Biological Conservation 188 (2015) 82–88

Contents lists available at ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon

Special Issue Article: Tropical Insectivores

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

Keith C. Hamer [a,*], Rob J. Newton [b], Felicity A. Edwards [a], Suzan Benedick [c], Simon H. Bottrell [b], David P. Edwards [a,d]

[a] *School of Biology, University of Leeds, Leeds LS2 9JT, UK*
[b] *School of Earth and Environment, University of Leeds, Leeds LS29JT, UK*
[c] *School of Sustainable Agriculture, Universiti Malaysia Sabah, Sandakan, Sabah, Malaysia*
[d] *Department of Animal and Plant Sciences, University of Sheffield, Sheffield S10 2TN, UK*

ARTICLE INFO

Article history:
Received 24 March 2014
Received in revised form 14 July 2014
Accepted 20 September 2014
Available online 12 October 2014

Keywords:
Biodiversity
Extinction
Foraging guild
Food-web
Southeast Asia
Tropical rainforest

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 unrecognised functional changes to species assemblages following logging, highlighting the importance of numerical assessments of trophic position within individual feeding guilds.

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., 2015). 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., 2015).

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., 2015). 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

---

* Corresponding author. Tel.: +44 (0)113 343 2983.
E-mail address: k.c.hamer@leeds.ac.uk (K.C. Hamer).

http://dx.doi.org/10.1016/j.biocon.2014.09.026
0006-3207/

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; Petchey 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 and Peres, 2008). Terrestrial foragers may also be more badly affected than understory foragers (Renjifo, 1999; Lees and 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 δ^{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 progressing beyond simply describing patterns of threat from habitat disturbance to understanding the evolutionary and ecological processes that lead to such patterns (Owens and Bennett, 2000; Gonzalez-Suarez and Revilla, 2013).

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 (4°58′N, 117°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 (12×2.7 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 $\geqslant$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 organisation.

Mist-nets were opened from 06:00 h to 12:00 h for three consecutive days (4860 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 Section 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 min).

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