

		Nepal	W. Himalayas	E. Himalayas	N.E. India	Bangladesh	N. Burma	N. Thailand	N. Laos	N. Viet Nam	Xizang Zhihiqu	S. China	Taiwan	Habitat
Pink-browed Rosefinch	<i>Carpodacus rhodochrous</i>	FC	U/C	+							+	+	C	F
Vinaceous Rosefinch	<i>Carpodacus vinaceus</i>	S	?				?				+	+		F
Dark-rumped Rosefinch	<i>Carpodacus edwardsii</i>	S		U							C	+		F/S
Spot-winged Rosefinch	<i>Carpodacus rhodopeplus</i>	FC	S	?			+				C	+		S
White-browed Rosefinch	<i>Carpodacus thura</i>	FC	C	C							C	+		S
Streaked Rosefinch	<i>Carpodacus rubicilloides</i>	+	FC	+							C	+		S
Crimson-browed Finch	<i>Pinicola subhimachala</i>	U		U	?		?				+	+		F/S
Scarlet Finch	<i>Haematospiza sipahi</i>	U	+	U	+		?	R	+	+				F
Gold-naped Finch	<i>Pyrhoptectes epanletta</i>	O	+	FC			?				FC	+		F
Red-headed Bullfinch	<i>Pyrhula erythrocephala</i>	FC	FC	FC			?				+	+		F
Collared Grosbeak	<i>Mycerobas affinis</i>	FC	LC	LC			?				FC	+		F
Spot-winged Grosbeak	<i>Mycerobas melanozanthus</i>	SP	U	U	+		?	S	?		+	+		F

Effects of selective logging on the ecological organization of a peninsular Malaysian rainforest avifauna

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Selective timber logging affects the avifauna in a variety of ways. There is a significant overall decrease in species richness. Families such as Alcedinidae, Trogonidae, Timaliidae, Muscicapidae and Dicaeidae were much reduced, both in species richness and overall abundance. Many species of the Pycnonotidae, and migrant insectivores such as *Hirundo rustica* and *Merops viridis* were observed far more frequently in logged (i.e. selectively logged) forest.

Species that possess a highly specialized diet or foraging behaviour, those exploiting resources that are evenly dispersed and predictable, and those that are physiologically intolerant of microclimatic changes were most often absent from logged forest. Terrestrial and sallying insectivores appear particularly susceptible. These birds tend to be replaced by more robust species, often those able to feed opportunistically on a variety of foods. The presence of some colonizing birds is highly ephemeral, but long-term changes in patterns of species abundance are to be expected in logged forest consistent with long-term changes in habitat parameters.

INTRODUCTION

Tropical rainforests support a high species richness among bird communities. This is partly due to historical factors (Pearson 1982) and partly due to environmental and habitat conditions promoting sympatry through specialization (Karr 1976); other factors may be involved.

Mean abundance per species may be very low in tropical compared to temperate forests (Karr 1971). Species may be rare for a number of reasons, usually because their food resources are rare or because their optimal living space along microclimatic gradients or within the habitat structure is small. Species which exist at very low densities are likely to be susceptible to any form of disturbance that alters features of their environment (Willis 1974, 1979): it is clear that species-rich rainforest communities are less constant (*sensu* Putman and Wratten 1984) in the face of environmental change than are simpler communities (e.g. Michael and Thornburgh 1971, Webb *et al.* 1977). Depending on the form of the disturbance, however, common species can be as seriously affected as rare ones. Abundance alone is not a reliable predictor of susceptibility to disturbance (Karr 1982a,b).

This paper examines the response of a species-rich avifauna to selective timber logging, a prevailing form of habitat disturbance in tropical rainforest. Logging operations in peninsular Malaysia rarely cut more than 5% of total stems for their timber, but incidental damage is considerable; destruction of less than 40% of the stand is unusual. The remnant is often left to regenerate, either naturally or with certain management procedures designed to promote the re-establishment of commercially important trees (see UNESCO 1978). The level of damage is sufficient to cause considerable change in patterns of resource abundance,

microhabitat diversity, predator/prey relationships and other controlling factors. The differing responses of species may be used as a basis to examine broad ecological attributes which permit or prohibit survival following habitat disturbance.

