiometer (Lemmon 1956). I averaged four readings, one from each of the four cardinal directions, about the central reference point. I also measured average canopy height and maximum height of standing vegetation with a laser rangefinder (Nikon Prostaff 3, Nikon Corporation, Japan), taking one measurement in each vegetation plot.

Species Traits

To explicitly test my predictions on species traits (*see Introduction*), I first obtained the corresponding traits from the literature (del Hoyo et al. 2005, 2006, 2007, Phillipps and Phillipps 2011) (Table 2-2). For details on selection of species traits, see Appendix C.

Processing of Acoustic Recordings

I divided each six-hour (6:00 AM – 12:00 PM) recording into five-minute clips and split stereo channels into individual mono tracks. Since I mounted the two microphones directly on the opposing sides of each ARU (29.5 cm apart), the recordings in the two channels from a given ARU are near replicas of each other. Therefore, I mostly used the left channel for all analyses. In some cases, when the left channel contained no acoustic data due to a failed microphone (animal or weather damage), I used the right channel. I subsampled my recordings by selecting three five-minute clips from 6:00-6:05, 7:00-7:05 and 8:00-8:05 AM (may be considered analogous to five-minute point counts) for each of the first three days of recording (*i.e.* 15 minutes/day \times 3 days). I then manually extracted the bird data for all analyses for this study from these five-minute clips with Avisoft SASLab Pro (Specht 1998). I performed a Fast Fourier Transform (sampling frequency 22050 Hz, FFT length 512, temporal overlap 50%, time resolution 11.6 ms, frequency resolution 43 Hz) with a Flat Top window function to suppress spectrum distortion (Specht 1998). I listened to each clip for diagnostic vocalizations of focal species while simultaneously viewing the spectrograms to distinguish the species-specific spectral

characteristics of different vocalizations. I extracted the following data: (i) *Counts of vocalizations (songs and duets)*: A bird may vocalize repeatedly within a five-minute interval. In many species, a song comprises several syllables that are grouped together and produced in rapid succession (< 0.5 s inter-syllable gap). In other species, songs comprise individual syllables that are > 0.5 s apart in time. Thus, my definition of song is species specific. In each five-minute clip, I counted individual songs that were separated in time from similar songs. I took care to count overlapping songs (*e.g.* two or more territorial males singing in rapid succession, or a breeding pair duetting), through careful listening and visual inspection of spectrograms. For duetting species, I only analyzed five-minute clips in which both the male and female were singing and counted the number of distinct male and female songs. (ii) *Detection histories*: I collapsed the counts of vocalizations above in each five-minute clip to obtain detection/non-detection data for each species in each clip. (iii) *Counts of individuals*: To estimate population density (individuals per plot or unit area) from acoustic cues, it is necessary to either distinguish songs from different individuals or convert song rate (*e.g.* songs per plot per minute) to population density (Dawson and Efford 2009). I chose to distinguish (and count) different individuals of each species vocalizing in each five-minute clip. Observers conducting point-count surveys leverage cues such as the intensity and direction of sound, and temporal overlap with conspecific vocalizations to identify species and count the number of individuals heard vocalizing (Ralph et al. 1995). Similar principles are applicable with respect to counting individuals with acoustic recordings (Rempel et al. 2005, Celis-Murillo et al. 2009). To do so, I first used Avisoft SASLab Pro to create multi-channel clips by combining the six channels (each coming from one of the six ARU's in an array) from a given time interval (*e.g.* 6:00-6:05 AM) for a particular day. I then visualized and listened to the six spectrograms simultaneously in Raven Pro 1.5 (Cornell Lab of

Ornithology, Ithaca, NY, U.S.A.). I counted the number of male individuals of each species heard vocalizing and visualized on spectrograms by leveraging the cues described above. For duetting species, in addition to counting the number of males, I also counted the number of female individuals heard and visualized on spectrograms responding to a male's song or initiating a duet. For plots with a single ARU, I used the intensity of sound and temporal overlap of conspecific cues (or the lack thereof) in the single channel to count individuals.

Statistical Analyses

With respect to the vegetation structure, occupancy and abundance analyses presented below, I fit models with Markov Chain Monte Carlo (MCMC) methods to estimate the posterior distribution for each model. I conducted these analyses with JAGS (v. 3.4.0) (Plummer 2013), called using R (v. 3.2.1) (R Development Core Team 2015) via the package R2jags (Su and Yajima 2015). I monitored model convergence via Gelman-Rubin statistics and a visual estimation of trace plots.

Analysis of vegetation structure

I transformed habitat variables on a proportion scale (mean understory density and canopy cover) with a logit transformation, adding a small constant (lowest non-zero value of the covariate) to both the numerator and denominator to account for zeros in the data (Warton and Hui 2011). I used a \log_{10} transformation on continuous covariates (mean canopy height and maximum height of standing vegetation). I estimated the pairwise correlations between forest type (categorical) and the above habitat variables with a Pearson's correlation test. Maximum height of standing vegetation was highly correlated with both canopy cover ($r = 0.66, p < 0.001$) and canopy height ($r = 0.97, p < 0.001$). Canopy height was also highly correlated with canopy cover ($r = 0.71, p < 0.001$) (Appendix D). I retained understory density and canopy cover as the variables capturing key elements of variation in vegetation structure between old growth and

logged forest. I then tested for differences in understory density and canopy cover between forest types with linear mixed models fit in a hierarchical Bayesian framework. I modeled understory density and canopy cover as a function of forest type with random intercepts for plots and random slopes for the effect of forest type. I fit three chains of 15,000 samples after an initial burn in period of 7000 samples for each model. I did not thin the chains (Link and Eaton 2012).

Correlation between species traits

I estimated the correlation between species traits with a Spearman's rank correlation test. Body size and mass were highly correlated ($r = 0.82$, $p < 0.001$) (Appendix E). I omitted body mass from further analyses.

Occupancy

I analyzed variation in occurrence between plots in old growth and logged forest only for species with a naïve occupancy estimate $\geq 10\%$ of plots ($n = 35$ species, Table 2-1). I used robust design occupancy models (MacKenzie et al. 2003) fit in a hierarchical Bayesian framework (Royle and Dorazio 2008). These models explicitly account for false negative errors that can bias estimates of occurrence and the estimated relationship between occurrence and habitat covariates (Royle and Dorazio 2008). I made the assumption that bird populations were closed to changes in occupancy across the three five-minute surveys in a day but open between the three sampling days. I also assumed that detection probability would not be confounded with random temporary emigration (Kendall 1999) due to our short sampling window spanning three consecutive days at each plot. Therefore, I used an implicit dynamics model where occupancy state at time $t + 1$ is not conditional on the state at time t (Kery and Schaub 2012). Estimating the Markovian transitions (*e.g.* colonization and extinction) between the days would also not have been biologically meaningful with respect to our questions (Rota et al. 2011, McCarthy et al. 2012). The full model (Appendix F) includes random site intercepts for both occupancy and detection,

among site random effects for occupancy, among survey random effects for detection as well as covariates for both occupancy and detection.

I specified all fixed and random effects to have flat normal priors with a mean of 0 and a precision of 0.001 (Gelman and Hill 2007, Royle and Dorazio 2008). I fit three chains of 20,000 samples after an initial burn in period of 6000 samples for each model. When 95% credible intervals of the slope parameters of a covariate overlapped zero (indicating ambiguous support for that covariate), I discarded the covariate and parameterized a simpler model (Royle and Dorazio 2008). I fit several models for each species with this manual, backward selection approach to model selection (Royle and Dorazio 2008, Kery and Schaub 2012).

Abundance

I analyzed variation in abundance of each species between plots in old growth and logged forest with N -mixture models (Royle 2004) fit in a hierarchical Bayesian framework (Royle and Dorazio 2008). In N -mixture models, repeated counts of individuals of a species from a number of sites are used to estimate abundance, while adjusting for imperfect detection of individuals (Royle 2004). I used an identical sampling design as the occupancy models above to fit robust design implicit dynamics N -mixture models. To account for zero-inflation (excess zeros) in the data, we fit the zero-truncated or hurdle N -mixture (Dorazio et al. 2013).

For each species, I modeled occupancy at site i as a Bernoulli process with site-specific occupancy probability $\psi_{i,k}$. I defined a binary latent variable $z_{i,k}$ for each site i . $z_{i,k} = 1$ if the species is present at site i over day k , and 0 if otherwise.

$$z_{i,k} \sim \text{Bernoulli}(\psi_{i,k}) \tag{2-1}$$

Conditional that the site i is occupied, I used the zero-truncated Poisson distribution to model abundance $N_{i,k}$. I parameterized this zero-truncated Poisson process by $\lambda_{i,k}$, which is the

mean and variance in abundance across the sites occupied by that species. I modeled abundance as:

$$N_{i,k}|Z_{i,k} \begin{cases} \sim \text{Poisson}(\lambda_{i,k}) \text{ Truncated}(1, \infty) & \text{if } z_{i,k} = 1 \\ = 0 & \text{if } z_{i,k} = 0 \end{cases} \quad (2-2)$$

The above parameterization of the hurdle model is similar to the standard N -mixture, but uses a conditional zero-truncated Poisson distribution instead of the standard Poisson distribution. I modeled the binomial observation process, conditional on true abundance $N_{i,k}$ of a species. I defined a latent variable $y_{i,j,k}$ representing the total number of individuals detected at site i , during survey j and day k .

$$y_{i,j,k} \sim \text{Binomial}(N_{i,k}, p_{i,j,k}) \quad (2-3)$$

I estimated site-specific variation in $\psi_{i,k}$, $\lambda_{i,k}$ and $p_{i,j,k}$ as a function of random intercepts, covariates and random effects using logit and log links, respectively. I fit covariates and random effects in an identical fashion as with the occupancy models and used the same manual, backward selection approach to model selection. For hurdle models, I fit three chains of 10,000 samples after an initial burn in period of 4000 samples for each model.

Song density

Song rate (songs per plot per minute) can be a function of species population density, *i.e.* it is intuitive to expect that song rate would increase with the density of breeding males in a given plot. Therefore, comparative studies of song rates between treatments must take population density into account. Per-capita song rate (song density henceforth) provides information on the number of songs each individual produces per minute in a given plot. I estimated song density for a species at site i as:

$$\text{Song density}_i = \frac{\text{Songs per minute}_i}{\text{Population density}_i} \quad (2-4)$$

Duet density

I calculated duet rate (duets per plot per minute) for each duetting species. I combined our counts of male and female individuals duetting and used hurdle models to estimate combined abundance at each plot. I estimated per-pair duet rate (duet density henceforth) for a species at site i as:

$$\text{Duet density}_i = \frac{\text{Duets per minute}_i}{\text{Population density (M+F)}_i} \quad (2-5)$$

Standardized differences in occupancy, abundance, song and duet density across old growth and logged forest

I estimated occupancy and abundance with statistical models and derived song and duet densities from counts of songs. To maintain consistency in calculating change in each of the above variables between old growth and logged forests, for each species, I estimated standardized differences (effect sizes) in each of the above response variables between old growth and logged plots. I calculated effect sizes with Cohen's d , the difference between logged and old growth group means of each response variable, standardized using the pooled standard deviation of the two groups (Borenstein et al. 2009), defined as:

$$d = \frac{y_{\text{logged}} - y_{\text{old growth}}}{SD_{\text{pooled}}}, \text{ where} \quad (2-6)$$

$$SD_{\text{pooled}} = \sqrt{\frac{(n_{\text{logged}} - 1)SD_{\text{logged}}^2 + (n_{\text{old growth}} - 1)SD_{\text{old growth}}^2}{n_{\text{logged}} + n_{\text{old growth}} - 2}} \quad (2-7)$$

Since Cohen's d may be a biased estimator of effect size, I used the conversion factor J to calculate a bias corrected metric referred to as Hedges g (Borenstein et al. 2009):

$$g = J \times d, \text{ where} \quad (2-8)$$

$$J = 1 - \frac{3}{4(n_{\text{logged}} + n_{\text{old growth}} - 2) - 1} \quad (2-9)$$

My definition of effect sizes for each response variable is therefore negative when a species shows a decline in that variable in logged forests and positive if vice versa. I resampled effect size estimates for each response variable for each species with 10,000 non-parametric bootstrap samples (with replacement) and generated 95% confidence intervals. I estimated all effect sizes with the package ‘bootES’ (Kirby and Gerlanc 2013) in R (v. 3.2.1).

Relationship between population and behavioral metrics

I used linear mixed models via *lmer* function in the package ‘lme4’ (Bates et al. 2015) in R to model the relationship between (i) abundance and song density, (ii) occupancy and song density and (iii) occupancy and abundance. I also modeled the relationships between (iv) abundance and duet density, (v) occupancy and duet density, and (vi) occupancy and abundance for duetting species. I included random effects for species nested within genus and family and location nested within block and forest type to control for potential phylogenetic non-independence (Hamer et al. 2015) and potential spatial autocorrelation between plots (Keitt et al. 2002, McCarthy et al. 2012), respectively.

Relationship between effect sizes and species traits

I used linear models via the *glm* function in R to conduct a series of weighted linear models between each effect size and all species traits. I used the inverse of the variance of Hedges g as a weight, which was calculated as: $v_g = J^2 v_d$ (Borenstein et al. 2009), where v_d , the variance of Cohen’s d , is:

$$v_d = \frac{n_{logged} + n_{old\ growth}}{n_{logged} n_{old\ growth}} + \frac{d^2}{2(n_{logged} + n_{old\ growth})} \quad (2-10)$$

Relationship between behavioral metrics and vegetation cover

I used linear mixed models via the *lmer* function in the package ‘lme4’ in R to examine how plot-level song density was related to forest type and vegetation cover. I included species

nested within genus and family as a random effect to control for potential phylogenetic non-independence.

Results

Vegetation Structure

As expected, logged forests had greater understory cover ($\beta = 0.71$; 95% CRI 0.35-1.04) and greatly reduced canopy cover ($\beta = -1.27$; CRI -1.67 - -0.86) (Figure 2-2).

Occupancy and Abundance

Fifteen of 35 species considered tended to decrease in occupancy (*i.e.* standard errors of bootstrapped effect size point estimates did not overlap zero) in logged forests compared to old growth forests, while 11 species tended to decline in abundance (Figure 2-3). Consistent with my predictions, these species include all the forest-interior sallying flycatchers and Monarch flycatchers (Families Muscicapidae and Monarchidae), ground and midstory gleaning babblers (Family Pellorneidae) and the only terrestrial thrush in our list of focal species (Family Turdidae). In contrast, the species that show increases in occurrence included understory babblers (Family Pellorneidae and Timaliidae) and flycatchers. Bulbuls (Family Pycnonotidae), midstory omnivores that forage by a combination of gleaning and sallying, also increased in occurrence and abundance in logged forests. The results of my modeling of occurrence and abundance as a function of understory density and canopy cover strongly indicated that understory insectivores tended to increase in occurrence with increasing understory cover, while for midstory insectivores, the converse was true.

