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1 **Impacts of selective logging on insectivorous birds in Borneo: the**
2 **importance of trophic position, body size and foraging height**

3

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14

15 **Abstract**

16 Habitat destruction and degradation are major drivers of biodiversity loss and attention is
17 increasingly focused on how different traits of species affect their vulnerability. Dietary traits
18 are critical in this respect, and are typically examined by assigning species to different
19 feeding and foraging guilds. However, such guilds may mask large variation in species'
20 trophic interactions, limiting our understanding of species' responses. Here we use stable
21 isotopes to quantify trophic positions within a Family of insectivorous understory birds, the
22 Timaliidae (babblers), within Bornean rainforests. We then relate changes in species'
23 abundances following intensive selective logging of forest to their trophic positions, body
24 sizes and foraging heights. We found that trophic positions within this single feeding guild
25 spanned more than an entire trophic level. Moreover, changes in abundance following
26 logging were significantly and independently related to mean trophic position in primary
27 forest, body size and foraging height: large ground-feeding species occupying high trophic
28 positions were more adversely affected than small understory-feeders with lower trophic
29 positions. These three variables together explained 81% of the variance in species' responses
30 to logging. The single most important predictor, however, was a species' mean trophic
31 position. Species recorded in both habitats also had significantly higher trophic positions in
32 logged forest. These data provide critical new understanding of species' responses to
33 disturbance. They also indicate previously unrecognized functional changes to species
34 assemblages following logging, highlighting the importance of numerical assessments of
35 trophic position within individual feeding guilds.

36 *Key-words:* Biodiversity; Extinction; Feeding guild; Food-web; Southeast Asia; Tropical
37 rainforest

38

39 **1. Introduction**

40 Destruction, fragmentation and degradation of natural habitats are among the greatest
41 threats to biodiversity, especially in the tropics (Fritz et al., 2009; Sodhi et al., 2010; Cordeiro
42 et al., this issue). Species differ widely in their responses to such drivers (Öckinger et al.,
43 2010; Newbold et al., 2013) and in some cases, these differences are demonstrably related to
44 ecological and morphological traits such as diet and body size (Benedick et al., 2006; Murray
45 et al., 2011; Gonzalez-Suarez and Revilla, 2013). However, results have been inconsistent
46 and we are still a long way from a general understanding of how species' traits determine
47 their responses to environmental change (Sekercioglu et al., 2002; Ewers and Didham, 2006;
48 Pavlacky et al., this issue).

49 The world's remaining rainforests are rapidly being logged, making the extent and form
50 of species' responses to logging a vital concern (Putz et al., 2012; Edwards et al., 2014).
51 Impacts of logging on species richness and composition have been well studied (Hamer et al.,
52 2003; Peters et al., 2006; Edwards et al., 2011) but fewer studies have examined how logging
53 affects species with different traits (Edwards et al., 2013a,b; Woodcock et al., 2013). For
54 instance, insectivorous birds are often less abundant in logged forest than in primary forest
55 (Peh et al., 2005; Powell et al., 2013), but not in all cases (Cleary et al., 2007; Edwards et al.,
56 2013c) and responses to other forms of forest management and disturbance are also unclear
57 (see meta-analysis by Gray et al., 2007; Edwards et al., 2009; Buechley et al., this issue). This
58 uncertainty may arise in part because many insectivorous species in tropical forests also feed
59 to some extent on plant material such as fruit. In addition, different species of strict
60 insectivore may occupy very different trophic positions (i.e. different positions in the food
61 web), for instance depending on whether their main prey are themselves herbivorous or
62 predatory arthropods. Higher predators often have small population sizes, slow population
63 growth and specialised ecological habitats, which are expected to make them more vulnerable

64 to local extinction (Purvis et al., 2000; Duffy, 2003), and empirical data confirm that higher
65 predators are differentially lost following habitat disturbance (Didham et al., 1998; Petchy et
66 al., 1999). Hence, within-guild variation in trophic position may greatly affect species'
67 responses to disturbance, but there are few data to address this issue.