STUDY AREA

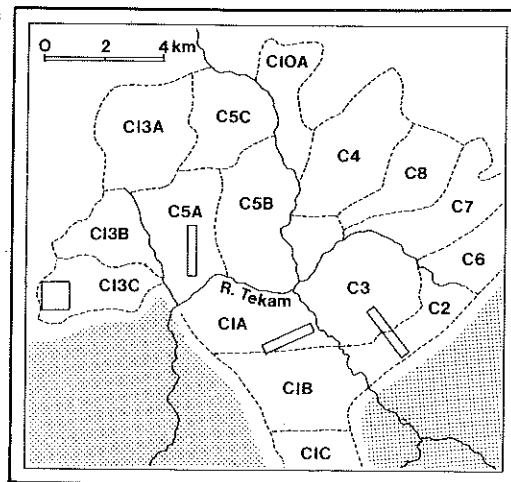
Data were collected in tropical dipterocarp forest (for a description of this vegetation type, see Whitmore 1984) in the Sungai Tekam Forestry Concession, Pahang, West Malaysia (4°10'N 102°40'E). This area is part of a large block of, until recently, entirely undisturbed primary rainforest. Observations were made in one compartment (C13C) before, during and after selective logging, and in 1–2 year-old (C5A), 3–4 year-old (C1A) and 5–6 year-old logged forests (C2). The period of study was from April 1979 until June 1981.

Study sites (Figure 1) ranged from around 80 m (C2) to 400 m above sea level (C5A), were of undulating to steep terrain and of a uniform vegetation type. None of the higher areas possessed the stands of the common dipterocarp *Shorea curtisii*, which does not occur below the hill-foot boundary and could have been a cause of variation between sites. The different altitudes of the study sites may be a cause of some variation (Wells 1985), but it will later be shown that this is a minor influence.

Site C13C remained adjacent to primary forest throughout the study; the older logged forests were progressively further from primary forest (see Figure 1). Birds would be expected to move freely between primary and logged forest in contiguous areas, unless constrained in some way, but (because of isolation) not between primary and older logged forests, at least on a regular basis.

Observations at C13C showed that 3.3% of trees were cut for their timber, but a

Figure 1. Location of study areas in the Sungai Tekam Forestry Concession. Shaded areas are clear-felled forest, now under plantation crops. All remaining areas are forested. Compartments logged at the time of the study are numbered. Boxed areas represent the study sites.



total of 51% was destroyed during the operation to fell and remove them. The high level of indiscriminate damage counteracts preferences shown by loggers for large specimens of selected tree taxa: the loss of most taxa and all size classes of tree is proportional to their abundance. Selective logging is not selective at all.

In addition to the loss of food resources, there are considerable changes in forest microclimate. Loss of a high proportion of canopy cover causes increased temperature, increased insolation, and decreased humidity in the understorey. Wind damage through desiccation and treefalls is also increased.

Extraction levels, and subsequent damage levels, were uniform between all sites studied. Environmental effects of the selective logging operation at Sungai Tekam have been discussed in detail elsewhere (Johns 1983).

METHODS

Data were collected in the form of spot observations; notes were made on first observing an individual bird and not subsequently. In most cases, however, individual birds did not remain visible for more than a few seconds. The majority of species were seen only rarely and many exhibited cryptic behaviour, which probably gives rise to under-representation in the population sample. Many species associated in mixed-species flocks, and in these there would be a bias towards recording the most conspicuous flock members. Cryptic species may, in some cases, be more effectively sampled by mist-netting programmes, but this is only really feasible in the understorey of rainforest and introduces a new set of biases (e.g. Lovejoy 1974). The importance of differential detectability is reduced since analyses compare relative abundances of the same sets of species between habitats.

Results presented for C13C were collected for five months (February to June 1980) prior to logging and six months (January to June 1981) after its completion (data collected during the six-month logging period are not here considered). Birds were observed by walking at random along a 100 × 100 m trail grid cut through an area of approximately 1 km². Observation times varied, but were generally between 06h00 and 18h00, and 19h30 and 22h00 daily. Between two and three weeks were spent at the study site each calendar month.

Results from C5A, C1A and C2 were collected by walking along three 3 km trails. Only the first kilometre was walked during the night. The entire length of the trail was covered at least once per day. Observation times were as at the main study site. Between 12 and 16 full days were spent at each site, but no more than six in any 30-day period.

The local abundance of some bird species may be a reaction to seasonal fluctuations of food abundance (e.g. Leighton 1982), thus comparative analyses are between matched monthly samples, unless indicated otherwise.

Before the onset of data collection, nine months were spent learning to recognize individual species. Not all vocalizations were reliably distinguished and all such data are dropped from the analyses. The use of these data would, in any case, overestimate the abundance of very vocal species such as hornbills Bucerotidae and barbets Capitonidae.