Song and Duet Density

Fifteen species that tended to increase in abundance also tended to increase per-capita singing rates in logged forests. Nine species that tended to show reduced abundance in logged forests also showed reduced per-capita singing rates (Table 2-3, Figure 2-3, 2-4). From the

perspective of contrasting population and behavioral metrics in the context of logging, this result suggests that behavioral metrics reveal similar trends as population metrics. Overall, the results indicate that (i) forest interior specialists that were vulnerable to logging in terms of occupancy and abundance were also producing fewer songs per breeding male and (ii) habitat generalists were increasing in occurrence and abundance in logged forests as well as producing more songs per breeding male. My comparisons of duetting rates of babblers (Figure 2-4) in the Family Pellorneidae revealed that midstory gleaning species such as the scaly-crowned and moustached babblers exhibited significantly lower duetting rates in logged forests. However, another midstory gleaning species, the sooty-capped babbler, exhibited greater duet density in logged forest. Among the Timaliid babblers, three understory generalists exhibited increased duetting rates in logged forest while a midstory species showed no change.

Relationship between Population and Behavioral Metrics

Curves of fitted values of song density from linear mixed models plotted against abundance revealed that the relationship between abundance and song density is non-linear, *i.e.* song density tends to increase initially with abundance but reaches an asymptote and then drops off (Figure 2-5A). This pattern was consistent across both forest types. The relationship between occupancy and song density was also asymptotic (Figure 2-5B) while the relationship between occupancy and abundance was positive (Figure 2-5C).

Relationship between Behavioral Metrics and Vegetation Cover

Contrary to predictions, neither understory cover ($\beta = 0.02$, $SE = 0.03$, $p > 0.60$) nor canopy cover ($\beta = 0.02$, $SE = 0.06$, $p > 0.28$) explained variation in song density.

Relationship between Effect Sizes and Species Traits

Habitat breadth had a weak positive association with change in occupancy of species ($\beta = 0.06$, $SE = 0.03$, $p = 0.04$), such that species with greater habitat breadth tended to be more likely

to occur in logged forests than old growth. However, I did not find a tendency for any species trait to be associated with change in abundance of species [body size ($p > 0.76$), trophic position ($p > 0.21$), dietary breadth ($p > 0.48$), foraging stratum ($p > 0.29$), foraging strategy ($p > 0.74$) or habitat breadth ($p > 0.12$)]. Habitat breadth was positively associated with change in song density ($\beta = 0.03$, $SE = 0.01$, $p = 0.005$), such that species with greater habitat breadth tended to have higher per-capita song rates in logged relative to old growth forests. There was also a weak negative association between trophic position and change in song density ($\beta = -0.02$, $SE = 0.01$, $p = 0.09$). I did not find a significant tendency for any species trait to be associated with change in duet density [body size ($p > 0.88$), trophic position ($p > 0.69$), dietary breadth ($p > 0.64$), foraging stratum ($p > 0.82$), or habitat breadth ($p > 0.43$)].

Discussion

Occupancy v Abundance v Birdsong

I present the first study, to my knowledge, which contrasts population and behavioral responses of a tropical songbird community to logging. Overall, across most species, I found that changes in vocalization behaviors in responses to logging reveal similar patterns as changes in occurrence and abundance. Species that showed negative responses to logging in terms of abundance also showed negative responses in terms of per-capita singing rate and per-pair duetting rate. On the other hand, species that responded positively to logging in terms of abundance also responded positively in terms of per-capita singing rate and per-pair duetting rate (Table 2-3). For several species, notably forest interior specialists that are vulnerable to anthropogenic change, I demonstrate declining song density in logged forests in addition to the effect of abundance. I also show that song density is not directly proportional to abundance. This suggests that logging may negatively impact singing behavior in breeding songbirds that are vulnerable to such anthropogenic impacts, with potential negative consequences downstream for

mate choice, pairing success and territory defense (Catchpole and Slater 1995, Grant and Grant 1997, Slabbekoorn and Smith 2002, Slabbekoorn and Ripmeester 2008). This behavioral impact has hitherto been masked, due to the focus on comparing population and community responses to logging. Behavioral measures can serve as complimentary response measures in monitoring the status of breeding birds in systems subjected to human disturbance.

Understanding Community Impacts via Species Traits

My analyses of effect sizes in relation to species traits reveals that species with greater habitat breadth, the majority of the old world babblers, bulbuls and a few species of ground babblers (Table 1-1), are more likely to increase in occurrence in logged forests (Figure 2-3). These species are likely best adapted to the early successional conditions that logged forests may represent. Prior to human dominance of Borneo, many of these early successional species, such as the bold-striped and fluffy-backed tit babblers, the sooty-capped babbler and many of the bulbuls, may have been rare and patchily distributed since the only habitats suitable for them would likely have been open canopy gaps created by landslides and tree falls. On the other hand, late successional or forest interior species would likely have been abundant and widely distributed (Phillipps and Phillipps 2011). The degradation of forest by humans may have reversed this situation, allowing species that readily exploit degraded habitats to increase in abundance and expand their distributional range while shrinking the populations and range of forest interior species (Phillipps and Phillipps 2011). Habitat breadth was also positively associated with change in song density in response to logging. In other words, the more habitats a species is adapted to, the more likely it is exhibit a high singing rate in the altered conditions of logged forests. This again reflects that early successional species may be well adapted to the conditions in logged forests and are therefore increasing breeding activity. Trophic position was negatively associated with change in song density in response to logging. In other words,

insectivores were more likely to exhibit a lower singing rate in logged forests than generalist omnivores. Many of the forest interior insectivorous flycatchers were indeed declining in logged forests (Figure 2-3) and were also exhibiting reduced song densities (Figure 2-4).

Breeding Behaviors and the Impacts of Logging

Mate attraction and territory defense are the two primary functions of birdsong (Searcy and Andersson 1986, Catchpole 1987). During mate selection by female songbirds, the quality of the territory may matter above male characteristics (e.g. age, body size, plumage color, etc.) or song repertoire (Alatalo et al. 1986). However, pairing success in songbirds is known to be related to singing rate (Gottlander 1987, Radesater et al. 1987), a behavioral trait that is limited by food availability (Gottlander 1987). Females may therefore use singing rate as a proximate cue indicating the quality of the territory held by a male (Yasukawa 1981, Hoi-Leitner et al. 1995). I suggest that males of many forest interior species, which are producing fewer songs per-capita, may be signaling a relatively low quality habitat in logged forest (e.g. sparse food resources, Ewers et al. 2015). The converse may be true for males of habitat generalist species that are producing more songs per-capita in logged forest than in old growth.

Pairing success in breeding songbirds is known to decline with habitat fragmentation, degradation, edge effects (Villard et al. 1993, van Horn et al. 1995, Bayne and Hobson 2001), and anthropogenic noise (Habib et al. 2007). However, the impact of selective logging on breeding success remains unknown. Srinivasan et al. (2015) attempt to step in this direction with their analysis of the impact of logging on vital rates (survival and recruitment) that drive population responses. Defying predictions, they discovered a positive relationship between avian reproduction and logging intensity. Surprisingly, their work also suggests that natal dispersal tends to occur from more logged to less logged and intact forest patches. My analysis of duetting birds indicates lower duetting rates for forest specialists in logged forests (Figure 2-4). This

result potentially indicates that the primary functions of duetting (maintenance of the pair bond after establishment, acoustic contact, territory defense by a breeding pair and mate guarding) may be compromised in logged forests. I suggest that the species showing declining duetting should be prioritized for further investigation to ascertain whether pair bonds are indeed weaker in logged forests and whether these species have lower breeding success.

Caveats and Limitations

I did not consider other human pressures such as poaching, which may intensify with logging and drive species responses (Burivalova et al. 2015). Poachers have been captured on camera-traps at SAFE. However, small passerines such as my focal species are less likely to be directly impacted by poaching. I also did not include logging covariates such as the number of logging cycles, logging intensity (volume of timber extracted) and time since logging (*e.g.* Burivalova et al. 2015). While data on these variables are available at the scale of the entire SAFE experimental site (see Methods – Study Area), there is uncertainty about the spatial variation of these variables in the different blocks. My fine-scale measures of understory density and canopy cover are likely direct proxies for spatial variation in logging intensity. Since I focused on territorial passerine songbirds during the breeding season in Sabah, my estimates of occupancy and abundance likely reflect actual territory occupancy and not simply transient habitat use. Variation in song and duet density between forest types may be an artifact of sampling if one forest type was sampled at a different time relative to the other. However, I conducted this work at the start of the breeding season and continued to the end. I found no trend in detection probability for any species with Julian date, indicating that my results are not driven by sampling artifact. It may be argued that lower song density for some species in old growth forest may be due to all males in old growth being paired. However, this is unlikely since I

commenced sampling at the beginning of the breeding season when male song rates would have been high everywhere.

Bioacoustic Monitoring in an Age of Anthropogenic Change

I present an application of bioacoustics, a technology that has recently exploded into the ecological sciences (Laiolo 2010, Blumstein et al. 2011, Mennill et al. 2012), to sample the avian community using a rigorous, novel study design. I leveraged this design to estimate abundance from acoustic counts using zero-truncated hurdle N -mixture models (Dorazio et al. 2013). N -mixture models have been applied to estimate avian abundance on numerous occasions (Royle 2004, Chandler et al. 2011). However, to the best of my knowledge, avian abundance has never before been estimated by linking acoustic counts to N -mixture models. I also demonstrate that acoustic technology coupled to statistical models can be applied to investigate nuances of animal behavior that would be challenging, if not impossible, to achieve with traditional survey methods such as point counts. Acoustic methods are applicable to any species with diagnostic vocalizations. My results strongly suggest that, when paired with behavioral and ecological questions germane to species responses to global change, nuances of animal behavior can inform conservation in crucial ways and complement population trend assessments.

Conservation Implications

My results indicate that many forest interior species are showing declining singing rates in logged forests in addition to the effects on abundance. These potentially suggest declining breeding success for these species. We know little about the long-term impacts of logging. More than 83% of the datasets included in the meta-analysis by Gibson et al. (2011) had a time since logging of ≤ 12 years. Such short timeframes are insufficient to conclude whether logged forests offer viable habitats (Gibson et al. 2011). Another recent meta-analysis by Burivalova et al. (2015) indicates that the species that decline the most in abundance due to logging, have not

recovered even 40 years after the disturbance. Logged forests could very well be ecological traps (Battin 2004, Fletcher et al. 2012), where species extinction debts are repaid generations after the initial perturbation event (Tilman et al. 1994, Kuussaari et al. 2009). Yet this potential issue has not yet been addressed. I echo prior research (Clark et al. 2009, Edwards et al. 2011) in emphasizing that logged forests need to be conserved and rehabilitated (Edwards et al. 2009, Ansell et al. 2011), as opposed to the current practice of eventually converting them into depauperate monoculture plantations (Sodhi et al. 2004). Yet, the importance of preventing logging from occurring in the remaining old growth forests worldwide cannot be overstated. Old growth forests are indispensable for the conservation of biodiversity (Gibson et al. 2011).

Table 2-1. The 43 species of oscines detected in least one plot. Naïve occupancy estimates for eight species (highlighted with *) are < 0.10 (*i.e.* I detected them at < 5 plots out of 50). I omitted these species in statistical analyses due to paucity of data.

Common Name	Scientific Name	Species Code	# Plots with Detections		Naïve Occupancy (n=50)
			OG (n=18)	LG (n=32)	
Family Monarchidae – Monarch flycatchers					
Black-naped monarch	<i>Hypothymis azurea</i> (Boddaert, 1783)	BNMO	17	30	0.94
Asian paradise flycatcher	<i>Terpsiphone paradisi</i> (Linnaeus, 1758)	APRF	13	8	0.42
Family Muscicapidae – Old world flycatchers					
White-crowned shama	<i>Copsychus stricklandii</i> (Scopoli, 1788)	WCRS	13	19	0.64
Rufous-tailed shama	<i>Trichixos pyrropygus</i> (Lesson, 1839)	RUFS	6	6	0.24
Grey-chested jungle-flycatcher	<i>Rhinomyias umbratilis</i> (Strickland, 1849)	GCJF	11	2	0.26
Pale blue flycatcher	<i>Cyornis unicolor</i> (Blyth, 1843)	PLBF	13	0	0.26
Grey-headed canary-flycatcher	<i>Culicicapa ceylonensis</i> (Swainson, 1820)	GHCF	10	1	0.22
Bornean blue flycatcher	<i>Cyornis superbus</i> (Stresemann, 1925)	BOBF	6	3	0.18
Large-billed blue flycatcher*	<i>Cyornis caerulatus</i> (Bonaparte, 1857)	LBBF	1	1	0.04
Rufous-chested flycatcher*	<i>Ficedula dumetoria</i> (Wallace, 1864)	RCHF	0	1	0.02
Family Pycnonotidae - Bulbuls					
Spectacled bulbul	<i>Pycnonotus erythrophthalmos</i> (Hume, 1878)	SPBL	13	31	0.88
Black-headed bulbul	<i>Pycnonotus atriceps</i> (Temminck, 1822)	BHBL	9	28	0.74
Buff-vented bulbul	<i>Iole olivacea</i> (Blyth, 1844)	BVBL	7	22	0.58
Hairy-backed bulbul	<i>Tricholestes criniger</i> (Blyth, 1845)	HBBL	9	16	0.50
Red-eyed bulbul	<i>Pycnonotus brunneus</i> (Blyth, 1845)	REBL	0	21	0.42
Grey-cheeked bulbul	<i>Alophoixus bres</i> (Lesson, 1832)	GCBL	4	17	0.42
Yellow-bellied bulbul	<i>Alophoixus phaeocephalus</i> (Hartlaub, 1844)	YBBL	6	14	0.40
Cream-vented bulbul	<i>Pycnonotus simplex</i> (Lesson, 1839)	CVBL	1	13	0.28
Puff-backed bulbul	<i>Pycnonotus eutilotus</i> (Jardine & Selby, 1837)	PBBL	2	8	0.20

Table 2-1. Continued

Common Name	Scientific Name	Species Code	# Plots with Detections		Naïve Occupancy (n=50)
			OG (n=18)	LG (n=32)	
Black-and-white bulbul*	<i>Pycnonotus melanoleucos</i> (Eyton, 1839)	BWBL	3	1	0.08
Streaked bulbul*	<i>Ixos malaccensis</i> (Blyth, 1845)	STBL	4	0	0.08
Olive-winged bulbul*	<i>Pycnonotus plumosus</i> (Blyth, 1845)	OWBL	0	2	0.04
Finsch's bulbul*	<i>Alophoixus finschii</i> (Salvadori, 1871)	FNBL	1	0	0.02
Family Timaliidae – Old world babblers					
Chestnut-rumped babbler [♪]	<i>Stachyris maculata</i> (Temminck, 1836)	CRMB	18	30	0.96
Chestnut-winged babbler [♪]	<i>Stachyris erythroptera</i> (Blyth, 1842)	CWNB	16	31	0.94
Rufous-fronted babbler	<i>Stachyris rufifrons</i> (Hume, 1873)	RFRB	15	23	0.76
Fluffy-backed tit-babbler [♪]	<i>Macronous ptilosus</i> (Jardine & Selby, 1835)	FBTB	3	27	0.60
Grey-headed babbler	<i>Stachyris poliocephala</i> (Temminck, 1836)	GRHB	5	22	0.54
Bold-striped tit-babbler [♪]	<i>Macronous bornensis</i> (Bonaparte, 1850)	BSTB	0	20	0.40
Chestnut-backed scimitar-babbler	<i>Pomatorhinus montanus</i> (Horsfield, 1821)	CBSB	5	10	0.30
Black-throated babbler*	<i>Stachyris nigricollis</i> (Temminck, 1836)	BTHB	1	0	0.02
Family Pellorneidae – Ground babblers					
Short-tailed babbler	<i>Malacocincla malaccensis</i> (Hartlaub, 1844)	SRTB	16	28	0.88
Brown fulvetta	<i>Alcippe brunneicauda</i> (Salvadori, 1879)	BRFL	18	22	0.80
Rufous-crowned babbler [♪]	<i>Malacopteron magnum</i> (Eyton, 1839)	RCRB	18	20	0.76
Ferruginous babbler	<i>Trichastoma bicolor</i> (Lesson, 1839)	FERB	11	26	0.74
Black-capped babbler	<i>Pellorneum capistratum</i> (Temminck, 1823)	BCPB	15	18	0.66
Moustached babbler [♪]	<i>Malacopteron magnirostre</i> (Moore, 1854)	MUSB	15	17	0.64
Sooty-capped babbler [♪]	<i>Malacopteron affine</i> (Blyth, 1842)	SCPB	1	26	0.54
Scaly-crowned babbler [♪]	<i>Malacopteron cinereum</i> (Eyton, 1839)	SCRB	12	6	0.36
Horsfield's babbler	<i>Malacocincla sepiaria</i> (Horsfield, 1821)	HORB	2	5	0.14
Striped wren-babbler	<i>Kenopia striata</i> (Blyth, 1842)	STWB	6	0	0.12

Table 2-1. Continued

Common Name	Scientific Name	Species Code	# Plots with Detections		Naïve Occupancy (n=50)
			OG (n=18)	LG (n=32)	
Bornean wren-babbler*	<i>Ptilocichla leucogrammica</i> (Bonaparte, 1850)	BOWB	1	3	0.08
Family Turdidae – Thrushes					
Chestnut-capped thrush	<i>Zoothera interpres</i> (Temminck, 1826)	CCPT	4	1	0.10

♫ indicates species in which a breeding pair engages in duetting behaviour.