68 In addition to trophic position, impacts of disturbance may also be related to body size,
69 although previous studies have found apparently conflicting results, with large-bodied species
70 found to be worst affected in some studies and least affected in others, possibly depending on
71 whether the main form of disturbance examined was habitat degradation (mainly affecting
72 larger species; Gray et al., 2007) or habitat loss and fragmentation (mainly affecting smaller
73 species; Lees & Peres, 2008). Terrestrial foragers may also be more badly affected than
74 understory foragers (Renjifo, 1999; Lees & Peres, 2008), although Cleary et al. (2007)
75 emphasised that impacts may in some cases be governed by complex interactions between
76 body size, vertical foraging position and diet, highlighting the need for further data to
77 examine how these different traits affect the responses of insectivores to logging of forests.

78 Species' diets and trophic positions are often particularly difficult to assess in complex
79 ecosystems such as rain forests but these limitations can be overcome to some extent by using
80 stable isotope analysis to provide a rapid means of precisely quantifying an organism's
81 average trophic position (Layman et al., 2012). Tissue ratios of ^{15}N to ^{14}N (expressed as $\delta^{15}\text{N}$)
82 are enriched by ~ 2-3‰ with each trophic transfer up the food chain (Vanderklift and
83 Ponsard, 2003) and thus indicate an organism's mean trophic position during the period of
84 tissue synthesis (Bearhop et al., 2003; Caut et al., 2009; Dammhahn et al., 2013). Using this
85 technique together with presence-absence data for 73 species of understory bird in rainforests
86 of northern Borneo, Edwards et al. (2013a) showed that dietary specialists were more
87 vulnerable to local extinction from logged forest. However, whether quantitative changes in
88 abundance post-logging were related to trophic position and how this trait was related to

89 other morphological and ecological traits such as body size and foraging height were not
90 considered. Yet these questions are vital for understanding what drives variation among
91 species in their responses to logging, and hence moving further beyond simply describing
92 patterns of threat from habitat disturbance to understanding the evolutionary and ecological
93 processes that led to such patterns (Owens & Bennett, 2000; Gonzalez-Suarez & Revilla,
94 2014).

95 Here we focus on a large and diverse Family of insectivorous birds, the Timaliidae
96 (babblers). These are highly sedentary residents and forage predominantly in the understory
97 (Myers, 2009), allowing us to examine variability in trophic position within a cohesive group
98 of species within a single foraging guild. In addition, some species of babbler are restricted to
99 foraging at ground level among leaf litter, which may make forest birds particularly
100 vulnerable to disturbance (Renjifo, 1999; Patten and Smith-Patten, 2012). Using stable
101 nitrogen isotope analysis, we first examine the trophic positions occupied by different
102 species. We then test the hypotheses that decreases in abundance post-logging are greater
103 among species that (i) occupy high trophic positions, (ii) are large-bodied and (iii) forage at
104 ground level.

105 **2. Material and methods**

106 *2.1. Study site*

107 We focused on the island of Borneo, which is a global hotspot for biodiversity of vascular
108 plants and vertebrates including birds (Myers et al., 2000). Primary forests in the region are
109 numerically dominated by large trees of the family Dipterocarpaceae, which are valuable
110 timber species, and much of the remaining forest there has undergone multiple rounds of
111 selective logging with nearly all medium to large diameter trees harvested (further details of
112 logging in Edwards et al., 2011). Our study area was the Yayasan Sabah logging concession
113 in Sabah, north-eastern Borneo (4° 58'N, 117° 48'E), encompassing production forest within

114 the Ulu Segama-Malua Forest Reserve (US-MFR; area = 238,000 ha) and unlogged primary
115 forest within the Danum Valley Conservation Area and Palum Tambun Watershed Reserve
116 (area = 45,200 ha), forming one contiguous forest (Reynolds et al., 2011). Much of the forest
117 within the US-MFR has been logged twice (first rotation: 1987-1991, second rotation: 2001-
118 2007), producing total timber yields of $\sim 145 \text{ m}^3 \text{ ha}^{-1}$, which are among the highest globally
119 (Fisher et al., 2011).