RESULTS

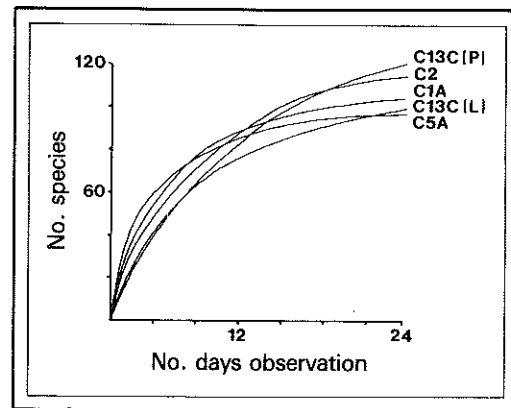
Species richness

Owing to the preponderance of rarity (i.e. of species living at very low densities), it may take a considerable time to record the full avifauna of an area of rainforest. In fact, owing to the dynamic nature of such an avifauna, it may be impossible to do so. Species accumulation curves (Figure 2) do not reach asymptotes. The differences in curve shape between primary and recently logged forests at C13C on the one hand, and the older logged forests on the other, indicate a greater abundance of birds in the latter. More species are recorded per day because more birds are recorded per day; the actual number of common species (i.e. those making up >1% of records) is in fact similar between sites (27 and 26 at C13C before and after logging, and a mean of 25.7 for the three older logged forests: see Appendix). The initial similarity of curves at C13C before and after logging indicates that results may not be significantly biased by differences in habitat-influenced observational ability (i.e. that the greater abundance of birds in the older logged forest is real).

Logged forests appear to support a lesser species richness than primary forest, however. Many species vacate the area as soon as logging begins and subsequently avoid it (pers. obs.). Others may be present in much reduced numbers and remain undetected. Significantly fewer species were observed per month following logging at C13C (Mann-Whitney U test: $U=1$, $n_1=n_2=4$, $p<0.05$). Species abundance curves indicate that logged forests accumulate species fairly quickly following an initial period of destabilization and loss of many species, but they do not necessarily regain species typical of primary rainforest (see Appendix).

The use of diversity indices to examine these data is inadvisable. Examining the whole avifauna by a single index ignores the fact that different subsets react to environmental disturbance in different ways (see Karr and Roth 1971).

Figure 2. Cumulative number of bird species in primary and selectively logged forests. Results from C13C are separated into those made before logging (P) and those made directly after logging (L).

*Species composition*

Degradation of forest habitat is certain to cause alterations in the composition of the avifauna. Such alterations may be temporary if the gene pool remains accessible and the forest is allowed to regenerate, or permanent if the logged area is isolated. Logging may be followed by the loss of some species, but will also be followed by the appearance of previously unrecorded species from secondary or edge habitat, many of which follow logging roads into forested areas (see Appendix).

The assemblages may first be examined in terms of sets of species (i.e. feeding guilds: Table 1). The number of species is a feature of sample size.

The primary forest avifauna is dissimilar to those of the older logged areas, but they are remarkably similar amongst themselves (Table 2). It should be noted that

Table 1. Comparison of feeding guild membership within primary and logged forest species assemblages. Feeding guild definitions follow those of Karr (1980), with the addition of the following: faunivore/frugivores (hornbills, which incorporate significant quantities of reptiles, etc., as well as fruit), sallying insectivores (birds that sally forth from a perch to capture flying insects) and sweeping insectivores (birds that fly swiftly in straight lines in open areas, normally above the canopy).

Trophic group	Feeding guild	Number of species		
		Unlogged (C13C)	Recent logged (C13C)	Old logged (C5A, C1A and C2)
Frugivores	Terrestrial	1	2	1
	Arboreal	16	10	9
Faunivore/frugivores	Arboreal	6	5	7
	Terrestrial	5	1	2
Insectivore/frugivores	Arboreal	28	23	30
	Terrestrial	10	8	9
Insectivore/nectarivores	Arboreal	16	6	4
	Terrestrial	11	7	11
Insectivores	Bark-gleaners	55	40	41
	Foliage-gleaners	20	17	9
Carnivores	Saltiers	9	7	7
	Raptors	15	9	11
	Piscivores	1	0	1
Number of species observed		193	135	142

Table 2. Pairwise comparison of the distribution of species between feeding guilds in different forests surveyed. Results are for chi-squared tests (the following groups are combined in the analyses: both frugivore guilds, both insectivore/frugivore guilds, raptors and piscivores). No areas are significantly different at the level $p<0.05$. Similarity is indicated: * = $p>0.95$, ** = $p>0.99$. It should be noted that effects of differential altitude of the study area appears inconsequential.