Table 2-2. Species traits of the focal songbirds in this study. Refer to footnote for abbreviations, units and details on various traits.

Species Code	Size	Mass	Trophic	Diet	Stratum	Strategy	Habitat
BNMO	16	11.1	2	2	3	3	7
APRF	20	18.5	2	1	3	3	3
WCRS	24.5	36.5	2	3	2	2	5
RUFS	21	40.9	2	1	2	1	2
GCJF	15	18.2	2	1	2	1	1
PLBF	17	21	2	1	3	3	1
GHCF	12.5	7.7	2	1	3	3	1
BOBF	15	NA	2	1	2	3	2
LBBF	14	NA	2	1	3	3	2
RCHF	10	9.5	2	1	2	3	2
SPBL	17	19.2	1	2	3	1	7
BHBL	17	25.5	1	3	3	2	8
BVBL	20	24	1	2	3	2	5
HBBL	16.5	17.1	1	2	2	2	3
REBL	19	28.8	1	4	2	2	8
GCBL	22	41.9	1	2	2	1	5
YBBL	20	32	1	2	2	1	3
CVBL	18	25.1	1	2	2	1	6
PBBL	21	35.3	1	2	3	1	6
BWBL	17	31	1	2	3	1	7
STBL	23	37.3	1	2	3	1	4
OWBL	20	36.7	1	2	2	1	7
FNBL	16	24.2	1	2	3	2	4
CRMB	17	29.2	2	2	3	1	6
CWNB	12	12.6	1	2	3	1	8
RFRB	12	10.6	1	2	3	1	7

Table 2-2. Continued

Species Code	Size	Mass	Trophic	Diet	Stratum	Strategy	Habitat
FBTB	15	18	2	1	2	1	5
GRHB	15	24.5	1	2	2	1	5
BSTB	13	10	1	3	2	1	4
CBSB	20	30.6	2	5	2	1	5
BTHB	16	26.2	2	2	3	1	8
SRTB	14	21.4	2	1	1	1	7
BRFL	14	14.3	2	2	3	1	4
RCRB	17	27.2	1	2	3	1	7
FERB	17	27.2	2	1	1	1	6
BCPB	17	25.1	2	3	1	1	7
MUSB	16	20.8	2	1	3	1	5
SCPB	16	18.6	2	1	3	1	6
SCRB	15	18.1	1	3	3	1	5
HORB	15.5	25.5	2	1	2	1	4
STWB	14	19.9	2	1	1	1	3
BOWB	16	40	2	1	1	1	5
CCPT	17	NA	1	4	3	1	3

Abbreviations and Units: Size = Body size (cm), Mass = Body mass (g), Trophic = Trophic Position (1 = Omnivore, 2 = Insectivore), Diet = Dietary breadth (larger number indicates that the species includes more items in its diet. Refer to Methods – Species traits for more details), Stratum = Foraging stratum (1 = ground, 2 = understory, 3 = midstory. Refer to Methods – Vegetation sampling for the definitions of each class), Strategy = Foraging strategy (1 = gleaning, 2 = both gleaning and sallying, 3 = sallying), Habitat = habitat breadth (larger number indicates that the species occurs in more habitats. Refer to Appendix A for definition of habitat types).

Table 2-3. Summary of species-level population and behavioral responses (effect sizes) to logging. Most species that show negative responses to logging (in terms of abundance) also show negative responses in terms of per-capita singing rates. On the other hand, most species that show positive abundance responses to logging also show positive responses in terms of per-capita singing rates.

Per-Capita Song Rate	Abundance		
	Positive	Negative	No Change
Forest Interior Specialists			
Positive	1	0	0
Negative	0	9	0
No Change	0	2	2
Habitat Generalists			
Positive	14	0	0
Negative	0	0	0
No Change	3	0	4

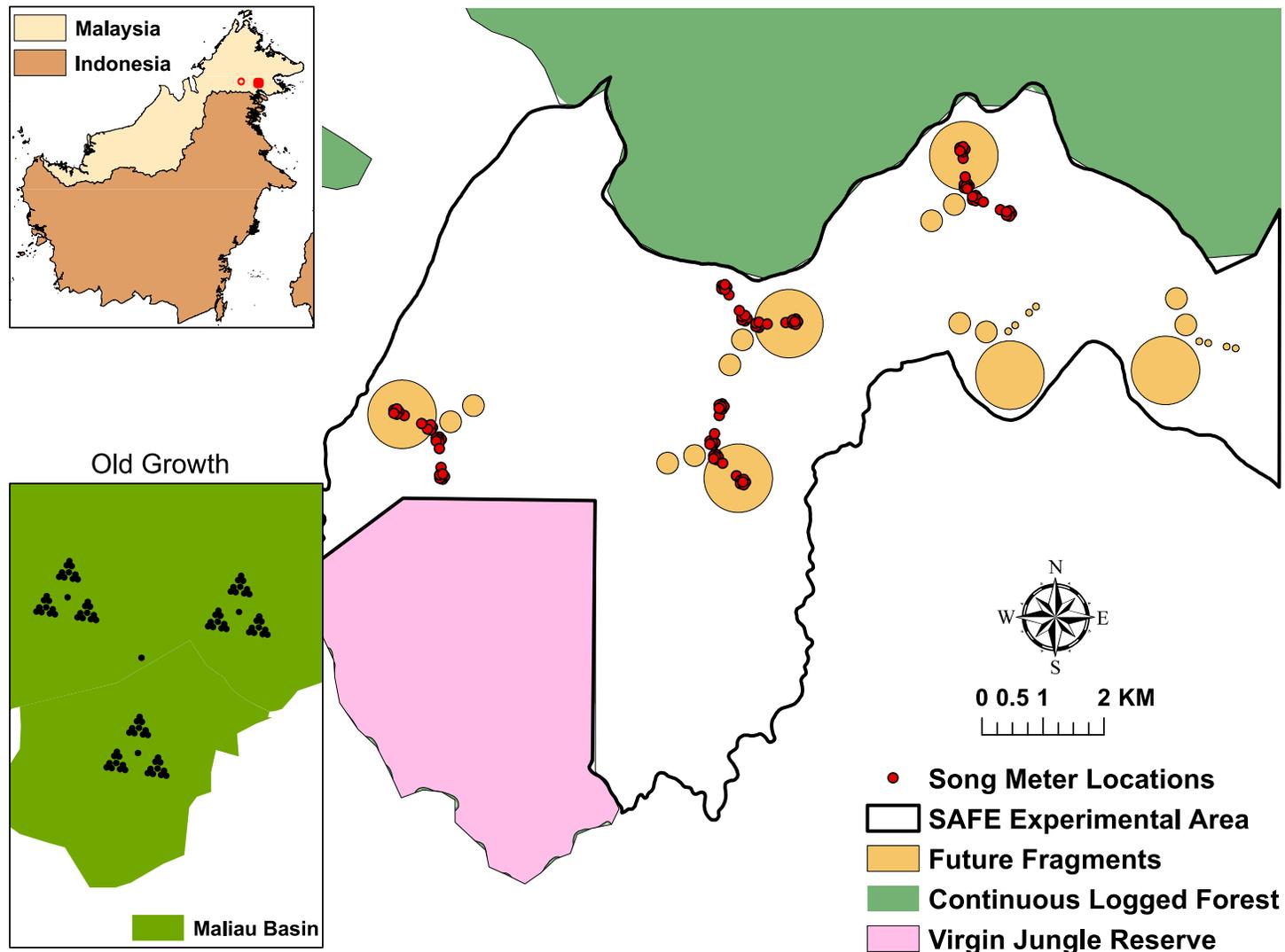


Figure 2-1. Study design showing location of the SAFE Project in Sabah, Malaysian Borneo (Inset – Top Left) and the placement of Song Meters or automated recording units (ARU’s) (red dots) in the various blocks at the SAFE Experimental Area (Ewers et al. 2011). I deployed ARU’s in the 1 ha fragments and replicated this design within the 100 ha fragments. I deployed ARU’s in an identical design at the SAFE old growth control sites (black dots) in the Maliau Basin (Inset-Bottom Left).

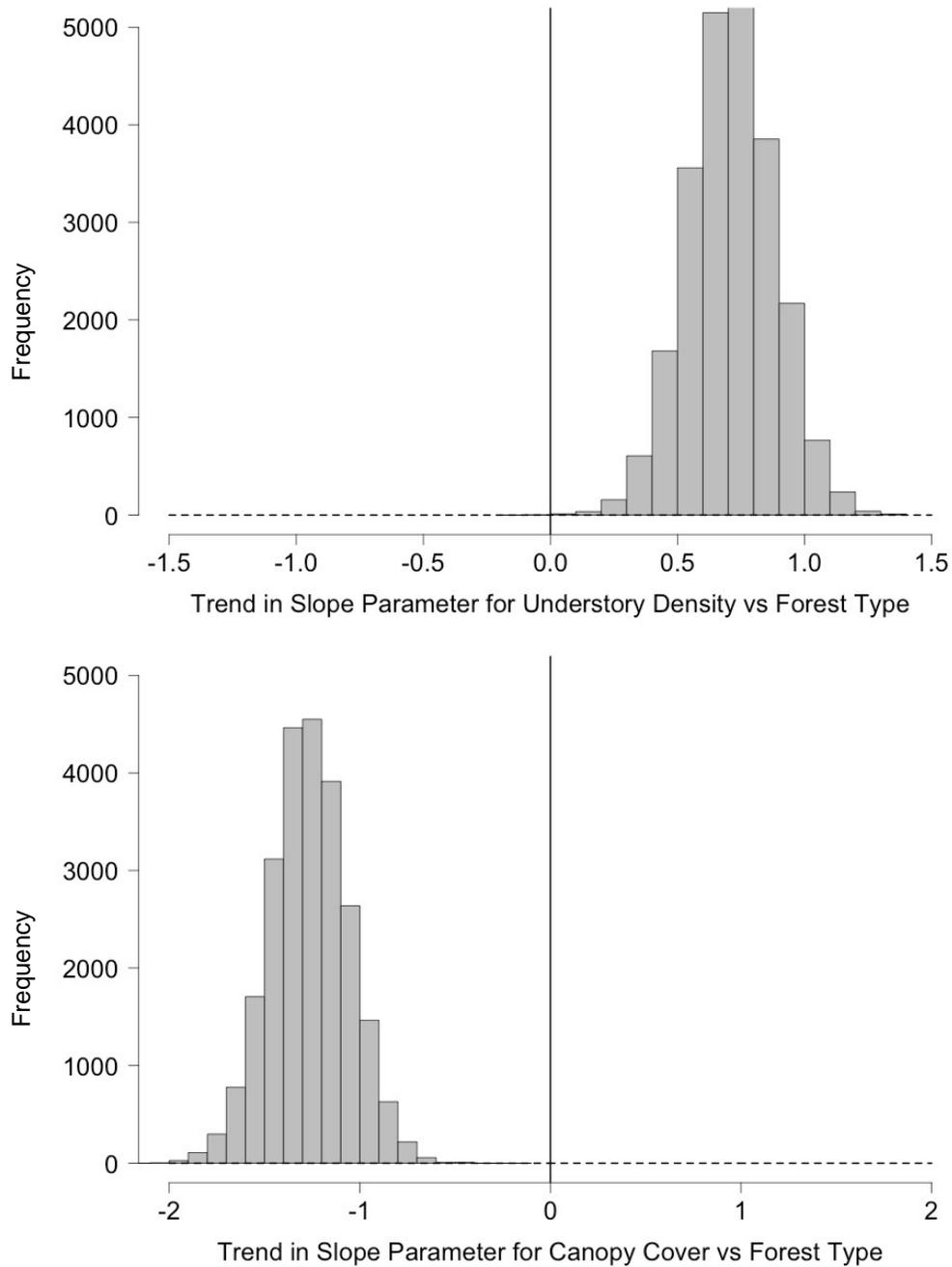


Figure 2-2. Posterior distributions for the effect of forest type on understory density and canopy cover. The vertical line represents the value of zero, *i.e.* no trend in vegetation variables as a function of logging. The dashed line represents the flat normal prior distribution that I specified in the linear mixed model. Understory density increases in logged forests (top) while canopy cover declines (bottom).