120 2.2. *Sampling of birds*

121 Fieldwork took place from July to August 2007 and May to August 2008. This
122 corresponds with the slightly drier period of each year (Walsh et al., 2011) but there is little
123 seasonal variation in rainfall at the study site, with no marked dry period, and sampling years
124 were similar in terms of environmental conditions (no mast-fruiting, droughts or floods). We
125 sampled birds along 16 transects, each comprising fifteen mist nets (12 x 2.7 m) erected end-
126 to-end in a straight line (eight transects each in primary and logged forest). Studies in tropical
127 forests have indicated that samples from mist nets separated by $> 200 \text{ m}$ are statistically
128 independent (Hill and Hamer, 2004) and in our study, all transects were spaced $\geq 500 \text{ m}$ apart,
129 with distances between logged transects ($28.3 \pm 3.7 \text{ km}$) being similar to those between
130 logged and primary transects ($23.6 \pm 0.5 \text{ km}$; see Edwards et al., 2013a for further details).
131 Babblers are not strong flyers (Myers, 2009) and in our study, no individuals were captured
132 in both forest types or on different transects within a forest type. Hence we are confident that
133 our data are representative of impacts of logging on species abundances and trophic
134 organization.

135 Mist-nets were opened from 06:00 h to 12:00 h for three consecutive days (4,860 mist-net
136 hours in total; see Edwards et al., 2013a) and every bird captured was marked with an
137 individually numbered metal ring to prevent re-sampling of individuals. Nail clippings, which
138 integrate diet over a period of several weeks (Bearhop et al., 2003), were taken from the

139 central front claw and rear claw of both feet for stable isotope analysis (see 2.3 below), and
140 were stored in a labelled vial. Nail clipping occasionally caused slight bleeding and in these
141 cases, pressure was applied to the cut end of the nail and the bird was released only when
142 bleeding had stopped (typically within 1-2 minutes).

143 2.3. Stable isotope analysis

144 In addition to sampling birds, we also collected pairs of leaves from two understory plants
145 every 15 m along each transect (n=20 plants per transect) to determine baseline isotope
146 compositions (see calculations below), against which trophic position could be assessed
147 (Woodcock et al., 2012). Claws were analysed whole and leaves were ground into a fine
148 powder using a mixer mill. Samples were weighed into tin capsules and analysed on a
149 continuous flow - isotope ratio monitoring mass spectrometer system comprising a
150 Eurovector – 3028HT elemental analyser with Costech zero-blank autosampler, coupled to a
151 GV Isoprime mass spectrometer (see Edwards et al., 2013a for further details).

152 The trophic position (TP) of each bird sampled was calculated as: $TP = \lambda + (\delta^{15}N_{\text{bird}} -$
153 $\delta^{15}N_{\text{baseline organism}})/E$, where λ is the trophic level of the organisms used to estimate $\delta^{15}N_{\text{baseline}}$
154 organism ($\lambda = 1$ for plants, which were used in this study) and E is the enrichment in $\delta^{15}N$ per
155 trophic level (Post et al., 2000). The value of $\delta^{15}N_{\text{baseline organism}}$ was the mean $\delta^{15}N$ for the
156 twenty leaves collected from the same transect as each bird sampled (see Woodcock et al.,
157 2012 for further details). We used $E = 2.5$ as the most appropriate enrichment factor
158 following two extensive reviews (Vanderklift and Ponsard, 2003; Caut et al., 2009). There is
159 a lack of experimental studies on the enrichment of ^{15}N in claws, but Caut et al. (2009) found
160 no significant variation in the enrichment of this isotope across different tissues including
161 feathers, which like claws comprise mainly keratin, and several studies have recorded a
162 strong correlation between N stable isotope ratios of feathers and claws (Bearhop et al., 2003;
163 Clark et al., 2006; Ferger et al., 2013). Enrichment factors can also differ between species

164 within a trophic level, between trophic levels and between environments, although we found
165 that the mean trophic position of presumed frugivores (doves) calculated using this method
166 was as expected within primary forest (TP = 2.0, SD \pm 0.5) and did not differ between
167 primary and logged forest while the mean trophic position of carnivorous species feeding
168 extensively on small fish and amphibians was also as expected (TP = 3.2, SD \pm 0.4; Table 1
169 in Edwards et al., 2013a), providing independent validation for our study system.

170 *2.4. Data analysis*

171 We used general linear modelling (GLM, in IBM SPSS Statistics 20) to examine how the
172 mean trophic position (MTP) of each species in primary forest was related to body size (data
173 on adult body length from Myers, 2009) and foraging height (terrestrial - i.e. foraging at
174 ground-level - or understory – i.e. foraging above ground-level; data from Myers, 2009).
175 Foraging height was included in the model as a fixed effect, with body size as a covariate and
176 an additional term for the interaction between these predictor variables. Data were
177 homoscedastic with normal error distributions. We also examined the relationship between
178 mean trophic position and abundance within primary forest using a Spearman correlation
179 because abundance data are integers and so abundance in primary forest cannot rigorously be
180 considered a continuous variable over the range of values observed in the study.