	C13C (primary)	C13C (logged)	C5A	C1A	C2
C13C (primary)	-				
C13C (logged)	3.03*	-			
C5A	11.58	7.62	-		
C1A	9.77	3.25*	1.99**	-	
C2	11.98	5.25	4.41	1.03**	-

the avifauna of C13C after logging was still in a state of change. This is also demonstrated by the shape of the species accumulation curve, which falls midway between that of undisturbed forest and that of the older logged forests (Figure 2). In effect, it was still losing species of primary forest but had not yet gained the edge species that were present in older logged areas. It should also be noted, however, that the areas with similar avifaunas were usually located close to each other.

The point should be emphasized that overall similarity of organization masks many changes of species composition, particularly between primary and older logged areas. If a correcting factor is applied to take into account the difference in time spent in unlogged and the old logged forests, i.e.:

$$d = \frac{n}{\left(\frac{t_1}{t_2}\right)}$$

where n = number of observations of species in unlogged forest,

t_1 = number of days observation in unlogged forest,

t_2 = number of days observation in the three old logged forests combined.

If species with a value of $d < 1.0$ are discounted, 22 species in total were judged to avoid logged forests (Table 3). On the other hand, 20 species were observed only in older logged forests or along logging roads.

Table 3. Intolerant and colonizing bird species at Sungai Tekam. Intolerant species are defined as those that occurred at C13C but not in older logged forests, taking the correction factor into account. Colonizing species are those occurring only at C5A, C1A and/or C2, and those associated with open logging roads (marked with an asterisk). Feeding guild codes are explained in the Appendix.

Intolerant species	Feeding guild	Colonizing species	Feeding guild
<i>Otus rufescens</i>	R	<i>Spizaetus cirrhatus</i>	R
<i>Hirundapus giganteus</i>	SwI	<i>Falco</i> sp.	R
<i>H. cochinchinensis</i>	SwI	<i>Clamator coromandus</i>	AIF
<i>Harpactes kasumba</i>	FGI	<i>Phodilus badius</i>	R
<i>Ceyx erithacus</i>	TI	<i>Caprimulgus indicus</i> *	SwI
<i>Lacedo pulchella</i>	TI	<i>C. macrurus</i> *	SwI
<i>Halcyon concreta</i>	TI	<i>Anthracoceros malayanus</i>	FF
<i>Buceros bicornis</i>	FF	<i>Muelleripicus pulverulentus</i>	BGI
<i>Sasia abnormis</i>	BGI	<i>Dryocopus javensis</i>	BGI
<i>Hemipus hirsuticeps</i>	Sal	<i>Cymbirhynchus macrorhynchus</i>	FGI
<i>Pericrocotus cinnamomeus</i>	FGI	<i>Pycnonotus goiavier</i> *	AIF
<i>Malacopteron affine</i>	FGI	<i>Hypsipetes charlottae</i>	AIF
<i>Stachyris poliocephala</i>	FGI	<i>Corvus enca</i>	FGI
<i>S. leucotis</i>	FGI	<i>Copsychus saularis</i> *	FGI
<i>Macronous ptilosus</i>	FGI	<i>Prinia rufescens</i> *	FGI
<i>Copsychus pyrropyga</i>	FGI	<i>Orthotomus ruficeps</i> *	FGI
<i>Emicurus leschenaulti</i>	TI	<i>Motacilla cinerea</i> *	TI
<i>Ficedula mugimaki</i>	Sal	<i>Lanius cristatus</i> *	FGI
<i>Culicapa ceylonensis</i>	Sal	<i>Zosterops everetti</i>	AIF
<i>Rhipidura perlata</i>	Sal	<i>Lonchura leucogastra</i>	AF
<i>Prionochilus percussus</i>	AF		
<i>Dicaeum concolor</i>	AF		

In general terms, there would appear to be less species of certain groups of insectivores in logged forests, notably terrestrial, foliage-gleaning and sallying species. Terrestrial species were uncommonly observed, but the lack of observations of almost all such species in old logged forests suggests they were avoiding such areas. A number of foliage-gleaners (e.g. babblers of genus *Stachyris*) and flycatchers (e.g. Mugimaki Flycatcher *Ficedula mugimaki* and Spotted Fantail *Rhipidura perlata*) were observed commonly in primary but never in logged forest. They may have been replaced to some extent by colonizing insectivore/frugivores (e.g. Yellow-vented Bulbuls *Pycnonotus goiavier* and Everett's White-eyes *Zosterops everetti*), but these species are present in large numbers only in very recently logged forest. There is some change in the species of frugivore present, although absolute numbers of frugivorous species are similar between study sites. For example, flowerpeckers Dicaeidae, which specialize on mistletoe (Loranthaceae) berries, are entirely absent from older logged forests.