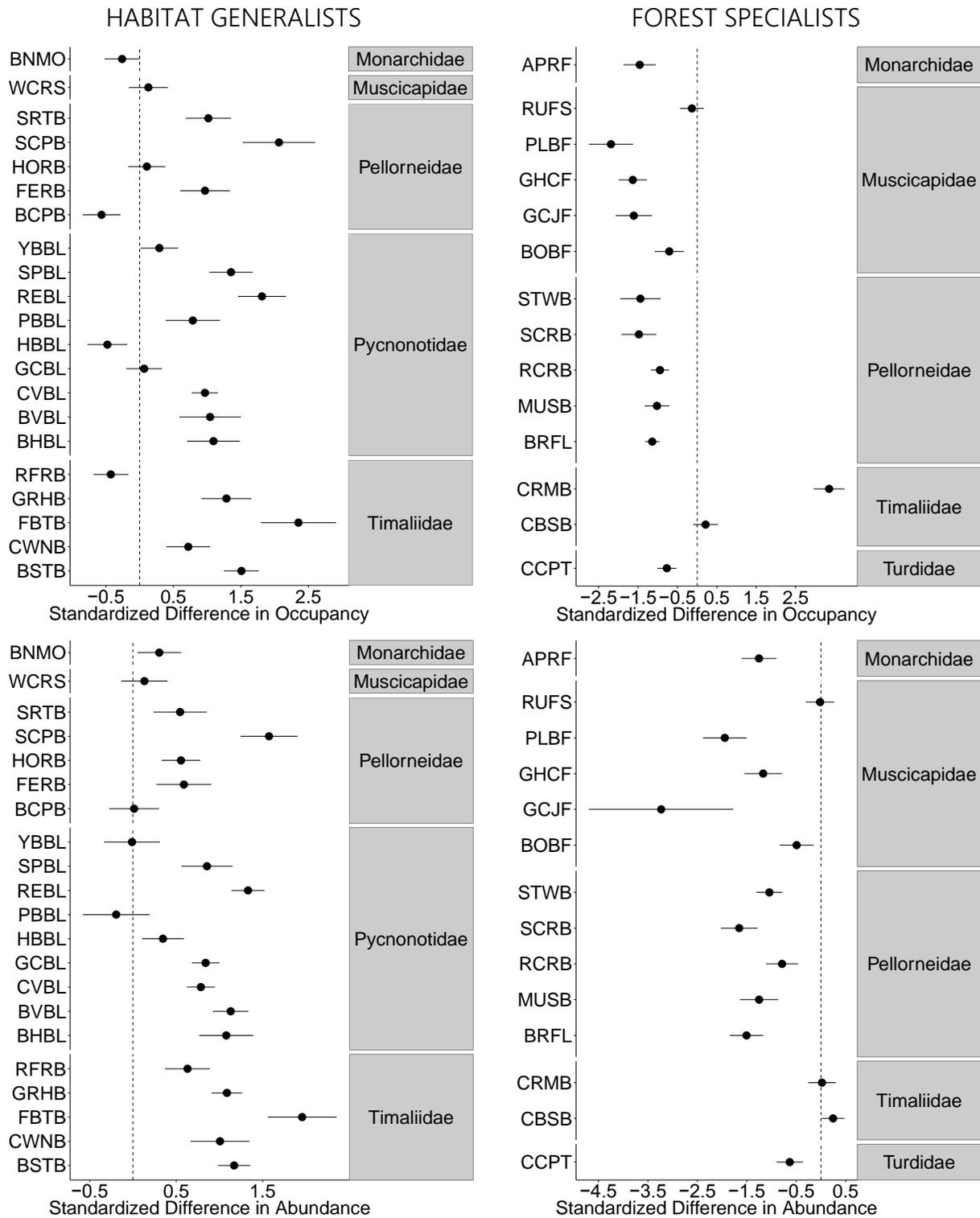


Figure 2-3. Standardized effect sizes (Hedges' g) for occupancy (top panel) and abundance (bottom panel) for habitat generalists and forest interior specialists respectively. Error bars represent ± 1 SE. Species are sorted by Family.

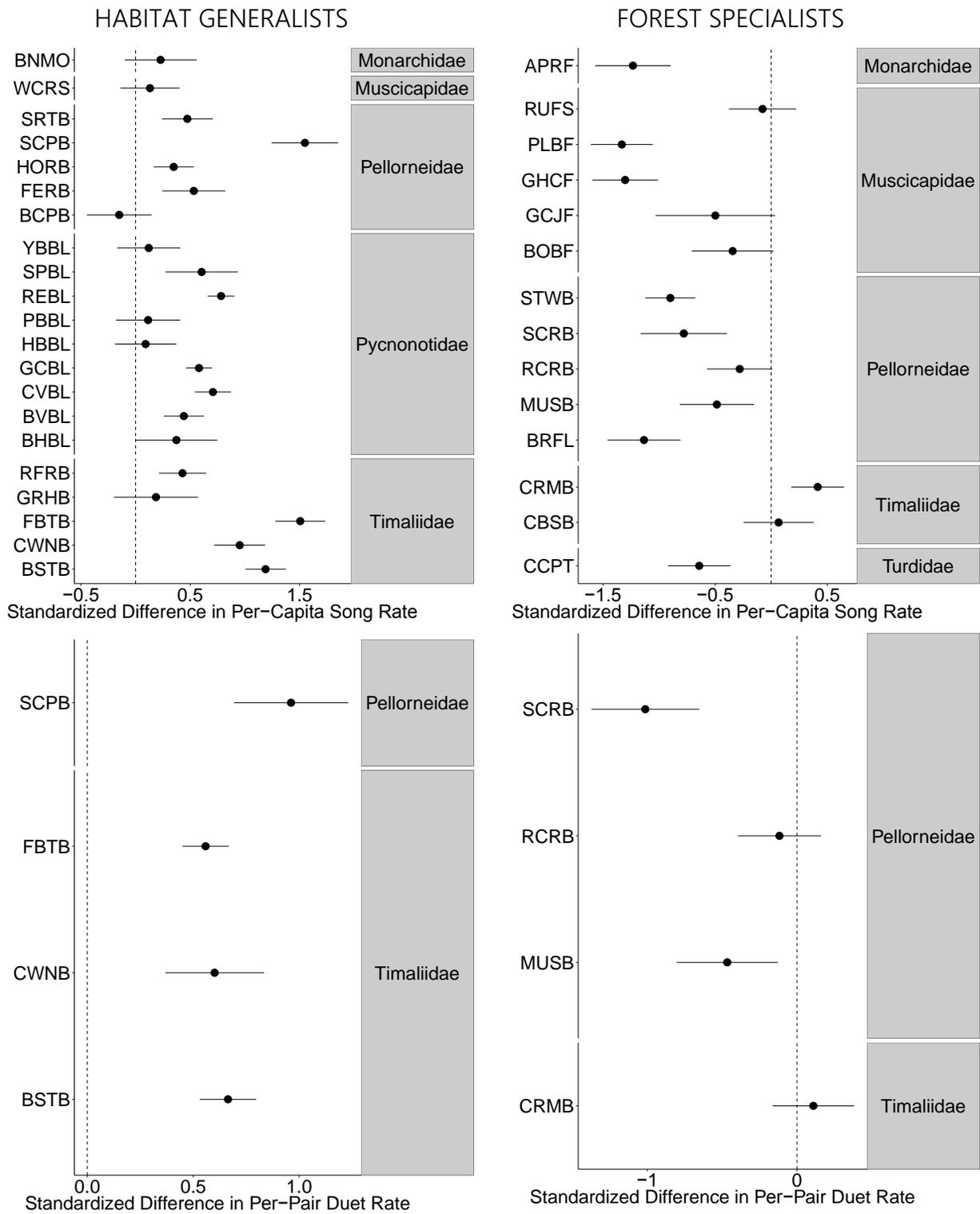


Figure 2-4. Standardized effect sizes (Hedges' g) for song density (top panel) and duet density (bottom panel) for habitat generalists and forest interior specialists respectively. Error bars represent ± 1 SE. Species are sorted by Family.

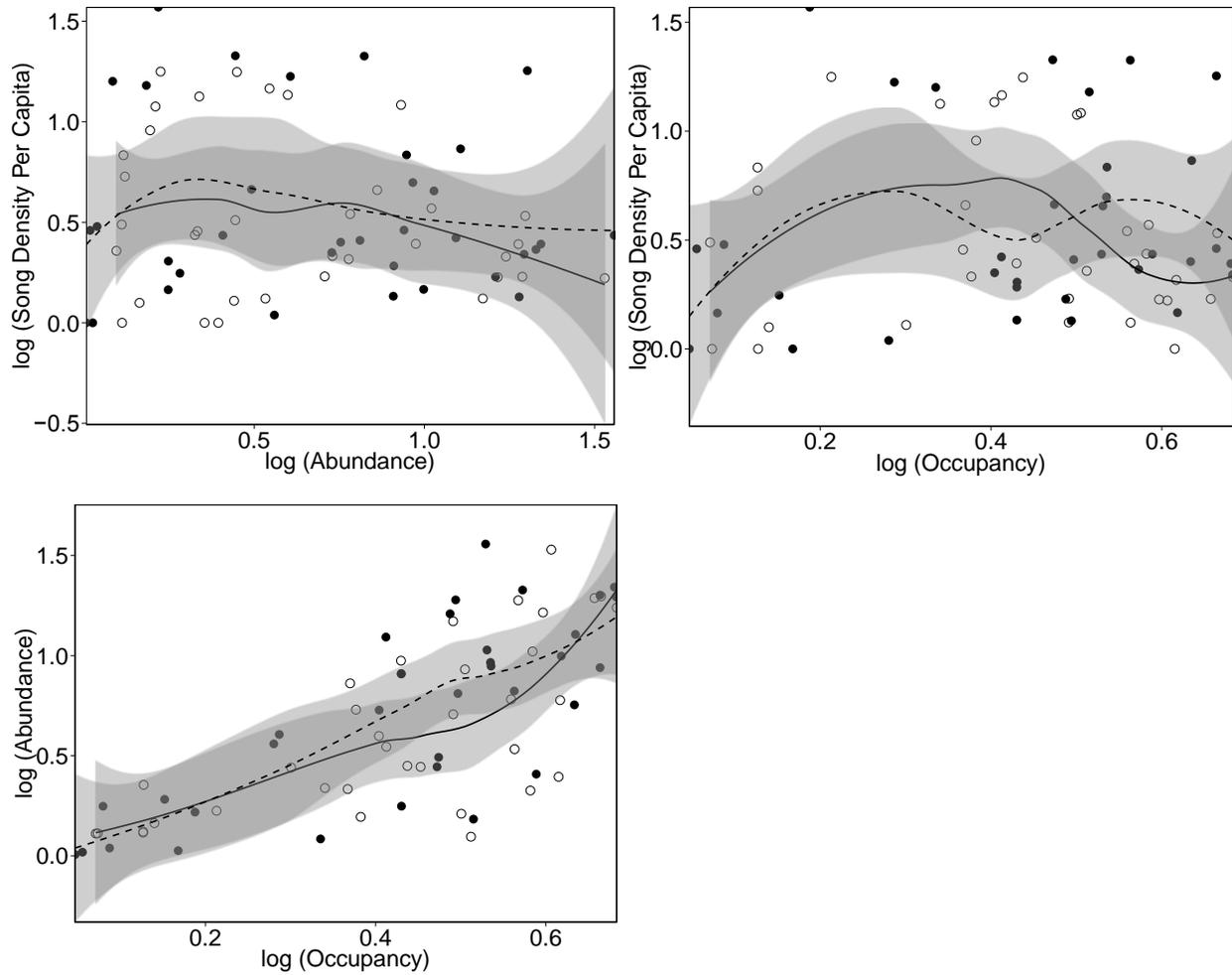


Figure 2-5. The relationships between abundance and song density (2-5A – top left), occupancy and song density (2-5B – top right) and occupancy and abundance (2-5C – bottom left). Closed circles = logged forest, open circles = old growth forest. Curve with the continuous line = fitted values of the linear model for old growth forest. Curve with the dashed line = fitted values for logged forest.

CHAPTER 3
FINE-SCALE POPULATION AND BEHAVIORAL RESPONSES OF SONGBIRDS TO
PERCEIVED PREDATION RISK ACROSS A LOGGING GRADIENT

Selective logging is a widespread and pernicious threat to tropical forests and biodiversity. Logging causes major shifts in vegetation structure, which may expose animals to altered predation risk. Predation may also have non-lethal, habitat-mediated behavioral impacts that may outweigh direct lethal effects. Thus, habitat change and perceived predation risk may have potential synergistic effects on animal behavior. In breeding songbirds, singing is a conspicuous behavioral activity and is critical for mate choice and pairing success. However, it can also attract the unwanted attention of predators. Alterations to singing behavior (*e.g.* reduced singing rates to escape detection) in the face of habitat change and predation risk may serve as an anti-predator strategy but may eventually have deleterious consequences for fitness and population dynamics. Little is known about the synergistic effects of habitat change and perceived predation risk on animal populations and behavior. I experimentally tested the effects of perceived predation risk on population and behavioral responses of two babbler species (Family Pellorneidae) in old growth and logged forests in Sabah, Malaysian Borneo. During the breeding season, I manipulated the cues of three avian predators that prey on adult passerines. I coupled this playback scheme with a novel, bioacoustic sampling design to estimate abundance and per-capita singing rates before and after playbacks. Finally, I tested whether behavioral responses of prey to enhanced risk vary with predator body size or with predator type. Contrary to expectations, I did not find synergistic effects of habitat change brought about by logging and perceived predation risk on either population or behavioral responses. However, my results suggest that breeding songbirds may respond to perceived predation risk by evacuating territories (reduced abundance post-playbacks) as well as by displaying cryptic behavior (reduced per-capita song rates post-playbacks). The effects of perceived predation risk may not necessarily

interact with habitat change caused by logging. My results suggest that the cost of fear can potentially have a negative impact on avian breeding success via both population and behavioral responses.

Introduction

Selective logging is a pervasive, yet often underrated, threat to tropical forests and biodiversity (Sodhi et al. 2004, Asner et al. 2009). Logging causes major changes to forest vegetation structure by eliminating much of the continuous canopy cover and by transforming the relatively open understory into a dense tangle of secondary growth over time (Johns 1988, Edwards et al. 2011). Such human-induced vegetation shifts may alter resource availability (Wilson and Johns 1982, Franzreb 1983, Zarette et al. 2000), and subsequently, impact the diversity, abundance and behavior of species in logged forests (Wilson and Johns 1982, Franzreb 1983, Johns 1986, 1987, Lampila et al. 2005).

Anthropogenic shifts in vegetation structure from logging may simultaneously influence other biotic processes, although these indirect effects have been largely neglected. In particular, changes in vegetation structure and cover may expose animals to altered predation risk (Gates and Gysel 1978, Flaspohler et al. 2001, Eggers et al. 2005). Predation may also have non-lethal, habitat-mediated behavioral impacts that may outweigh direct lethal effects (Rodríguez et al. 2001, Preisser et al. 2005, Cresswell 2008, Martin 2011). Thus habitat change and perceived predation risk may interact to influence animal behaviors such as altering pairing success (Lampila et al. 2005) or creating ecological traps (Battin 2004, Fletcher et al. 2012). Such modifications to behavior may have eventual deleterious consequences for fitness and population dynamics. Yet, little is known about the synergistic effects of habitat change and perceived predation risk on animal populations and behavior (Evans 2004).

Singing is a prominent behavior in oscine birds during the breeding season (Catchpole and Slater 1995). It is aimed at attracting mates and defending territories (Lima 2009) but may also attract the unwanted attention of predators (Zuk and Kolluru 1998). The risk of predation, therefore, has the potential to influence singing behavior (Lima 2009). Many species of breeding songbirds may rely on vegetation cover for protection when engaging in conspicuous singing behavior (Niemi and Hanowski 1984, Lima et al. 1987, Lima 1990, Rodríguez et al. 2001, Duncan and Bednekoff 2006, Moller et al. 2008). When faced with enhanced predation risk, some evidence suggests that birds may respond by singing from more protected perches (Duncan and Bednekoff 2006) or, by reducing singing rates, a form of cryptic behavior (Fontaine and Martin 2006). Cryptic behavior may be a successful strategy at predator avoidance, particularly when it may neither be possible nor optimal to seek new territory or additional protective cover within the current territory (Lima 2009). Such anti-predator strategies may have an eventual cost on successful pairing (Catchpole and Slater 1995). Yet, tests of the impact of perceived predation risk on avian singing behavior are sparse (Zuk and Kolluru 1998, Lima 2009). Furthermore, it is unknown whether habitat change from disturbances such as logging interacts synergistically with perceived predation risk to influence avian singing behavior.