181 To assess the importance of different traits in determining the numerical responses of
182 species to forest degradation, we compared the relative abundances of species in primary
183 forest with those in logged forest. Sampling effort was constant across sites and so we used
184 the number of individuals of a species recorded in each habitat as an index of relative
185 abundance. We restricted our analysis to the 20 species with $n \geq 4$ (excluding three species
186 with fewer samples), giving us a mean of 20.3 ± 3.9 individuals per species. The proportional
187 difference in abundance between primary and logged forest was calculated for each of these

188 species, as [(abundance in primary forest – abundance in logged forest) / (abundance in
189 primary forest + abundance in logged forest)] (following Benedick et al., 2006). The resulting
190 logging sensitivity index (LSI), which was independent of sample size ($r = -0.1$, $n = 20$, $P >$
191 0.5), was positive for species with lower abundances in logged forest and negative for species
192 with higher abundances in logged forest, with a theoretical maximum range of -1 (species
193 only in logged forest) to +1 (species only in primary forest). We then used a general linear
194 model to examine how arcsine-transformed LSIs of each species were related to mean trophic
195 position in primary forest, body size and foraging height. Trophic position and body size
196 were included in the model as covariates and foraging height as a fixed effect, with additional
197 terms for interactions between variables, as above. We also used a further general linear
198 model of the same form to examine how the difference between primary and logged forest in
199 the mean trophic position of each species was related to each of these three predictor
200 variables.

201 The uncertain systematics of Southeast Asian babblers (Alström et al., 2006; Collar,
202 2006) precluded the use of phylogenetic contrasts to control for evolutionary non-
203 independence. As an alternative, following Edwards et al., (2013a) and Koh et al., (2004), we
204 included Subfamily (Gelang et al., 2009; Moyle et al., 2012) as a random effect in our
205 analysis. Fulvettas (*Alcippe* spp) have been placed within both the Pelorneinae (presented
206 here) and the Leiothrichinae (Cibois, 2003; Moyle et al., 2012) but this difference in
207 classification had no qualitative effect on our results.

208 We also used linear mixed-effects models (LMEs; Pinheiro and Bates, 2000), in the lme
209 function in the nlme package of R v.2.13.0 (Pinheiro et al., 2013), to determine whether the
210 trophic positions of individuals differed between primary and logged forest. This analysis
211 was carried out at the level of individuals rather than species because in contrast to LSI,
212 trophic positions were measured for individual birds. We included Subfamily as a random

213 effect in our analysis to control for phylogenetic non-independence, with species identities of
214 individuals nested within Subfamily to account for repeated measures per species (models
215 had the form $TP \sim \text{forest, random} = \sim 1 | \text{Subfamily} | \text{species}$). For all analyses involving multiple
216 predictor variables, to find the best-fitting models and check the robustness of our results,
217 non-significant terms ($P \geq 0.05$) were serially deleted to ensure that this did not qualitatively
218 affect the significance of the remaining terms, producing a minimum adequate model (MAM)
219 in each case (Crawley, 2007). Means are presented ± 1 SE throughout unless stated
220 otherwise.

221 **3. Results**

222 Stable isotope data were consistent with species being broadly insectivorous (trophic levels 3
223 to 4) but there was marked variation among species, with mean trophic positions (MTPs) in
224 primary forest spanning more than an entire trophic level (range = 2.87 ± 0.07 to 3.94 ± 0.15 ;
225 Table 1). MTP was significantly higher among terrestrial foragers (mean \pm SE = 3.5 ± 0.1)
226 than among understory foragers (3.0 ± 0.1 ; GLM; $F_{1,14} = 11.7$, $P < 0.001$) but was not related
227 to body size or Subfamily and there was no interaction between predictor variables ($P \geq 0.6$
228 in each case). There was also a significant negative relationship between MTP and
229 abundance within primary forest (Table 1; Spearman correlation; $r_s = -0.51$, $P < 0.05$).