Individual species abundances

Pairwise comparisons of the distribution of individuals between feeding guilds in all combinations of the different forest types give no conclusive results. Using chi-squared tests, all sites are significantly different from all others ($p < 0.001$ in every case) regardless of proximity or altitude. This is probably a reflection upon vagaries of small sample sizes: the older logged forests would have been expected to be more similar to each other than to primary forest.

The response of particular species (see Appendix) may in some cases be attributed to particular effects of logging. For example, logging causes blockage and eutrophication of forest streams, and this adversely affects piscivorous kingfishers Alcedinidae and stream-feeding passerines, such as White-crowned Forktails *Enicurus leschenaulti*. Concentration of logging activity on ridgetops destroys a high proportion of traditional dancing-grounds of Great Argus Pheasants *Argusianus argus*, which are preferentially established in such areas (G. W. H. Davison verbally); their reproductive success, although not their immediate population density, is likely to be affected as a result.

Logging causes contrasting shifts in the abundance of certain species groups (Figure 3), which often reflects the dominance or demise of particular species. Babblers Timaliidae of such genera as *Malacopteron* and *Stachyris* were observed commonly in primary forest but far less so following logging. Comparing observations before and after logging at C13C, a significant drop in numbers was evident (Mann-Whitney U test: $U=0$, $n_1=n_2=4$, $p < 0.05$). There was also a significant drop in the numbers of understory flycatchers Muscicapidae in logged forests (comparing primary forest at C13C with the three logged forest sites: $U=0$, $n_1=4$, $n_2=3$, $p < 0.05$). By contrast, significantly higher numbers of bulbuls Pycnonotidae were recorded (comparing primary with older logged forest sites: $U=0$, $n_1=4$, $n_2=3$, $p < 0.05$). This was largely due to the appearance in the sample of large numbers of the colonizing Cream-vented and Yellow-vented Bulbuls *Pycnonotus simplex* and *P. goiavier*. The opening-up of the canopy by logging allowed invasion of lower levels by large numbers of sweeping insectivores, notably

by migrant Barn Swallows *Hirundo rustica*. Migrant Blue-throated Bee-eaters *Merops viridis* were also commonly observed in the lower levels of logged forest.

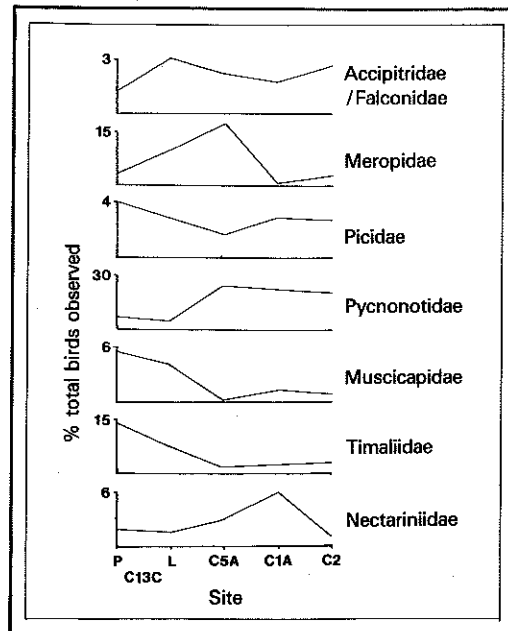
It should be noted that although species are here classified into discrete feeding guilds, some may alter foraging strategies in response to changes in the resource profile. For example, bark gleaners such as Crimson-winged and Banded Woodpeckers *Picus puniceus* and *P. miniaceus* switch to foliage-gleaning when faced with a shortage of bark insects. In view of the predominance of specialized feeders in rainforest, however, major changes in food chosen or feeding behaviour are unlikely to be widespread.

DISCUSSION

Rarity

There is no pattern in the abundance of species in the sample at C13C before logging in relation to their abundance in logged forests. Many species rarely observed in primary forest were equally infrequent in logged areas while others were encountered regularly (e.g. Crested Jay *Platylophus galericulatus*). Some species that were observed frequently in primary forest survive well in logged forest (e.g. Bushy-crested Hornbill *Anorrhinus galeritus*) whereas others do not (e.g. Spotted Fantail *Rhipidura perlata*).

Figure 3. Changes in the relative abundance of selected families of birds in primary and logged forests. Results from C13C are separated into those made before logging (P) and those made directly after logging (L).



