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

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Abstract

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

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

1. Introduction

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

The world's remaining rainforests are rapidly being logged, making the extent and form of species' responses to logging a vital concern (Putz et al., 2012; Edwards et al., 2014). Impacts of logging on species richness and composition have been well studied (Hamer et al., 2003; Peters et al., 2006; Edwards et al., 2011) but fewer studies have examined how logging affects species with different traits (Edwards et al., 2013a,b; Woodcock et al., 2013). For instance, insectivorous birds are often less abundant in logged forest than in primary forest (Peh et al., 2005; Powell et al., 2013), but not in all cases (Cleary et al., 2007; Edwards et al., 2013c) and responses to other forms of forest management and disturbance are also unclear (see meta-analysis by Gray et al., 2007; Edwards et al., 2009; Buechley et al., this issue). This uncertainty may arise in part because many insectivorous species in tropical forests also feed to some extent on plant material such as fruit. In addition, different species of strict insectivore may occupy very different trophic positions (i.e. different positions in the food web), for instance depending on whether their main prey are themselves herbivorous or predatory arthropods. Higher predators often have small population sizes, slow population growth and specialised ecological habitats, which are expected to make them more vulnerable to local extinction (Purvis et al., 2000; Duffy, 2003), and empirical data confirm that higher predators are differentially lost following habitat disturbance (Didham et al., 1998; Petchy et al., 1999). Hence, within-guild variation in trophic position may greatly affect species' responses to disturbance, but there are few data to address this issue.

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

Species' diets and trophic positions are often particularly difficult to assess in complex ecosystems such as rain forests but these limitations can be overcome to some extent by using stable isotope analysis to provide a rapid means of precisely quantifying an organism's average trophic position (Layman et al., 2012). Tissue ratios of ^{15}N to ^{14}N (expressed as $\delta^{15}N$) are enriched by ~ 2-3‰ with each trophic transfer up the food chain (Vanderklift and Ponsard, 2003) and thus indicate an organism's mean trophic position during the period of tissue synthesis (Bearhop et al., 2003; Caut et al., 2009; Dammhahn et al., 2013). Using this technique together with presence-absence data for 73 species of understory bird in rainforests of northern Borneo, Edwards et al. (2013a) showed that dietary specialists were more vulnerable to local extinction from logged forest. However, whether quantitative changes in abundance post-logging were related to trophic position and how this trait was related to other morphological and ecological traits such as body size and foraging height were not considered. Yet these questions are vital for understanding what drives variation among species in their responses to logging, and hence moving further beyond simply describing patterns of threat from habitat disturbance to understanding the evolutionary and ecological processes that led to such patterns (Owens & Bennett, 2000; Gonzalez-Suarez & Revilla, 2014).

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

2. Material and methods

2.1. Study site

We focused on the island of Borneo, which is a global hotspot for biodiversity of vascular plants and vertebrates including birds (Myers et al., 2000). Primary forests in the region are numerically dominated by large trees of the family Dipterocarpaceae, which are valuable timber species, and much of the remaining forest there has undergone multiple rounds of selective logging with nearly all medium to large diameter trees harvested (further details of logging in Edwards et al., 2011). Our study area was the Yayasan Sabah logging concession in Sabah, north-eastern Borneo (4º 58’N, 117º 48’E), encompassing production forest within the Ulu Segama-Malua Forest Reserve (US-MFR; area = 238,000 ha) and unlogged primary forest within the Danum Valley Conservation Area and Palum Tambun Watershed Reserve (area = 45,200 ha), forming one contiguous forest (Reynolds et al., 2011). Much of the forest within the US-MFR has been logged twice (first rotation: 1987-1991, second rotation: 2001-2007), producing total timber yields of ~145 m^3 ha^{-1}, which are among the highest globally (Fisher et al., 2011).

2.2. Sampling of birds

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

Mist-nets were opened from 06:00 h to 12:00 h for three consecutive days (4,860 mist-net hours in total; see Edwards et al., 2013a) and every bird captured was marked with an individually numbered metal ring to prevent re-sampling of individuals. Nail clippings, which integrate diet over a period of several weeks (Bearhop et al., 2003), were taken from the central front claw and rear claw of both feet for stable isotope analysis (see 2.3 below), and were stored in a labelled vial. Nail clipping occasionally caused slight bleeding and in these cases, pressure was applied to the cut end of the nail and the bird was released only when bleeding had stopped (typically within 1-2 minutes).