I present the first experimental test of the synergistic effects of logging-induced habitat change and perceived predation risk on two babbler species (Family Pellorneidae) along a logging gradient in the Asian tropics. I examined two potential effects of experimental manipulations of predation risk: (a) population responses (changes in abundance) and (b) behavioral responses (changes in per-capita singing rates). I expected no change in per-capita singing rates for the black-capped babbler (*Pellorneum capistratum*), an understory insectivore that may seek cover in the dense understory of logged forests and continue to sing even when

perceiving greater predation risk. In contrast, I expected that the brown fulvetta (*Alcippe brunneicauda*), a mid-story insectivore, would reduce per-capita singing rates (*i.e.* display cryptic behavior) in the potentially riskier open midstory and canopy conditions of logged forests, when faced with enhanced threat. I manipulated the cues of three avian predators (2 accipiters of varying body size and 1 owl) that are known to prey on adult passerine birds and coupled this playback scheme to a novel, large-scale bioacoustic sampling design to measure species responses to enhanced risk. I first estimated abundance of prey species before and after experimental manipulations to test for population-level responses. I then tested for potential anti-predator cryptic behavior by estimating per-capita singing rates for each species in response to the same risk. Finally, I tested whether behavioral responses of prey to enhanced risk vary with predator body size or with predator type (Templeton et al. 2005).

Methods

Study Area

I conducted this study in Sabah, Malaysian Borneo in logged forest at the experimental site of the Stability of Altered Forest Ecosystems (SAFE) Project (Ewers et al. 2011) and in nearby old growth controls in the Maliau Basin Conservation Area (MBCA) (Figure 3-1). SAFE is located in the Kalabakan Forest Reserve, a logging concession comprised of hill dipterocarp forest within the Yayasan Sabah Forest Management Area. As part of SAFE, experimental forest fragments are being created of different sizes (1, 10 and 100 ha) and landscape context, with clearing for fragment creation initiating in 2013. However, for the results shown here, all sampling occurred in areas prior to any land clearing and fragment creation. Prior to this experiment, this area was subjected to multiple rotations of logging, the first of which began in the 1970's (Chong 2005, Fisher et al. 2011). Commercially valuable trees > 60 cm DBH were extracted and 112.96 m³ ha⁻¹ of timber was removed (Fisher et al. 2011). The second rotation,

commencing in the 2000's (Chong 2005, Fisher et al. 2011), encompassed three rounds (Struebig et al. 2013). Trees > 40 cm DBH were targeted (Fisher et al. 2011). 25.87, 22.32 and 18.16 m³ ha⁻¹ of timber was extracted during each round respectively (Yayasan Sabah, unpublished data). Logging ended in 2007-08 (Fisher et al. 2011), by which time 179 m³ ha⁻¹ of timber had been cumulatively removed (Struebig et al. 2013). Extensive collateral damage to forest structure also occurred due to the establishment of a grid of skid trails, access roads and log-landing zones (Wearn et al. 2013). Forest quality is highly varied and ranges from grassy open areas and low scrub vegetation, to nearly intact remnants on steep inclines and in rocky sections.

MBCA (~ 70 km from the SAFE experimental site) is a 588.4 km²-protected area designated by the Sabah State Government as a Class I Protection Forest Reserve. It mostly comprises undisturbed old growth hill dipterocarp forest although some parts of the periphery were lightly logged in the 1970's. In MBCA, I sampled only in the two SAFE old growth control sites (OG1, OG2) that have never been logged (Ewers et al. 2011).

Bioacoustic Sampling

I sampled the avian community in 28 plots [16 logged – SAFE, 12 old growth – MBCA] with Song Meter SM2+ GPS (Wildlife Acoustics Inc., Concord, MA, U.S.A.) automated recording units (ARU's) during April-July 2014 (Figure 3-1). For the purpose of my study, a plot refers to the size of a 1 ha circular fragment, the smallest experimental unit at SAFE (Ewers et al. 2011). My sampling window coincides with the major part of the breeding season for my focal species, which stretches from March-September in Sabah (Phillipps and Phillipps 2011). I set up microphone arrays at each of our plots. I used measuring tape, a compass (Suunto KB-20, Suunto Oy, Finland) and a GPS receiver (Garmin GPSMAP 60CSx, Garmin Ltd., Switzerland) to configure arrays that covered the entire 1 ha plot: I placed one ARU at the center of each plot and the remaining five at radii of 50 m from the center and adjacent to the plot boundary (the

radius of a 1 ha fragment is ~ 56 m) (Figure 3-1). I sampled the 1 and 100 ha fragments (prior to fragment creation) in each of the abovementioned blocks at SAFE. In the 1 ha fragments, I deployed arrays in the fragments closest to and furthest away from the adjacent 100 ha fragment. In the 100 ha fragments, I deployed arrays at the core and edge, thus mirroring the design in the 1 ha fragments (Figure 3-1). In old growth controls, I deployed arrays in identical fashion at plots in OG1 and OG2. I sampled each plot for five consecutive days, and programmed the ARU's to record bird vocalizations continuously for six hours each day, commencing with the dawn chorus at 6:00 AM and ending at 12:00 PM.

Experimental Design

In the above plots, I broadcast playbacks of predator vocalizations on the last two days of the five-day sampling period to enhance predator cues and the potential risk perceived by the prey bird community. I broadcast the vocalizations of two diurnal raptors native to the region: the crested goshawk (*Accipiter trivirgatus*) and the besra (*Accipiter virgatus*). I also broadcast the calls of a crepuscular/nocturnal predator: the Sunda scops-owl (*Otus lempiji*), since it was observed during the dawn hours (*direct personal observation and two detections by ARU's*). Each of these species is known to predate on adult passerine birds in the forests of Sabah (Phillipps and Phillipps 2011). The crested goshawk is also reported to prey on nestlings of passerine birds (Phillipps and Phillipps 2011). The two raptors differ in body size, with the goshawk being larger (37-46 cm, from beak tip to tail tip) than the besra (24-36 cm) (Phillipps and Phillipps 2011). Predator body size is a reliable predictor of risk in songbirds since small raptors tend to be more maneuverable than larger counterparts and may thus represent a greater degree of risk (Templeton et al. 2005). Therefore, I expected the calls of the besra would likely elicit a stronger negative behavioral response (cryptic behavior) than those of the crested goshawk (Templeton et al. 2005). I expected no cryptic behavior to the playbacks of the owl,

since songbirds are known to actively mob owls that they encounter during the daytime (Altmann 1956).

I assigned each plot to one of three treatments on days 4 and 5 of sampling using a randomized complete block design (Table 3-2): (i) predator playbacks with goshawk, besra and owl vocalizations, (ii) procedural control with playbacks of the Malayan long-nosed horned frog (*Megophrys nasuta*), a diurnal amphibian with distinctive and frequent vocalizations in our study area and, (iii) no playbacks *i.e.* silent control. I only manipulated cues and did not alter the predator community (*e.g.*, through removals; Fontaine and Martin 2006).

I deployed four playback stations within each 1-ha plot. Each playback station consisted of a waterproof loudspeaker [EcoXGear EcoExtreme (color: black for camouflage), Grace Digital Corporation, San Diego, CA, U.S.A.] and a digital audio player (SanDisk Sansa Clip+, SanDisk Corporation, Milpitas, CA, U.S.A.) that was sealed within the loudspeaker. I set up each station along four randomly selected radii of the microphone array at distances of 25 m (two stations) and 40 m (two stations) from the central ARU. I mounted the loudspeakers on trees at a standard height of 2 m above ground and additionally camouflaged them with leaves and twigs. I oriented each loudspeaker upwards at an angle of 45° and facing inwards into the plot so that the sound would carry into the center.

For each species of predator, I obtained recordings of three different individuals or exemplars from different locations (Appendix G). I randomly assigned one exemplar of each species to each plot, to avoid over-stimulating birds with the presence of too many predators (Kroodsma et al. 2001). I commenced playbacks at each plot between 6:00 – 8:15 AM. The first station (randomly selected) broadcast the first series of calls from a predator for three minutes. This was followed by 27 minutes of silence after which another station broadcast another

predator for three minutes. Another 27 minutes of silence followed after which the third predator started calling from the third station and so on. A complete playback cycle therefore comprised 63 minutes during which each predator called for three minutes once every 27 minutes. Over the course of the day (~12-16 hours until audio player batteries were depleted), playbacks were thus cycled through the four stations to provide the impression of three individuals of three species of predators calling at four different locations within the plot at different times. On the second day of treatments, I replaced audio players and loudspeaker batteries, reversed the distances of the stations and also reversed the direction of the playbacks to minimize habituation. For the procedural control, I recorded two *Megophrys nasuta* individuals vocalizing in our study area at SAFE with a solid-state recorder (Marantz PMD661, Marantz Corporation, Kanagawa, Japan) and a directional microphone (Sennheiser ME66/K6, Sennheiser GmbH & Co., Hanover, Germany) and used these for playbacks in identical fashion. In plots assigned as silent controls, I set up similar stations but with aluminum trays painted and moulded to resemble the speakers and shifted them in the same manner.

For each predator and procedural control, I prepared the playback files such that the vocalization rate (per unit time) mimicked the rate in the original recording. However, since these predators are relatively uncommon, the total amount of predator vocalizations provided within each plot likely exceeded the natural amounts of vocalizations of these predators in my study area. I used Audacity 2.0.5 (Audacity 2014) sound analysis software to remove background noise and normalize all recordings to the same amplitude for playbacks. I used a sound level meter (RadioShack 33-2055, RadioShack Corporation, Fort Worth, TX, U.S.A.) to standardize loudspeaker amplitude to 80 dB at 1 m horizontal distance.

Acoustic Analyses

I subsampled my acoustic recordings and manually extracted data from fifteen 1-minute clips for each day of sampling. I chose clips from one playback cycle commencing between 7:45-8:15 AM in a plot (depending on when playbacks were started in a given plot). To measure songbird responses immediately after the 3-minute playbacks of each predator, I extracted data from clips on a \log_2 scale at 1-2, 2-3, 4-5, 8-9 and 16-17 minutes after the calls of each predator respectively in the cycle. I extracted two types of data: counts of vocalizations and counts of individuals. The former enabled me to estimate song rates per minute, while the latter enabled me to estimate plot-level abundance. Thereafter, I used plot-level abundance estimates to calculate per-capita song rates before and after playbacks. See Appendix H for complete details on acoustic analyses.

Statistical Analyses

I analyzed species responses to treatments in terms of abundance and per-capita singing rates, first during the first three days of sampling when no treatments were applied and then during the last two days of sampling when different treatments were applied to each plot. I used the plot-level abundance estimates for each species to calculate per-capita song rates per minute for each species in each plot before and after treatments. Changes in song rates may be simply due to variation in abundance. Alternatively, they may be due to changes in risk perception and subsequent behavioral adjustments. I was able to disentangle density effects from treatment effects by estimating per-capita song rates in the above manner.

Abundance

To test for plot-level abundance responses of different species to treatments, I used N -mixture models fit in a hierarchical Bayesian framework (Royle and Dorazio 2008). To account

for zero-inflation (excess zeros) in the data, I fit zero-truncated (or hurdle) N -mixture models (Dorazio et al. 2013). See Appendix I for complete details on abundance estimation.

Effects of procedural control

Prior to testing the effects of predator playback treatments on population and behavioral responses of songbirds, I tested whether songbirds respond to all playbacks in a similar manner by examining the data from the procedural and silent controls. I used Welch's two-tailed t -tests to compare differences in the means of plot-level abundance and per-capita song rate of both species across the two controls. I also performed individual two-tailed t -tests for each species.

Population and behavioral responses to predator treatments

I first tested for a general effect of predator treatment (not considering predator identity) on the abundance and per-capita song rate of pre species. I used linear models via the *glm* function in R (v.3.2.1) (R Development Core Team 2015) to model (a) plot-level abundance estimates and (b) plot-level per-capita singing rates post-playbacks (days 4-5) as a function of forest type, treatment (predator v controls) and their interaction. I included pre-playback (days 1-3) plot-level estimates of abundance and per-capita singing rates as an additive effect and assumed a normal error distribution.

Next, I used generalized estimation equations via the package 'geepack' (Halekoh et al. 2006) in R to isolate short-term predator identity effects on per-capita singing rates of each species over the fine time-scale post-playbacks of each predator. Generalized estimation equations account for the non-independent nature of the data that results from sampling the same individuals of each species repeatedly over time in the same plots. I specified an identity link and a normal distribution since per-capita song rate is a continuous measure. I used an autoregressive correlation structure to account for the longitudinal nature of the data and to account for the fact that measurements taken immediately after playbacks were more likely to be correlated with

each other than those taken further apart in time. I modeled per-capita song rate post-playback as a function of forest type, predator identity and time since playback and included all two-way interactions between each of these predictor variables. I generally expected playbacks to have a non-linear effect on prey vocalization behaviors with prey reducing the rates of vocalizations immediately after playbacks and gradually increasing them over time. However, I ran separate models with time specified as linear, logarithmic and quadratic functions to account for potential linear and quadratic effects of playbacks. Finally, I ran a model with time specified as a factor (exchangeable correlation structure, potential autocorrelation not accounted for). For all models, I included plot as a within-subjects variable. I compared different models based on quasi-Akaike's Information Criterion (QIC) via the package 'MuMIn' (Bartoń 2016) in R.

Results

Effects of Procedural Control

Procedural control playbacks may have unexpected effects on focal species (Fletcher 2008). However, I found that the application of procedural controls did not significantly alter abundance ($p > 0.46$) or per-capita singing rates ($p > 0.12$) relative to silent controls for either species. Therefore, I combined silent and procedural controls into a single control group for all subsequent analyses (See Appendix J for t-test results on individual species).

Population Responses to Predator Treatments

Post-playback abundance did not vary by forest type for either the black-capped babbler ($\beta_{\text{ftype: old growth}} = 0.09$, SE = 0.44, $p > 0.83$) or for the brown fulvetta ($\beta_{\text{ftype: old growth}} = -0.14$, SE = 0.28, $p > 0.64$). However, there was a weak tendency for the black-capped babbler to have higher plot-level abundance pre-playbacks (days 1-3) ($\beta_{\text{pre}} = 0.43$, SE = 0.20, $p = 0.04$). This was much more pronounced for the brown fulvetta ($\beta_{\text{pre}} = 0.86$, SE = 0.14, $p < 0.001$), which tended to occur at higher abundance before predator playbacks were initiated.

Behavioral Responses to Predator Treatments

I found a general effect of predator treatments (not considering predator identity) on per-capita song rate of the black-capped babbler. There was a tendency for this species to have higher per-capita song rates pre-playbacks ($\beta_{\text{pre}} = 0.43$, SE = 0.18, $p = 0.03$). I also found a weak tendency for this species to exhibit a slightly higher per-capita singing rate in old growth forest ($\beta_{\text{ftype: old growth}} = 1.44$, SE = 0.59, $p = 0.05$). The brown fulvetta also showed a weak tendency to exhibit higher per-capita song rates pre-playbacks ($\beta_{\text{pre}} = 0.76$, SE = 0.39, $p > 0.06$) (Figure 3-1). However, per-capita song rate for this species was not higher in old growth forest ($\beta_{\text{ftype: old growth}} = 0.49$, SE = 0.63, $p > 0.45$). Per-capita song rates for the brown fulvetta were significantly higher in the plots assigned as silent controls in old growth forest ($\beta_{\text{ftype: old growth*silent}} = 4.01$, SE = 1.23, $p = 0.004$).