230 The proportional reduction in abundance of a species following logging (Logging
231 Sensitivity Index; LSI) was significantly positively related to both mean trophic position in
232 primary forest (GLM using arcsine-transformed data; $F_{1,12} = 45.1$, $P < 0.001$; Fig. 1a) and
233 body size ($F_{1,12} = 7.9$, $P = 0.016$; Fig. 1b), and was also significantly higher among terrestrial
234 foragers (LSI = 0.21 ± 0.34) than among understory foragers (LSI = -0.05 ± 0.17 ; $F_{1,12} = 8.0$,
235 $P = 0.015$; R^2 of MAM = 0.81; Table 1). Hence those species most adversely affected by
236 logging were large-bodied, ground-feeding species with high trophic positions. Subfamily did
237 not significantly affect the variance in LSI ($P > 0.9$) and there were no two-way or three-way

238 interactions between predictor variables ($P > 0.2$ in each case). Species recorded in both
239 habitats maintained similar relative trophic positions following logging (Pearson correlation;
240 $r = 0.79$, $n = 13$, $P = 0.001$) but with significantly higher trophic positions in logged forest
241 than in primary forest (mean increase \pm SE = 0.36 ± 0.04 trophic levels; LME; $F_{1,365} = 128.8$,
242 $P < 0.0001$; Fig. 2). The difference in MTP between primary and logged forest was, however,
243 not related to MTP in primary forest, body size, foraging height or Subfamily (GLM; $P > 0.5$
244 in each case) and trophic positions within logged forest did not differ between species
245 recorded only in that habitat and species recorded in both habitats (MTP in logged forest =
246 3.54 ± 0.15 and 3.43 ± 0.06 , respectively; $F_{1,15} = 0.7$, $P = 0.4$).

247 **4. Discussion**

248 Many researchers have grouped birds into feeding guilds to determine the effects of
249 disturbance on community composition (Lambert, 1992; Plumptre, 1997; Cleary et al., 2007;
250 Gray et al., 2007; Edwards et al., 2009) and functional diversity (Flynn et al., 2009; Hidasi-
251 Neto et al., 2012; Edwards et al., 2013c). Such groupings have important implications for our
252 understanding of changes to ecosystem processes and functioning. However, our study
253 reveals that the ecological roles of species within a guild may differ widely, as also found in a
254 behavioural study of foraging specialization among babblers (Styring et al., this study) and
255 among tropical rainforest birds in Mexico (Herrera et al., 2003; Herrera M. et al., 2006). We
256 found that the trophic positions of insectivorous birds in primary forest spanned more than an
257 entire trophic level, indicating marked variation in the proportions of herbivorous and
258 predatory arthropods in the diets of different species, with the highest values (mean trophic
259 position ~ 3.5 or more) overlapping those seen in many birds of prey (Arim et al., 2007;
260 Symes and Woodborne, 2009). These high trophic positions were found mainly among
261 terrestrial foragers, and probably reflected a greater abundance of predatory arthropods in the
262 leaf litter than in higher strata (Blüthgen et al., 2003; Davidson et al., 2003) whereas the

263 lowest values may have indicated occasional feeding on understory fruit (D. Edwards 2007-
264 2009 personal observation) and are consistent with findings from studies elsewhere that
265 insectivorous species may occasionally feed on fruits in the forest understory (Schleuning et
266 al. 2011; Ferger et al. 2013).

267 In a recent extensive analysis of pan-tropical bird data, Newbold et al. (2013) found that
268 forest specialists with primarily frugivorous or insectivorous diets were both less likely to
269 occur and less abundant in more intensively used habitats than non-frugivorous/insectivorous
270 habitat generalists. However their analysis was based on guild membership and they were not
271 able to consider variation in trophic position within guilds. We found, using quantitative data
272 on trophic position, that insectivorous species occupying higher trophic positions were more
273 adversely affected by logging (Fig. 1a). This variation in species' sensitivity to impacts of
274 logging probably occurred because predatory arthropods within the leaf-litter, where birds
275 with the highest trophic positions foraged, had lower abundance in logged forest than in
276 primary forest at this site (Edwards et al., 2012). We also found that insectivorous birds at
277 higher trophic positions were less abundant than species at lower trophic positions in primary
278 forest, which additionally supports the hypothesis that species higher up the food chain are
279 more vulnerable to environmental changes because they occur at lower densities (Duffy,
280 2003; Henle et al., 2004).