2.3. Stable isotope analysis

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

The trophic position (TP) of each bird sampled was calculated as: $TP = \lambda + (\delta^{15}N_{bird} - \delta^{15}N_{baseline\ organism})/E$, where λ is the trophic level of the organisms used to estimate $\delta^{15}N_{baseline\ organism}$ ($\lambda = 1$ for plants, which were used in this study) and E is the enrichment in $\delta^{15}N$ per trophic level (Post et al., 2000). The value of $\delta^{15}N_{baseline\ organism}$ was the mean $\delta^{15}N$ for the twenty leaves collected from the same transect as each bird sampled (see Woodcock et al., 2012 for further details). We used E = 2.5 as the most appropriate enrichment factor following two extensive reviews (Vanderklift and Ponsard, 2003; Caut et al., 2009). There is a lack of experimental studies on the enrichment of ^{15}N in claws, but Caut et al. (2009) found no significant variation in the enrichment of this isotope across different tissues including feathers, which like claws comprise mainly keratin, and several studies have recorded a strong correlation between N stable isotope ratios of feathers and claws (Bearhop et al., 2003; Clark et al., 2006; Ferger et al., 2013). Enrichment factors can also differ between species within a trophic level, between trophic levels and between environments, although we found that the mean trophic position of presumed frugivores (doves) calculated using this method was as expected within primary forest (TP = 2.0, SD ± 0.5) and did not differ between primary and logged forest while the mean trophic position of carnivorous species feeding extensively on small fish and amphibians was also as expected (TP = 3.2, SD ± 0.4; Table 1 in Edwards et al., 2013a), providing independent validation for our study system.

2.4. Data analysis

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

To assess the importance of different traits in determining the numerical responses of species to forest degradation, we compared the relative abundances of species in primary forest with those in logged forest. Sampling effort was constant across sites and so we used the number of individuals of a species recorded in each habitat as an index of relative abundance. We restricted our analysis to the 20 species with $n \geq 4$ (excluding three species with fewer samples), giving us a mean of 20.3 ± 3.9 individuals per species. The proportional difference in abundance between primary and logged forest was calculated for each of these species, as [(abundance in primary forest – abundance in logged forest) / (abundance in primary forest + abundance in logged forest)] (following Benedick et al., 2006). The resulting logging sensitivity index (LSI), which was independent of sample size ($r = -0.1$, $n = 20$, $P > 0.5$), was positive for species with lower abundances in logged forest and negative for species with higher abundances in logged forest, with a theoretical maximum range of -1 (species only in logged forest) to +1 (species only in primary forest). We then used a general linear model to examine how arcsine-transformed LSIs of each species were related to mean trophic position in primary forest, body size and foraging height. Trophic position and body size were included in the model as covariates and foraging height as a fixed effect, with additional terms for interactions between variables, as above. We also used a further general linear model of the same form to examine how the difference between primary and logged forest in the mean trophic position of each species was related to each of these three predictor variables.

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

We also used linear mixed-effects models (LMEs; Pinheiro and Bates, 2000), in the lme function in the nlme package of R v.2.13.0 (Pinheiro et al., 2013), to determine whether the trophic positions of individuals differed between primary and logged forest. This analysis was carried out at the level of individuals rather than species because in contrast to LSI, trophic positions were measured for individual birds. We included Subfamily as a random effect in our analysis to control for phylogenetic non-independence, with species identities of individuals nested within Subfamily to account for repeated measures per species (models had the form TP~forest, random = ~1|Subfamily|species). For all analyses involving multiple predictor variables, to find the best-fitting models and check the robustness of our results, non-significant terms ($P \geq 0.05$) were serially deleted to ensure that this did not qualitatively affect the significance of the remaining terms, producing a minimum adequate model (MAM) in each case (Crawley, 2007). Means are presented ± 1 SE throughout unless stated otherwise.