With respect to the short-term effects of each predator on prey vocalization behaviors, I found that the model parameterized with time as a logarithmic function was selected as the best model for both the black-capped babbler (quasi-likelihood= -197, QIC = 137, $w = 0.48$) and the brown fulvetta (quasi-likelihood= -45.3, QIC = -212, $w = 0.38$). This indicates that the response of both species to predators is to initially exhibit cryptic behavior and then gradually increase per-capita singing rate. The black-capped babbler showed a tendency to reduce singing rates slightly more upon perceiving the goshawk ($\beta_{\text{goshawk}} = -0.65$, SE = 0.39, $p > 0.09$) than on perceiving a besra or a Sunda scops-owl. I observed a similar tendency for the brown fulvetta to respond more negatively to goshawks but in old growth forest ($\beta_{\text{goshawk: old growth}} = -0.35$, SE = 0.21, $p > 0.08$). (Figure 3-2, Figure 3-3). The black-capped babbler also increased its singing rate post-playbacks more rapidly in old growth forest ($\beta_{\text{ftype: old growth: log2 (time)}} = -0.35$, SE = 0.21, $p > 0.08$). I did not observe a similar tendency for the brown fulvetta ($\beta_{\text{ftype: old growth: log2 (time)}} = -0.07$, SE = 0.06, $p > 0.23$).

Discussion

My results indicate that breeding songbirds may respond to perceived predation risk by evacuating currently held territories (reduced abundance post-playbacks) as well as by displaying cryptic behavior (reduced per-capita song rates post-playbacks). I initiated playbacks during April-May, just after the commencement of the breeding season for most species in Sabah (March-September) (Phillipps and Phillipps 2011). Furthermore, the duration of playbacks at my plots was short (two days), relative to prior studies that conducted playbacks over the entire breeding season (*e.g.* Zanette et al. 2011). Breeding males of both prey species may already have established territories when I commenced playbacks. It has been suggested that evacuating current territories to set up new ones may neither be possible nor optimal for breeding males (Lima 2009). However, despite commencing playbacks after many males had likely established territories and despite the short duration of playbacks, I observed population-level responses. Furthermore, I found a tendency for both species to exhibit higher per-capita singing rates before playbacks, indicating that the individual males that chose to remain within their territories after initiation of playbacks display cryptic anti-predator behavior (Figure 3-1). Avian singing behavior has direct links to breeding success (Catchpole and Slater 1995). Although cryptic behavior by reducing singing rates in response to a perceived predator may be an effective strategy in avoiding detection, it may have ramifications on fitness and population dynamics. These results suggest that perceived predation risk can potentially have a negative impact on avian breeding success via behavior (Martin 2011).

As expected, I did not observe a significant tendency for either species to respond cryptically to the calls of the Sunda scops-owl. Contrary to expectations, however, I observed a stronger negative behavioral response to the larger goshawk than for the likely more maneuverable besra (Figure 3-2, Figure 3-3). The goshawk is relatively more common (25-30

detections by ARU's) in my study sites than the besra (only one detection by ARU's). Both prey species may have a keener awareness of the goshawk than the besra, which may be one likely reason for this result.

There may be several reasons for the relatively weak treatment effects observed. Prey species may respond to the playbacks of predators by singing from more protected perches (Duncan and Bednekoff 2006). It is possible that several individuals may have continued to sing after moving to denser cover within their territories. Microphone arrays can be used to localize birds on the basis of time-of-arrival differences of sounds at different microphones within an array (Mennill et al. 2012). These data can then be coupled to measurements of understory and canopy cover, to potentially reveal fine-scale movements to relatively protected microhabitats within territories. Second, there is a possibility that songbirds may respond to enhanced predation risk via another form of cryptic behavior: shifting song frequencies and varying temporal modulation of sounds. It is known that birds in urban areas may shift song frequencies in order to be heard above the noise produced by traffic (Slabbekoorn and Peet 2003, Slabbekoorn and den Boer-Visser 2006). However, it is unknown whether songbirds may adapt their frequencies in response to enhanced predation risk. Predators use time-of-arrival and phase differences of sounds to cue in on singing prey (Marler 1955). Changing the spectral characteristics of songs may therefore enable avoiding predation (Marler 1955, Richards and Wiley 1980, Wiley and Richards 1982) but may have fitness consequences as songs altered in frequency may be less attractive to potential mates. Third, I considered only two species of oscines. It is likely that examining the wider community of songbirds and the responses of each species to enhanced risk may reveal more variation in terms of behavioral responses. Fourth, I sampled only one playback cycle. Sampling additional playback cycles to encompass slices of

time spread throughout the day may reveal time of day effects. For instance, it may be expected that owl playbacks may have more of an effect at dusk and dawn (Lima 2009).

Contrary to expectations, I did not find synergistic effects of habitat change brought about by logging and perceived predation risk on either population or behavioral responses. Rather, the black-capped babbler showed a tendency to exhibit higher per-capita singing rates in old growth forest, indicating that the effect of habitat may outweigh interactions between habitat and predator cues. The impacts of selective logging have been the subject of intense debate, with several studies indicating minimal impacts to the majority of species in certain taxonomic groups (Berry et al. 2010, Edwards et al. 2011, Woodcock et al. 2011, Wearn et al. 2013). The inferences of these studies, made on the basis of population and community measures such as occurrence, abundance and species richness, have been criticized as misleading (Didham 2011, Michalski and Peres 2013), since they rely on the assumption that the presence of a species is correlated with the absence of an impact (van Horne 1983, Bock and Jones 2004). I show that some species may respond negatively to habitat change brought about by logging by reducing singing rates, a behavioral modification that may likely have negative effects on pairing success. Such impacts cannot be revealed by population measures alone.

Experimental studies on the fine-scale effects of predation risk on terrestrial vertebrates are sparse, especially with regard the impact of perceived risk on avian behavior (Laiolo et al. 2004, Templeton et al. 2005, Emmering and Schmidt 2011). My study adds important experimental evidence that the cost of fear has the potential to interfere with avian breeding, potentially causing male songbirds to evacuate territories and display cryptic anti-predator behavior.

Table 3-1. The focal species of oscines in this study.

Common Name	Scientific Name	Species Code	# Plots with Detections		Naïve Occupancy (n=28)
			OG (n=12)	LG (n=16)	
Family Pellorneidae – Ground babblers					
Brown fulvetta	<i>Alcippe brunneicauda</i> (Salvadori, 1879)	BRFL	12	12	0.86
Black-capped babbler	<i>Pellorneum capistratum</i> (Temminck, 1823)	BCPB	11	14	0.89

Table 3-2. Assignment of microphone-array plots to different treatments on sampling days four and five

Forest type	Treatment		
	Control-Silence	Control-Procedural	Predator (Accipiter: 2, Owl: 1)
Logged (16)	3	3	10
Old growth (12)	2	2	8

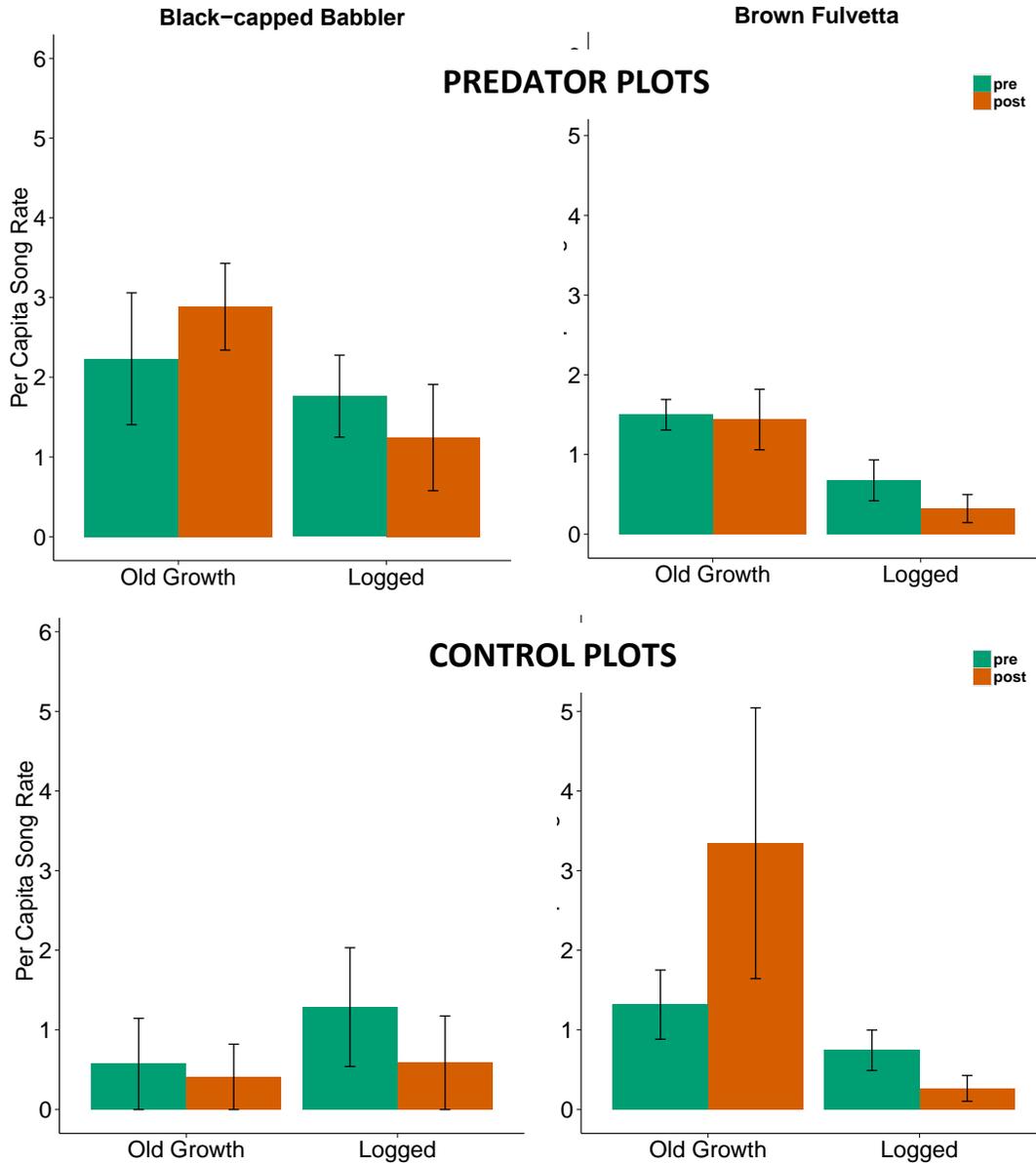


Figure 3-1. Behavioral responses (per capita singing rate) of the black-capped babbler (*Pellorneum capistratum*) and the brown fulvetta (*Alcippe brunneicauda*) to overall perceived predation risk from three predators (besra, crested goshawk and Sunda scops-owl) in old growth and logged forests. The brown fulvetta, a mid-story gleaning insectivore, displayed cryptic behavior by reducing its singing rate in logged forests following playbacks of predator calls. The black-capped babbler, an understory insectivore, displayed a similar tendency. We pooled silent and procedural control plots into one ‘control’ group (bottom panel).

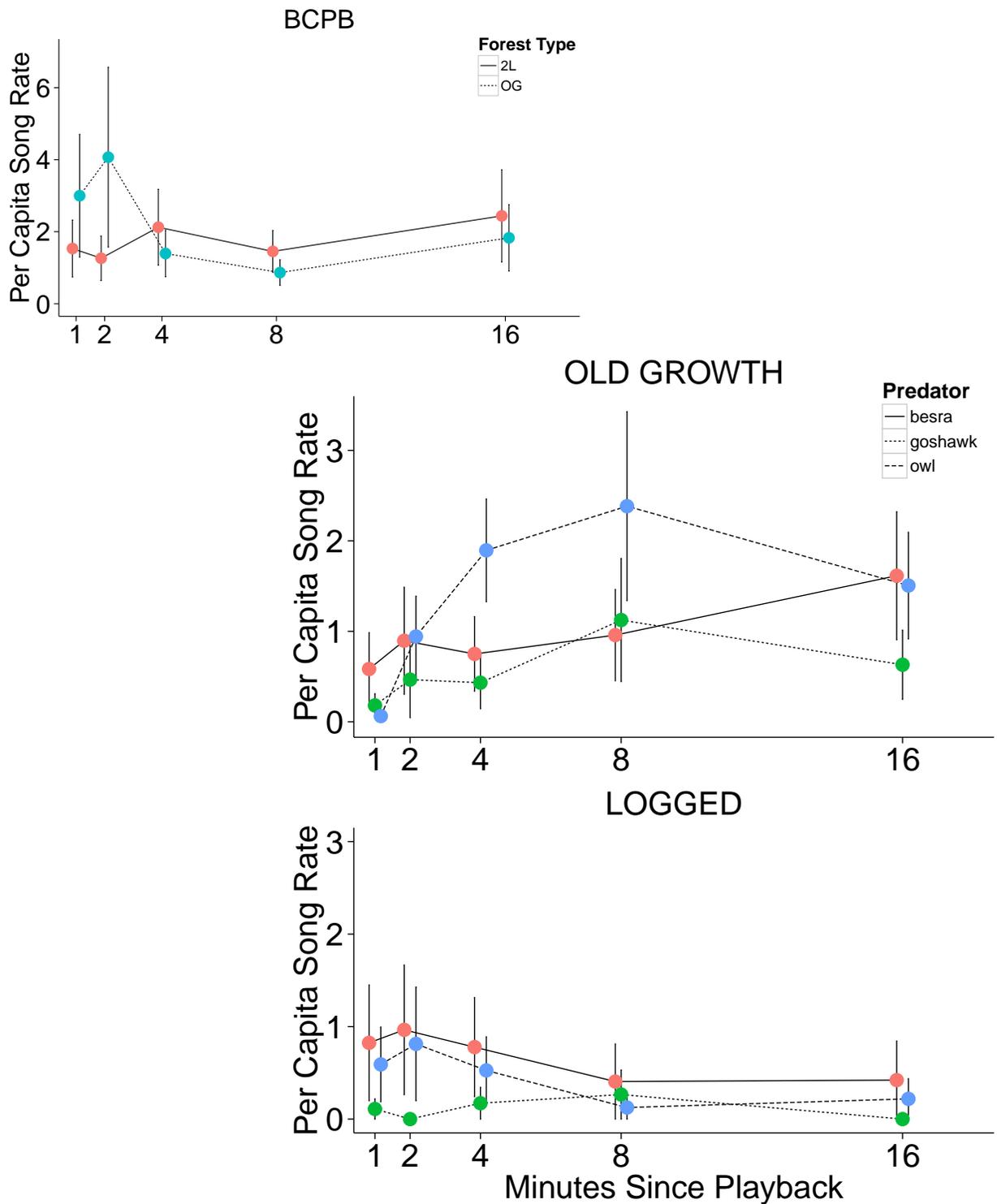


Figure 3-2. Differential behavioral responses of the black-capped babbler (BCPB) to the three predator species we used for playbacks. (Besra=red circles, continuous line; Goshawk=green circles, dotted line, Owl=blue circles, dashed line). Inset (top left panel): Per-capita singing rates in old growth (OG=blue circles, dotted line) and logged (2L=red circles, continuous line) forest on the three days of sampling preceding playbacks.