281 Our finding that ground-feeding insectivores declined more in abundance than understory
282 foragers agrees with previous studies in disturbed and fragmented forests (Cleary et al. 2007;
283 Lees & Peres 2008). Ground-nesting species are more vulnerable than canopy species to
284 elevated numbers of small and medium-sized predators in small fragments (meso-predator
285 release; Terborgh, 1988). In addition, ground-feeding species, which often forage in dense
286 shade, may have impaired vision in disturbed forest due to elevated light intensity beneath the
287 canopy (Patten and Smith-Patten, 2012; Pollock et al., this issue).

288 In addition to trophic position and vertical foraging position, we also found that species'
289 responses to logging depended on body size, with larger species decreasing more in
290 abundance than smaller species. This finding agrees with previous studies examining
291 insectivores' responses to forest disturbance (Gray et al., 2007; Newbold et al., 2013) but
292 contrasts with fragmentation studies recording that small-bodied insectivores were less likely
293 to occur within forest fragments, probably due to their poor dispersal ability and
294 metapopulation persistence within fragmented landscapes (Sekercioglu et al. 2002; Lees &
295 Peres 2008). These data emphasise the importance of distinguishing between the impacts of
296 different forms of forest disturbance (Durães et al. 2013; Moura et al. 2013) in addition to
297 distinguishing pressures related directly to changes in land-use from other threats such as
298 hunting, which mainly affects large-bodied species (Owens & Bennett 2000).

299 Previous studies have highlighted the complexity of insectivores' responses to logging,
300 with multiple interactions among different ecological and morphological traits (Dale et al.,
301 2000; Cleary et al., 2007; Edwards et al., 2009). We found that body size, foraging height and
302 mean trophic position together explained 81% of the variance in species' responses to
303 logging. However, mean trophic position alone explained more than half the variance ($R^2 =$
304 0.59), suggesting that this was the most important single factor. Edwards et al. (2013a) found,
305 using presence-absence data for a wide range of understory bird species in different feeding
306 guilds at this study site, that there was no systematic effect of trophic position on the
307 persistence of species post-logging but that species showing little variability in trophic
308 position were less likely to persist. These contrasting results strongly suggest that in addition
309 to depending on the type of disturbance (see above) the pattern of variation in species'
310 sensitivity to disturbance also depends on the type of response and the set of species being
311 considered: the persistence of species across a broad range of guilds was explained mainly by
312 trophic flexibility (Edwards et al., 2013a) whereas changes in abundance within a single guild

313 (insectivores) were best explained by trophic position, with additional influences of body size
314 and foraging height (this study). Further data are now required for other taxa and other
315 regions to determine the universality of these patterns and provide a clearer understanding of
316 species' responses to human modification of tropical forests.

317 Elevation of trophic positions in logged forest may have resulted directly from species
318 altering their diets (feeding more on predatory arthropods) or indirectly from increases in the
319 trophic positions of their prey (McHugh et al., 2010; Edwards et al., 2013a). Both
320 mechanisms are likely to operate to some extent, although changes in the diets of prey cannot
321 explain increases in trophic position among species that, in primary forest, feed
322 predominantly on obligate herbivores. In Borneo, carnivorous arthropods were more
323 abundant in the understory of logged forest, in contrast to the leaf litter, which may have
324 encouraged prey-switching among birds feeding in the understory (Edwards et al., 2012). In
325 addition, leaf-litter ants had significantly higher trophic positions in logged forest (Woodcock
326 et al., 2013). Thus the mechanisms responsible for trophic elevation among insectivorous
327 birds may differ between rainforest strata. Nonetheless, for birds, both changes in the relative
328 abundances of species with different trophic positions and elevations in the trophic positions
329 of remaining species indicate important functional changes to species composition following
330 logging.

331 In natural communities, food chain length is positively related to basal productivity
332 (Takimoto et al., 2012; Takimoto and Post, 2013). Disturbance may then reduce food chain
333 length due to a lowering in the abundance of species at higher trophic levels (Jenkins et al.,
334 1992; this study). However, disturbance such as selective logging that results in a marked
335 increase in net primary production (Berry et al., 2010) could also increase food chain length.
336 In our study, the geometric mean trophic position of species sampled was ~0.3 trophic levels
337 higher in degraded forest than in primary forest (3.45 and 3.11, respectively; calculated from

338 data in Table 1). This was very similar to the increase recorded for ants in the same forests
339 (0.2 trophic levels; Woodcock et al., 2013), suggesting a net overall increase in functional
340 food chain length following intensive selective logging.