3. Results

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

The proportional reduction in abundance of a species following logging (Logging Sensitivity Index; LSI) was significantly positively related to both mean trophic position in primary forest (GLM using arcsine-transformed data; $F_{1,12} = 45.1$, $P < 0.001$; Fig. 1a) and body size ($F_{1,12} = 7.9$, $P = 0.016$; Fig. 1b), and was also significantly higher among terrestrial foragers (LSI = 0.21 ± 0.34) than among understory foragers (LSI = -0.05 ± 0.17; $F_{1,12} = 8.0$, $P = 0.015$; R^2 of MAM = 0.81; Table 1). Hence those species most adversely affected by logging were large-bodied, ground-feeding species with high trophic positions. Subfamily did not significantly affect the variance in LSI ($P > 0.9$) and there were no two-way or three-way interactions between predictor variables ($P > 0.2$ in each case). Species recorded in both habitats maintained similar relative trophic positions following logging (Pearson correlation; $r = 0.79$, $n = 13$, $P = 0.001$) but with significantly higher trophic positions in logged forest than in primary forest (mean increase ± SE = 0.36 ± 0.04 trophic levels; LME; $F_{1,365} = 128.8$, $P < 0.0001$; Fig. 2). The difference in MTP between primary and logged forest was, however, not related to MTP in primary forest, body size, foraging height or Subfamily (GLM; $P > 0.5$ in each case) and trophic positions within logged forest did not differ between species recorded only in that habitat and species recorded in both habitats (MTP in logged forest = 3.54 ± 0.15 and 3.43 ± 0.06, respectively; $F_{1,15} = 0.7$, $P = 0.4$).

4. Discussion

Many researchers have grouped birds into feeding guilds to determine the effects of disturbance on community composition (Lambert, 1992; Plumptre, 1997; Cleary et al., 2007; Gray et al., 2007; Edwards et al., 2009) and functional diversity (Flynn et al., 2009; Hidasi-Neto et al., 2012; Edwards et al., 2013c). Such groupings have important implications for our understanding of changes to ecosystem processes and functioning. However, our study reveals that the ecological roles of species within a guild may differ widely, as also found in a behavioural study of foraging specialization among babblers (Styring et al., this study) and among tropical rainforest birds in Mexico (Herrera et al., 2003; Herrera M. et al., 2006). We found that the trophic positions of insectivorous birds in primary forest spanned more than an entire trophic level, indicating marked variation in the proportions of herbivorous and predatory arthropods in the diets of different species, with the highest values (mean trophic position ~ 3.5 or more) overlapping those seen in many birds of prey (Arim et al., 2007; Symes and Woodborne, 2009). These high trophic positions were found mainly among terrestrial foragers, and probably reflected a greater abundance of predatory arthropods in the leaf litter than in higher strata (Blüthgen et al., 2003; Davidson et al., 2003) whereas the lowest values may have indicated occasional feeding on understory fruit (D. Edwards 2007-2009 personal observation) and are consistent with findings from studies elsewhere that insectivorous species may occasionally feed on fruits in the forest understory (Schleuning et al. 2011; Ferger et al. 2013).

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

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

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

Previous studies have highlighted the complexity of insectivores' responses to logging, with multiple interactions among different ecological and morphological traits (Dale et al., 2000; Cleary et al., 2007; Edwards et al., 2009). We found that body size, foraging height and mean trophic position together explained 81% of the variance in species' responses to logging. However, mean trophic position alone explained more than half the variance ($R^2 = 0.59$), suggesting that this was the most important single factor. Edwards et al. (2013a) found, using presence-absence data for a wide range of understory bird species in different feeding guilds at this study site, that there was no systematic effect of trophic position on the persistence of species post-logging but that species showing little variability in trophic position were less likely to persist. These contrasting results strongly suggest that in addition to depending on the type of disturbance (see above) the pattern of variation in species' sensitivity to disturbance also depends on the type of response and the set of species being considered: the persistence of species across a broad range of guilds was explained mainly by trophic flexibility (Edwards et al., 2013a) whereas changes in abundance within a single guild (insectivores) were best explained by trophic position, with additional influences of body size and foraging height (this study). Further data are now required for other taxa and other regions to determine the universality of these patterns and provide a clearer understanding of species' responses to human modification of tropical forests.

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

In natural communities, food chain length is positively related to basal productivity (Takimoto et al., 2012; Takimoto and Post, 2013). Disturbance may then reduce food chain length due to a lowering in the abundance of species at higher trophic levels (Jenkins et al., 1992; this study). However, disturbance such as selective logging that results in a marked increase in net primary production (Berry et al., 2010) could also increase food chain length. In our study, the geometric mean trophic position of species sampled was ~0.3 trophic levels higher in degraded forest than in primary forest (3.45 and 3.11, respectively; calculated from data in Table 1). This was very similar to the increase recorded for ants in the same forests (0.2 trophic levels; Woodcock et al., 2013), suggesting a net overall increase in functional food chain length following intensive selective logging.

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

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

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

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

Figure legends

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

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