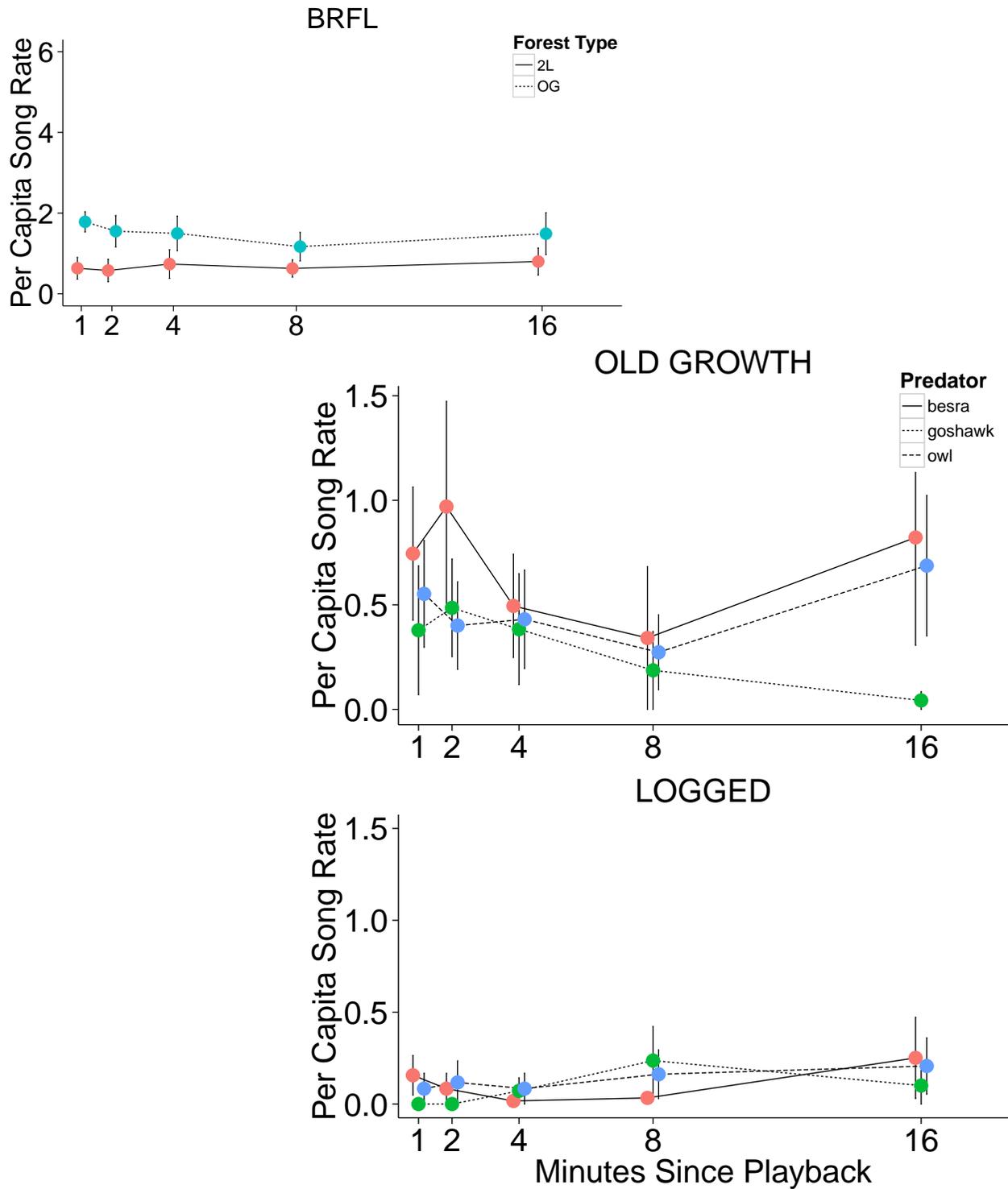


Figure 3-3. Differential behavioral responses of the brown fulvetta (BRFL) to the three predator species we used for playbacks. (Besra=red circles, continuous line; Goshawk=green circles, dotted line, Owl=blue circles, dashed line). Inset (top left panel): Per-capita singing rates in old growth (OG=blue circles, dotted line) and logged (2L=red circles, continuous line) forest on the three days of sampling preceding playbacks.

APPENDIX A
MEAN TREE DBH, HEIGHT AND CROWN DIAMETER OF *D. LANCEOLATA* TREES IN
OLD GROWTH AND LOGGED FOREST

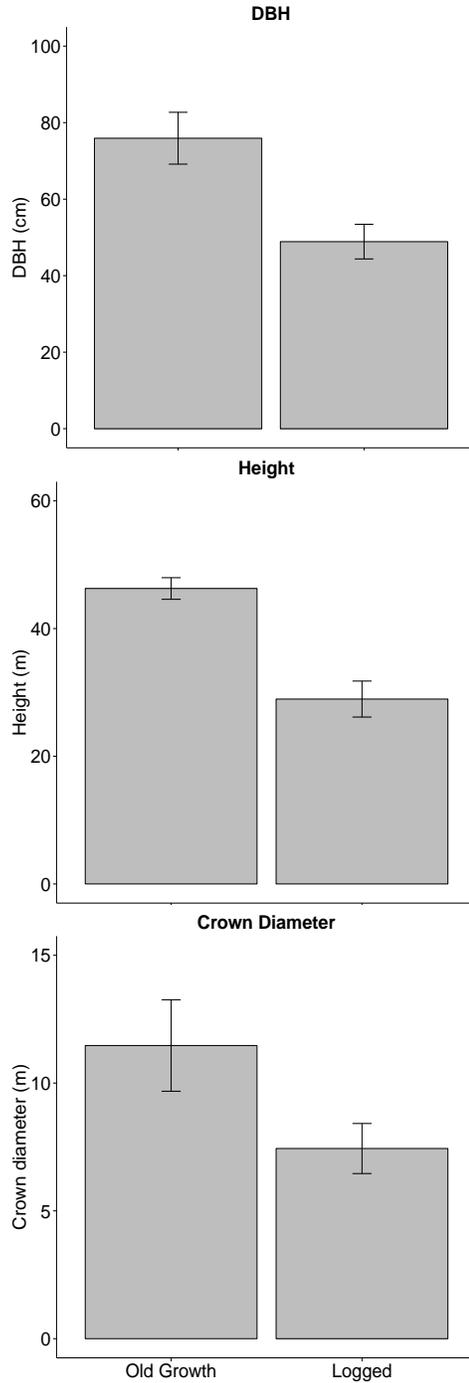


Figure A-1. Size measurements of individual experimental trees. Reproductive adult trees in old growth forest are significantly larger and taller than those in logged forest (n = 7 individuals in each forest type).

APPENDIX B
PATTERNS OF SEED LIMITATION IN THE WIDER PLANT COMMUNITY IN LOGGED
FOREST DURING THE 2014 MAST-FRUITING EVENT

Table B-1. Patterns of seed limitation in the wider plant community. I observed 9574 seeds of 13 species of heterospecific dipterocarps and 7 species of non-dipterocarps in the seedfall traps and unmanipulated plots around our seven experimental trees in old growth forest. In contrast, I observed only 745 seeds of 7 species of heterospecific dipterocarps and 2 species of non-dipterocarps in the seedfall traps and unmanipulated plots around our seven experimental individuals in logged forest.

Seed species/Family	# Seeds	
	Old Growth	Logged
Family Dipterocarpaceae		
<i>Hopea</i> sp.	0	343
<i>Parashorea malaanonan</i>	94	0
<i>Parashorea tomentella</i>	2871	56
<i>Shorea agamii</i>	38	0
<i>Shorea almon</i>	64	0
<i>Shorea atrinervosa</i>	170	6
<i>Shorea faguetiana</i>	187	44
<i>Shorea gibbosa</i>	569	0
<i>Shorea johorensis</i>	2105	166
<i>Shorea leprosula</i>	133	75
<i>Shorea ovata</i>	437	0
<i>Shorea parvifolia</i>	1534	52
<i>Shorea platyclados</i>	277	0
<i>Vatica</i> sp.	1	0
Family Phyllanthaceae		
<i>Baccaurea parviflora</i>	26	0
Family Myristicaceae		
<i>Knema</i> sp.	7	0
Family Fabaceae		
<i>Koompassia excelsa</i>	575	0
Family Meliaceae		
<i>Lansium</i> sp.	14	0
Identified to Family Only		
Family Fagaceae	12	1
Family Combretaceae	24	0
Family Clusiaceae	436	0
Unidentified	0	2
TOTAL	9574	745

APPENDIX C SPECIES TRAITS

I calculated body size and mass as the average of male and female body size and mass respectively, when available. Else, I used the midpoint of a range (del Hoyo et al. 2005, 2006, 2007, Dunning 2008, Phillipps and Phillipps 2011). I categorized trophic position as omnivore (insects, other invertebrates, fruits and other vegetable matter) or insectivore (insects and other invertebrates) (del Hoyo et al. 2005, 2006, 2007). I estimated dietary breadth as the number of categories of different prey types eaten by a species. Categories included insects/other arthropods, crustaceans, annelids, molluscs, other invertebrates, flowers, fruit and seeds (del Hoyo et al. 2005, 2006, 2007). I estimated habitat breadth as the number of habitat categories used by a species. Habitat categories included: primary broadleaf evergreen forest (comprising closed canopy mixed dipterocarp and naturally regenerating dipterocarp forest), moist deciduous or semi-evergreen forest, *kerangas* or Sundaland heath forest, upland heath, peatswamp forest, riverine forest (riparian areas adjacent to rivers or streams), grasslands, tidal riverine swamp forest, coastal heath, mangroves, logged forest (comprising secondary forest created by intensive and selective logging), scrub (dense tangles of undergrowth, bamboo thickets and cane brakes in both primary and logged forest), forest edges (roads, logging tracks and fragmented areas), plantations (includes mature and young *Eucalyptus*, *Albizia*, *Gmelina*, rubber and oil palm plantations), and cultivated areas and gardens (del Hoyo et al. 2005, 2006, 2007, Phillipps and Phillipps 2011). I categorized foraging stratum as ground, understory or midstory (del Hoyo et al. 2005, 2006, 2007, Wunderle Jr. et al. 2006, Hamer et al. 2015) and foraging strategy as primarily gleaning, both gleaning and sallying or primarily sallying (del Hoyo et al. 2005, 2006, 2007).

APPENDIX D
PEARSON'S CORRELATION MATRIX (R) BETWEEN HABITAT VARIABLES

Table D-1. Pearson's correlation matrix between habitat variables. Significant correlations are highlighted in italics.

Habitat Variable	Ftype	Udens	CC	Can.Ht	Max.Canopy
Ftype	1.00	0.49	-0.58	-0.83	-0.84
Udens		1.00	-0.33	-0.56	-0.48
CC			1.00	<i>0.71</i>	<i>0.66</i>
Can.Ht				1.00	<i>0.97</i>
Max.Canopy					1.00

Abbreviations: Ftype = forest type, Udens = mean proportion understory density, CC = mean proportion canopy cover, Can.Ht = mean canopy height, Max.Canopy = maximum height of standing vegetation.

APPENDIX E
SPEARMAN'S RANK CORRELATION MATRIX (*R*) BETWEEN SPECIES TRAITS

Table E-1. Spearman's rank correlation matrix between species traits. Significant correlations are highlighted in italics.

Trait	Size	Mass	Trophic	Dietary	Stratum	Strategy	Habitat
Size	1.00	<i>0.82</i>	-0.18	0.35	-0.07	0.08	-0.07
Mass		1.00	-0.13	0.16	-0.31	-0.30	-0.04
Trophic			1.00	-0.45	-0.18	0.18	-0.34
Dietary				1.00	0.00	-0.03	0.45
Stratum					1.00	0.28	0.08
Strategy						1.00	-0.07
Habitat							1.00

Abbreviations and Units: Size = body size (*cm*), Mass = body mass (*g*), Trophic: trophic position (omnivore, insectivore), Dietary = dietary breadth, Stratum = foraging stratum (ground, understory, midstory), Strategy = foraging strategy (gleaning, sallying, both), Habitat = habitat breadth.

APPENDIX F
DESCRIPTION OF THE FULL MODEL PARAMETERIZED FOR OCCUPANCY
ANALYSES

For each species, I modeled occupancy at each site i ($i = 1 \dots 50$) and day k ($k = 1, 2, 3$) as a Bernoulli process with site-specific occupancy probability $\psi_{i,k}$. I defined a binary latent variable $z_{i,k}$ for each site i . $z_{i,k} = 1$ if the species is present at site i over day k , and 0 if otherwise.

$$z_{i,k} \sim \text{Bernoulli}(\psi_{i,k}) \quad (\text{F-1})$$

Next, I modeled the observation process as another Bernoulli trial governed by the product of the occupancy state at i and k and detection probability $p_{i,j,k}$. Observation $y_{i,j,k} = 1$ if the species is detected at site i , during temporal replicate or survey j ($j = 1, 2, 3$) and day k , and 0 if otherwise:

$$y_{i,j,k} | z_{i,k} \sim \text{Bernoulli}(z_{i,k} \times p_{i,j,k}) \quad (\text{F-2})$$

I modeled $\psi_{i,k}$ as a function of both fixed and random effects through a logit link function: $\text{logit}(\psi_{i,k}) = \alpha_i + \beta_1 \times \text{forest}_i + \beta_2 \times \text{udens}_i + \beta_3 \times \text{cc}_i + \varepsilon_i$, (F-3) where α_i is a random intercept term for a site i , β_1 is the beta coefficient for covariate forest_i , forest_i is the categorical covariate for forest type (old growth = 0, logged = 1) at site i , β_2 is the beta coefficient for the understory density covariate udens_i at site i , β_3 is the beta coefficient for the canopy cover covariate cc_i at site i , and ε_i is the random effect of site i on $\psi_{i,k}$.

I modeled $p_{i,j,k}$ through a logit link function as a function of random intercepts for each site, covariates likely to influence detection probability, and a random survey effect to account for variation in detection probability of a species over time of day. I added a random survey effect because, for several species, I observed higher vocalization activity during the dawn chorus at 6:00 AM than at 7:00 and 8:00 AM. The covariates likely to influence detection probability are understory density and a quadratic relationship with Julian date (Rota et al. 2011,

McCarthy et al. 2012). Understory density, being different in the old growth and logged forests, may cause forest-specific variation in sound propagation (Wiley 1991) and subsequent detection of avian vocalizations by the microphones of an ARU. I considered the quadratic term of Julian date because songbirds may be most detectable in the early part of the breeding season when singing rates are at their highest during territory establishment but less so as nesting activity commences (Wilson and Bart 1985):

$$\text{logit}(p_{i,j,k}) = \alpha_i + \beta_1 \times \text{udens}_i + \beta_2 \times \text{Julian date}_i + \beta_3 \times (\text{Julian date}_i)^2 + \varepsilon_j, \quad (\text{F-4})$$

where α_i is a random intercept term for site i , β_1 is the beta coefficient for covariate udens_i , β_2 is the beta coefficient for covariate Julian date_i , β_3 is the beta coefficient for the quadratic term of Julian date_i , and ε_j is the random effect of time of day (survey) on $p_{i,j,k}$.