341 In conclusion, our data provide new understanding of species' trophic relationships and
342 responses to disturbance, highlighting the vulnerability of large-bodied ground-feeding
343 species occupying high trophic positions and indicating previously unrecognized functional
344 changes to species assemblages following logging. They also highlight the likely importance
345 of objective numerical assessments of trophic position within other feeding guilds such as
346 carnivores and omnivores, where guild membership may likewise mask large variation
347 among species in their trophic positions and responses to environmental change.

348

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576 **Table 1.** Ecological and morphological traits of Timaliidae (babblers) in primary and logged rainforest in northern Borneo

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		Trophic position				Body length (mm)	Foraging position	Abundance		Logging Sensitivity Index
		Primary mean	SD	Logged mean	SD			Primary	Logged	
582	Timaliinae									
583	<i>Stachyris nigricollis</i>	-	-	3.59	0.23	15.5	2	0(0)	7(7)	-1.00
584	<i>S. leucotis</i>	3.56	0.21	-	-	14.5	2	4(4)	0(0)	1.00
585	<i>S. poliocephala</i>	3.09	0.24	3.61	0.17	14.0	2	10(10)	5(5)	0.33
586	<i>S. erythroptera</i>	2.99	0.28	3.40	0.30	13.0	2	21(17)	40(38)	-0.32
587	<i>S. maculata</i>	3.08	0.26	-	-	17.8	2	11(11)	1(0)	0.83
588	<i>Stachyridopsis rufifrons</i>	-	-	3.19	0.22	11.5	2	0(0)	5(5)	-1.00
589	<i>Macronous bornensis</i>	-	-	3.47	0.12	12.0	2	0(0)	11(11)	-1.00
590	<i>M. ptilosus</i>	2.91	0.24	3.26	0.25	16.5	2	12(11)	32(32)	-0.45
591	Pelorneinae									
592	<i>Alcippe brunneicauda</i>	3.22	0.18	3.32	0.15	14.5	2	15(14)	5(5)	0.50
593	<i>Pellorneum capistratum</i>	3.17	0.45	3.59	0.26	16.0	1	6(6)	13(12)	-0.37
594	<i>Malacopteron mignirostre</i>	2.94	0.25	3.16	0.23	17.0	2	14(14)	9(9)	0.22
595	<i>M. cinereum</i>	2.87	0.27	3.16	0.29	15.0	2	14(13)	9(9)	0.22
596	<i>M. magnum</i>	2.92	0.27	3.32	0.18	18.0	2	5(5)	4(4)	0.11
597	<i>Ptilocichla leucogrammica</i>	3.94	0.30	-	-	15.5	1	4(4)	0(0)	1.00
598	<i>Trichastoma rostratum</i>	-	-	3.92	0.30	14.5	1	0(0)	10(10)	-1.00
599	<i>T. bicolor</i>	2.91	0.23	3.30	0.31	17.0	2	19(18)	22(22)	-0.07
600	<i>Malacocincla sepiaria</i>	3.01	0.28	3.64	0.32	15.0	2	11(11)	11(11)	0.00
601	<i>M. malaccensis</i>	3.28	0.26	3.56	0.25	13.5	1	25(21)	35(35)	-0.17
602	<i>Kenopia striata</i>	3.52	0.29	-	-	14.5	1	9(9)	1(0)	0.80
603	<i>Turdinus atrigularis</i>	3.44	0.32	-	-	18.0	1	5(4)	0(0)	1.00

604

605 Data on body length and foraging position from Myers (2009). For foraging position, 1 = ground, 2 = understory. For abundance, figures in brackets are
 606 numbers of isotope samples.

607 **Figure legends**

608 **Fig. 1.** Relationship between changes in the abundance of Tamaliidae (babblers) following
609 selective logging of Bornean rainforests (logging sensitivity index) and (a) mean trophic
610 position in primary forest (indicating average position in the food chain) and (b) body length
611 (cm). See text for calculation of logging sensitivity index (arcsine-transformed prior to
612 analysis; higher values indicate a stronger adverse effect of logging). Squares, ground-
613 feeders; circles, understory feeders. Blue symbols, Timaliinae; green symbols, Pelorneinae.

614

615 **Fig. 2.** Mean trophic positions of species in primary and logged forest. Solid line shows
616 observed relationship; dotted line shows expected relationship if species did not alter their
617 trophic positions post-logging.

618