Furthermore, there is no pattern in the survival of sets of species of different body weight: some large-bodied species survive successfully (e.g. hornbills Bucerotidae) whereas others do not (e.g. partridges Phasianidae). Responses are more likely to be due to changes in habitat parameters than due to body weight *per se*, although it should be noted that large-bodied species are often more specialized feeders (*cf.* Cope's Law; Ricklefs 1979).

No direct conclusions can be drawn concerning patterns of rarity since samples are limited and serendipity would be a major influence. Seasonal or periodic fluctuations cannot be taken into account, and it is clear that there are high proportions of itinerants among many bird populations, some species (e.g. green pigeons *Treron* and some hornbills *Rhyticeros*) being entirely nomadic (Leighton 1982, Wells 1985). It is necessary to examine features of the environment that are likely to affect patterns of bird distribution.

Food resources

Frugivorous birds may be divided into two main groups: those that feed primarily on small fruits (e.g. bulbuls Pycnonotidae) and those that feed primarily on large fruits (e.g. hornbills Bucerotidae). Both types of fruit are distributed patchily in dipterocarp forest, largely because very few of the tree species produce fruit that is edible to birds (McClure 1966, Fogden 1972).

Small fruits are characteristically produced by small and early-maturing trees, which are often commoner in early successional patches or in riparian habitat, and thus show a highly clumped distribution (Fogden 1972). Large bird-edible fruit are usually produced by rare and widely dispersed canopy trees, and are exploited by large-bodied species capable of travelling long distances and which frequently form cohesive flocking units (e.g. green pigeons *Treron* and Mountain Imperial Pigeon *Ducula badia*).

Specialization towards exploiting a resource that is both patchily distributed and erratic in its seasonality is, to a certain extent, preadaptive to survival in conditions of habitat disturbance. In logged forest, dispersion of large fruit sources will become increasingly irregular, but those species which are physiologically and anatomically adapted for extensive ranging are likely to persist. Less wide-ranging species which feed on sugar-rich fruits are often able to exploit colonizing trees and shrubs (Fogden 1972) and may be less vulnerable than those species which specialize on large fruits produced by trees which are eliminated by logging; for example, disproportionate loss of strangling fig trees *Ficus* subgenus *Urostigma* may adversely affect large hornbills (Leighton and Leighton 1983).

Among the most susceptible frugivores may be small species which feed on lipid-rich fruit (e.g. Green Broadbill *Calypotomena viridis*). Lipid-rich fruit are not often borne by colonizing trees. Flowerpeckers Dicaeidae would appear to be severely restricted in logged forest for similar reasons: in this case, a reliance on a single group of plants (Loranthaceae) which are parasites of canopy trees.

Insectivore/nectarivores, which feed in association with flowers to a major extent, share many behavioural traits with frugivores. Although not well adapted for flying long distances, the species in question typically show considerable local population

shifts, even in primary forests, consistent with the spatial and temporal patterning of food resources. This feature would enable species to exploit patchy food resources in logged forest, and most appear to persist at Sungai Tekam. The more open habitat in recently logged forest contains higher densities of many flowering plants visited by sunbirds of the genera *Anthreptes* and *Hypogramma*, and supports the thick, tangled pioneer community of bananas Musaceae and gingers Zingiberaceae that is occupied by many spiderhunters *Arachnothera*.

Foliage insects are a largely predictable resource in primary forest, but become less so following logging. The overall abundance of insects is less in logged forest, and periods when they are a scarce resource are longer (Wong 1982). Such periods of low abundance of foliage insects are marked by shifts in the feeding habits of some species; bulbuls Pycnonotidae and malkohas *Phaenicophaeus* add fruit or increase the proportion of fruit in their diet. Species which are obligate insectivores will not remain in habitat where shortages of insect prey occur. For example, a severe reduction in the numbers of large foliage insects favoured by trogons *Harpactes* may account for the low numbers of these birds in logged forests.

Babblers Timaliidae are extremely abundant in primary forest and may make up a major portion of the biomass (Wong 1985). They are mostly gleaning insectivores and may find less food in regenerating vegetation. Certain understorey flycatchers, in such genera as *Muscicapa* and *Philentoma*, were also observed far less frequently in logged forests. This is not likely to be correlated with food abundance since the numbers of some flying insects (notably mosquitos Culicidae) increases considerably. There are, however, two ways in which the insects may be less accessible to flycatchers in logged forests. First, sallying species might be limited in their feeding by an absence of suitable perches in the vicinity of food resources, for example, along logging roads and in cleared areas where the insects congregate to breed in water-filled ruts. Second, in such open areas, flying insects become increasingly exploited by sweeping insectivores such as swifts Apodidae and Barn Swallows *Hirundo rustica*, which are restricted to foraging above the canopy in primary forest. These birds, and especially migrant Blue-throated Bee-eaters *Merops viridis*, occupy foraging volume normally used by understorey flycatchers.