APPENDIX G
PREDATOR VOCALIZATION EXEMPLARS

Table G-1. Vocalization exemplars for the three predators used for playbacks in this study. I obtained three vocalization exemplars from different locations for each of the three predators used in this study. I randomly assigned each exemplar to various plots as shown below:

Predator and Exemplar Location	Recordist	Plots – Old Growth n = 8	Plots – Logged n = 10
<i>Crested goshawk (Accipiter trivirgatus)</i>			
Danum Valley, Sabah, Malaysian Borneo Mindanao, Philippines*	Jelle Scharringa	OG1-712, OG1-715, OG1-721	B-1-4, B-100-1, D-100-4, F-100-1
	Stijn De Win	OG1-717, OG1-718	D-1-1, E-1-1, F-100-4
Java, Indonesia*	Bas van Balen	OG1-711, OG2-724, OG2-728	D-100-1, E-1-4, F-1-1
<i>Besra (Accipiter virgatus)</i>			
Kinabalu National Park, Sabah, Malaysian Borneo Gunung Merapi, Java, Indonesia*	Andrew Boyce	OG1-712, OG2-724, OG2-728	B-1-4, B-100-1, D-1-1, E-1-1
	Bas van Balen	OG1-711, OG2-721	D-100-1, E-1-4, F-1-1
Gunung Salak, Java, Indonesia	Jelle Scharringa	OG1-715, OG1-717, OG1-718	D-100-4, F-100-1, F-100-4
<i>Sunda scops-owl (Otus lempiji)</i>			
West Kalimantan, Indonesian Borneo*	Bas van Balen	OG1-712, OG2-728	B-1-4, F-1-1, F-100-4
Central Kalimantan, Indonesian Borneo*	David Marques	OG1-715, OG1-718, OG2-724	B-100-1, D-100-1, F-100-1
Brumas, Sabah, Malaysian Borneo*	David Edwards	OG1-711, OG1-717, OG2-721	D-1-1, D-100-4, E-1-1, E-1-4

* Indicates that the recording was obtained from the online birdsong database Xeno-Canto (www.xeno-canto.org). I obtained the remaining recordings directly from the recordists.

APPENDIX H ACOUSTIC ANALYSES FOR PREDATOR PLAYBACK EXPERIMENT

I divided each six-hour (6:00 AM – 12:00 PM) recording into five-minute clips and split stereo channels into individual mono tracks. Since I mounted the two microphones directly on the opposing sides of each ARU (29.5 cm apart), the recordings in the two channels from a given ARU are near replicas of each other. Therefore, I mostly used the left channel for all analyses. In some cases, when the left channel contained no acoustic data due to a failed microphone (animal or weather damage), I used the right channel. I subsampled our recordings by selecting five one-minute clips in a playback cycle of 63 minutes. The cycle I used commenced from ~ 7:45 AM – 8:10 AM depending upon when playbacks were started at a given plot. I then manually extracted the bird data for all analyses for this study from these one-minute clips with Avisoft SASLab Pro (Specht 1998). I performed a Fast Fourier Transform (sampling frequency 22050 Hz, FFT length 512, temporal overlap 50%, time resolution 11.6 ms, frequency resolution 43 Hz) with a Flat Top window function to suppress spectrum distortion (Specht 1998). I listened to each clip for diagnostic vocalizations of focal species while simultaneously viewing the spectrograms to distinguish the species-specific spectral characteristics of different vocalizations. I extracted the following data: (i) *Counts of vocalizations (songs and duets)*: A bird may vocalize repeatedly within a five-minute interval. In many species, a song comprises several syllables that are grouped together and produced in rapid succession (< 0.5 s inter-syllable gap). In other species, songs comprise individual syllables that are > 0.5 s apart in time. Thus, my definition of song is species specific. In each one-minute clip, I counted individual songs that were separated in time from similar songs. I took care to count overlapping songs (*e.g.* two or more territorial males singing in rapid succession, or a breeding pair duetting), through careful listening and visual inspection of spectrograms. For duetting species, I only analyzed five-minute clips in which both

the male and female were singing and counted the number of distinct male and female songs. (ii) *Detection histories*: I collapsed the counts of vocalizations above in each five-minute clip to obtain detection/non-detection data for each species in each clip. (iii) *Counts of individuals*: To estimate population density (individuals per plot or unit area) from acoustic cues, it is necessary to either distinguish songs from different individuals or convert song rate (*e.g.* songs per plot per minute) to population density (Dawson and Efford 2009). I chose to distinguish (and count) different individuals of each species vocalizing in each five-minute clip. Observers conducting point count surveys leverage cues such as the intensity and direction of sound, and temporal overlap with conspecific vocalizations to identify species and count the number of individuals heard vocalizing (Ralph et al. 1995). Similar principles are applicable with respect to counting individuals with acoustic recordings (Rempel et al. 2005, Celis-Murillo et al. 2009). To do so, I first used Avisoft SASLab Pro to create multi-channel clips by combining the six channels (each coming from one of the six ARU's in an array) from a given time interval (*e.g.* 6:00-6:05 AM) for a particular day. I then visualized and listened to the six spectrograms simultaneously in Raven Pro 1.5 (Cornell Lab of Ornithology, Ithaca, NY, U.S.A.). I counted the number of male individuals of each species heard vocalizing and visualized on spectrograms by leveraging the cues described above. For duetting species, in addition to counting the number of males, I also counted the number of female individuals heard and visualized on spectrograms responding to a male's song or initiating a duet. For plots with a single ARU, I used the intensity of sound and temporal overlap of conspecific cues (or the lack thereof) in the single channel to count individuals.

APPENDIX I HURDLE *N*-MIXTURE MODELING

I analyzed variation in abundance of each species between plots in old growth and logged forest with robust-design *N*-mixture models (Royle 2004) fit in a hierarchical Bayesian framework (Royle and Dorazio 2008). In *N*-mixture models, repeated counts of individuals of a species from a number of sites are used to estimate abundance, while adjusting for imperfect detection of individuals (Royle 2004) that can bias estimates of abundance. I made the assumption that bird populations were closed to changes in abundance within the three five-minute surveys in a day but open between the sampling days. I also assumed that detection probability would not be confounded with random temporary emigration (Kendall 1999) due to our short sampling window spanning three consecutive days at each plot. Therefore, I used an implicit dynamics model where occupancy state at time $t + 1$ is not conditional on the state at time t (Kery and Schaub 2012). Estimating the Markovian transitions (*e.g.* colonization and extinction) between the days would also not have been biologically meaningful with respect to my questions. To account for zero-inflation (excess zeros) in the data for some species, I fit the zero-truncated or hurdle *N*-mixture (Dorazio et al. 2013). I did so for all species, to ensure uniformity of model type used to estimate abundance. My full model (presented below) includes random site intercepts for both occupancy and detection, among site random effects for occupancy and abundance conditional on occupancy, among survey random effects for detection as well as covariates for both occupancy and detection.

For each species, I modeled occupancy at site i as a Bernoulli process with site-specific occupancy probability $\psi_{i,k}$. I defined a binary latent variable $z_{i,k}$ for each site i . $z_{i,k} = 1$ if the species is present at site i over day k , and 0 if otherwise.

$$z_{i,k} \sim \text{Bernoulli}(\psi_{i,k}) \tag{I-1}$$

Conditional that the site i is occupied, I used the zero-truncated Poisson distribution to model abundance $N_{i,k}$. I parameterized this zero-truncated Poisson process by $\lambda_{i,k}$, which is the mean and variance in abundance across the sites occupied by that species. I modeled abundance as:

$$N_{i,k}|z_{i,k} \begin{cases} \sim \text{Poisson}(\lambda_{i,k}) \text{ Truncated } (1, \infty) & \text{if } z_{i,k} = 1 \\ = 0 & \text{if } z_{i,k} = 0 \end{cases} \quad (\text{I-2})$$

The above parameterization of the hurdle model is similar to the standard N -mixture, the difference being in how the zero-truncated distribution is used instead of a Poisson distribution. Next, I modeled the observation process, conditional on true abundance $N_{i,k}$ of a species. I defined a latent variable $y_{i,j,k}$ representing the total number of individuals detected at site i , during survey j and day k :

$$y_{i,j,k}|z_{i,k} \sim \text{Binomial } N_{i,k}, p_{i,j,k} \quad (\text{I-3})$$

I estimated site-specific variation in $\psi_{i,k}$, $\lambda_{i,k}$ and $p_{i,j,k}$ as a function of random intercepts, covariates and random effects using logit and log links respectively. I fit covariates and random effects as follows: I modeled $\psi_{i,k}$ as a function of both fixed and random effects through a logit link function: $\text{logit}(\psi_{i,k}) = \alpha_i + \beta_1 \times \text{forest}_i + \beta_2 \times \text{udens}_i + \beta_3 \times \text{cc}_i + \varepsilon_i$, (I-4) where α_i is a random intercept term for a site i , β_1 is the beta coefficient for covariate forest_i , forest_i is the categorical covariate for forest type (old growth = 0, logged = 1) at site i , β_2 is the beta coefficient for the understory density covariate udens_i at site i , β_3 is the beta coefficient for the canopy cover covariate cc_i at site i , and ε_i is the random effect of site i on $\psi_{i,k}$. I used an identical parameterization for $\lambda_{i,k}$.

I modeled $p_{i,j,k}$ through a logit link function as a function of random intercepts for each site, covariates likely to influence detection probability, and a random survey effect to account for

variation in detection probability of a species over time of day. I added a random survey effect because, for several species, I observed higher vocalization activity during the dawn chorus at 6:00 AM than at 7:00 and 8:00 AM. The covariates likely to influence detection probability are understory density, Julian date and the quadratic term of Julian date (Rota et al. 2011, McCarthy et al. 2012). Understory density, being different in the old growth and logged forests, may cause forest-specific variation in sound propagation (Wiley 1991) and subsequent detection of avian vocalizations by the microphones of an ARU. I considered the quadratic term of Julian date because songbirds may be most detectable in the early part of the breeding season when singing rates are at their highest during territory establishment but less so as nesting activity commences (Wilson and Bart 1985):

$$\text{logit}(p_{i,j,k}) = \alpha_i + \beta_1 \times \text{udens}_i + \beta_2 \times \text{Julian date}_i + \beta_3 \times (\text{Julian date}_i)^2 + \varepsilon_j, \quad (\text{I-5})$$

where α_i is a random intercept term for site i , β_1 is the beta coefficient for covariate udens_i , β_2 is the beta coefficient for covariate Julian date_i , β_3 is the beta coefficient for the quadratic term of Julian date_i , and ε_j is the random effect of time of day (survey) on $p_{i,j,k}$.

I specified all fixed and random effects to have flat normal priors with a mean of 0 and standard deviation 0.001 (Gelman and Hill 2007, Royle and Dorazio 2008) and fit all models with Markov Chain Monte Carlo (MCMC) methods to estimate the posterior distribution for each model. I conducted our analyses with JAGS (v. 3.4.0) (Plummer 2013), called using R (v. 3.2.1) (R Development Core Team 2015) via the package R2jags (Su and Yajima 2015). I fit three chains of 20,000 samples after an initial burn in period of 8000 samples for each model. I did not thin the chains (Link and Eaton 2012). I monitored model convergence via Gelman-Rubin statistics and a visual estimation of trace plots and evaluated the fit of the model to the data through a posterior predictive check (Kery and Schaub 2012). When 95% credible intervals

of the slope parameters of a covariate overlapped zero (indicating ambiguous support for that covariate), I discarded the covariate and parameterized a simpler model (Royle and Dorazio 2008).

APPENDIX J
T-TEST RESULTS FOR EFFECTS OF PROCEDURAL CONTROL

Table J-1. Results of Welch’s two-tailed *t*-tests (*p*-values) to ascertain the effects of procedural control (playbacks of *Megophrys nasuta*) on plot-level abundance and per-capita song rates of our two focal species. I found no effect of procedural control on either species.

Species	N	Song Rate
Family Pellorneidae – Ground babblers		
BCPB	0.89	0.15
BRFL	0.21	0.35

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BIOGRAPHICAL SKETCH

Rajeev Pillay was born in Kolkata, India. He was an avid urban birder as a child and a voracious reader of wildlife books. Jim Corbett, a British hunter and naturalist who shot several man-eating tigers and leopards in the Himalayan foothills of northern India during colonial times, was among his favorite authors. In his teens, he was hooked to nature documentaries on the Discovery and National Geographic Channels. When in the eighth grade, he read 'Elephant Days and Nights', a non-technical version of the doctoral research of Dr. Raman Sukumar, arguably the world's foremost expert on the Asian elephant. Rajeev found his life's purpose. Up to that point, he had not imagined that one could actually pursue a career studying wild animals in their natural habitats. He studied biology in high school and thereafter, majored in zoology for his bachelor's and master's degrees. He joined the Wildlife Institute of India immediately after being awarded his master's degree in 2004. The job was a dream come true: monitoring the populations of tigers and their prey in the deciduous forests of the central Indian highlands, in Kanha, Pench and Satpura Tiger Reserves. These forests are some of the most beautiful in India. Kanha boasts the third highest density of tigers in the country (and the world), behind Corbett and Kaziranga Tiger Reserves. Nine glorious months of fieldwork followed, which included line-transect sampling, camera trapping and tracking radio-collared tigers. Rajeev then worked for a year and a half with the Wildlife Trust of India in New Delhi, managing various large mammal conservation projects. There he met Milind Pariwakam, who, at the time had just completed his master's degree on estimating populations of prey species for tigers at the National Center for Biological Sciences in Bangalore, southern India. They quickly became fast friends. In 2007, Milind introduced Rajeev to Dr. M.D. Madhusudan, a scientist at the Nature Conservation Foundation, an organization in the city of Mysore in southern India that focuses on science-based conservation. Madhu offered Rajeev a research position on large mammal occupancy dynamics

in the Western Ghats biodiversity hotspot. The Western Ghats is a narrow strip of mountains that stretches along the entire west coast of India. It is home to an amazing diversity of habitats and wildlife. This was also Rajeev's opportunity to work closely with Dr. A.J.T. Johnsingh, widely regarded as the father of field biology in India. Rajeev grabbed the opportunity with both hands and spent the next three and a half years traveling the length and breadth of the Western Ghats south of the state of Maharashtra, collecting data on the occurrence of large mammals, analyzing, writing and publishing. He considers his field trips with Dr. Johnsingh to several parts of the southern Western Ghats, some of the most memorable in his life. Dr. Johnsingh is primarily a large mammal biologist but has a deep love for plants. During fieldwork, he would always bring up the point that plants are as just important as tigers and elephants. His enthusiasm for plants slowly rubbed on to Rajeev and he began to maintain lists of plants species he had observed during each of those field visits. Little did Rajeev know that plant-animal interactions would become a crucial (and exciting) part of his doctoral research a few years down the line. In 2010, Rajeev accepted a Ph.D. position at the University of Florida. His original research plans were completely different from what he ended up doing and where he ended up working. A year into his Ph.D., his advisor Dr. Rob Fletcher sensed that he loved being in the field and offered him an opportunity to work in in the tropical rainforests of Borneo in Southeast Asia. At the time, the Stability of Altered Forest Ecosystems (SAFE) Project had just been initiated. SAFE is a world-class experiment on the impact of logging and rainforest fragmentation on biodiversity and ecosystem processes. From 2012-14, Rajeev cumulatively spent 14 months in Sabah, focusing on avian singing behavior and seed predation. He was awestruck at the grandeur of a mast-fruiting event in 2014, a phenomenon unique to Southeast Asian rainforests when the majority of trees come into fruit. He was awarded his Ph.D. in 2016.