Their position at the top of the food chain might be expected to render carnivores susceptible to disturbances affecting the food web, but most appear to exploit a variety of prey species opportunistically and are able to move over very large areas. Many species take advantage of the fact that prey have to cross open areas more frequently in logged forest and are thus more easily seen and captured. Patrolling or scanning of roadways was observed in many species, such as Collared Scops Owls *Otus bakkamoena*, which catch beetles, and hawk eagles *Spizaetus* and Crested Serpent Eagles *Spilornis cheela*, which catch mostly reptiles.

Microhabitat gradients

Karr and Freemark (1983) suggest that selection of optimal microhabitats is a primary determinant of activity, particularly among understorey species. Optimal microhabitats will be selected on the basis of foraging volume (habitat structure) and conditions of temperature and humidity. The activity of many small birds is limited

by temperature fluctuations; some are known never to cross sunlit patches (Bell 1982). Microclimatic changes associated with logging probably limit populations of understorey groups such as babblers Timaliidae more than do alterations of food supply. Babblers are known to become heat-stressed very easily outside of their preferred environment (M. Wong verbally). Species which normally follow the outer surface ('skin') of the forest searching for food (e.g. drongos *Dicrurus*, malkohas *Phaenicophaeus*, leafbirds *Chloropsis*) do not show such physiological limitations and are more likely to respond to features of resource abundance than to microclimatic gradients. As the canopy is broken up by logging, these species will also occupy foraging volume normally exploited by (but now rendered unsuitable for) understorey species.

Logging acts directly to eliminate or reduce certain parts of the microhabitat mosaic. The bark of some forest trees is scorched by sunlight, which also kills the covering of mosses and epiphytes. This change causes a reduction in the numbers of some bark-gleaning insectivores and those that probe among moss and epiphytes for their food. Drying and hardening of the soil severely reduces the availability of soil arthropods and has a marked effect upon litter-gleaning birds: this group may be the most vulnerable to elimination by logging. Terrestrial babblers (e.g. Black-capped Babbler *Pellorneum capistratum*, Large Wren-Babbler *Napothera macrodactyla*, and *Trichastoma* species) were rarely observed in logged forest at Sungai Tekam, and no species of pitta Pittidae was encountered (these birds are normally easily detected because of their characteristic calls).

Nest sites

Loss of suitable nest sites is another factor that may restrict the populations of certain birds in logged forest (e.g. cavity nesters: McClure 1968). Reproductive success of birds has been reported to be depressed even in forest logged 25 years previously (Wong 1985), although it is not clear whether a lack of nest sites or other factors give rise to this difference. No data are provided by this study (see Johns 1985).

Cautionary note

Many large-bodied forest birds travel over large distances and may range between logged and primary forests at Sungai Tekam, although in the case of areas C1A and C2 this would require travelling at least 6 km. Their exploitation of logged forest indicates that it is not wholly unsuitable habitat, but they may not be able to persist solely within it. Most small-bodied itinerant birds would not range so far on less than a seasonal basis, however. Differences in species composition between sites may to some extent be due to the limited observation time, the patchy distribution of birds, the serendipity of encounters, and slight differences caused by altitude, but a consideration of microhabitat parameters suggests that avoidance of logged forest by some species is likely.

The persistence of a large number of bird species in logged areas some distance from primary forest might be taken to indicate resilience to disturbance. It should be borne in mind, however, that following logging the land was left to regenerate

naturally, apart from some replanting in heavily damaged areas: there was no further disturbance. This is atypical of many regions, where logged forests are invaded by hunters and agriculturalists (Johns 1985).

Furthermore, the study considers only short-term results. It would be expected that the most critical period of resident birds is immediately following logging; it is at this time that the species assemblage shows characteristics of instability (notably a predominance of generalist species: see Pimm and Lawton 1978). Itinerant birds may not be stressed at this time, however, because of the proximity of primary forest. While many species persist in the primary/logged forest mosaic at Sungai Tekam, it has yet to be proven that forest avifaunas can be maintained in discrete areas that are completely logged (i.e. selectively logged throughout).

As logging continues at Sungai Tekam, primary forest will become increasingly remote from the older regenerating forests and their use by nomadic and perhaps by itinerant birds may thus fall off over time (unless they regenerate quickly to a stage whereby they can support these birds). In time, primary forest may remain only on steeper land. Many species' distributions are limited by slope (i.e. the hill-foot boundary: Wells 1985) and the source of colonists may thus be curtailed (unless older logged forests support the susceptible species by this time). It is hoped that longer-term observations at Sungai Tekam will provide answers to some of these outstanding questions.

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APPENDIX
BIRD SPECIES RECORDED IN PRIMARY AND SELECTIVELY LOGGED FORESTS AT SUNGAI TEKAM.

Migrant species are marked (Mig); montane species, probably accidental at Sungai Tekam, are marked (Mont).

Feeding guild data are from D. R. Wells (*in litt.*) and my own personal observations. Feeding guild codes are as follows: TF, terrestrial frugivore; AF, arboreal frugivore; FF, arboreal faunivore/frugivore; TIF, terrestrial insectivore/frugivore; AIF, arboreal insectivore/frugivore; IN, insectivore/nectarivore; TI, terrestrial insectivore; BGI, bark-gleaning insectivore; FGI, foliage-gleaning insectivore; Sal, sallying insectivore; SwI, sweeping insectivore; R, raptor; P, piscivore.

Observations made at C13C are divided into those made in primary forest (P) and those made directly after logging (L). Species abundances are noted as follows: -, not observed; x, <0.5% of sample; xx, between 0.5 and 1.0% of the sample; xxx, >1.0% of the sample; p, present (these species were not included in the population sample since they are above-canopy feeders and would thus be underestimated in primary forest where the canopy is closed). Species which follow logging roads, and may thus occur along open roads even within otherwise primary forest, are marked with an asterisk (*).

Nomenclature follows Wells (1985), with minor additions.

Family and species	Feeding guild	C13C (P)	C13C (L)	C5A	C1A	C2	Family and species	Feeding guild	C13C (P)	C13C (L)	C5A	C1A	C2
ACCIPITRIDAE							<i>Keops ketupu</i>	R	x	-	-	-	xx
<i>Aviceda jerdoni</i> (Mig)	R	-	x	-	-	-	<i>Olancheilus brodiei</i> (Mont)	R	x	x	-	-	-
<i>Peris pilorhynchus</i> (Mig)	R	x	-	-	-	-	<i>Ninox scutulata</i>	R	x	-	-	-	-
<i>Accipiter trivirgatus</i>	R	x	xx	x	-	x	CAPRIMULGIDAE						
<i>A. gularis</i> (Mig)	R	x	-	-	-	-	<i>Burystropus tenuirostris</i>	SwI	xx	xx	x	x	xxx
<i>Buteo indicus</i> (Mig)	R	x	x	-	-	-	<i>Coprimachus indicus</i> (Mig)*	SwI	-	-	-	-	x
<i>Spizaetus cirrhatus</i>	R	-	-	-	-	-	<i>C. macrurus</i>	SwI	x	-	x	-	-
<i>S. nomen</i>	R	x	-	-	-	-	AFODIDAE						
<i>S. albinger</i>	R	x	x	-	-	-	<i>Calocitta sp.</i>	SwI	p	p	p	p	-
<i>Hieronax hiemalis</i>	R	x	xx	x	-	-	<i>Hirundinidae</i>	SwI	p	p	-	-	-
<i>Lanius malayensis</i> (Mont)	R	x	-	-	-	-	<i>H. ochirophana</i>	SwI	p	p	-	-	-
<i>Spilornis cheela</i>	R	x	xx	xx	xx	xxx	<i>Raphidura leucopygia</i>	SwI	p	p	p	p	p
FALCONIDAE													
<i>Microbuteo fringillarius</i> *	R	x	x	xx	x	xxx	HEMIPROCNIDAE						
<i>Falco sp.</i>	R	-	-	-	-	-	<i>Hemiprocne longipennis</i>	SwI	x	xxx	xxx	xxx	xx
PHASIANIDAE													
<i>Rhinoceros longirostris</i>	TIF	x	-	-	-	-	<i>H. comata</i>	SwI	x	x	xxx	xx	xxx
<i>Arborophila chartonii</i>	TIF	x	-	-	-	-	TROGONIDAE						
<i>Rallulus rufus</i>	TIF	x	-	-	-	-	<i>Harpactes kaumba</i>	FGI	xx	x	-	-	-
<i>Polyplectron malacense</i>	TIF	x	-	-	-	-	<i>H. alardi</i>	FGI	x	-	-	-	-
<i>Argusianus argus</i>	TIF	xx	xx	xx	xxx	xxx	<i>H. orriophanus</i>	FGI	x	x	-	xx	x
COLUMBIDAE													
<i>Trogon curvirostris</i>	AF	xxx	xxx	-	-	x	<i>H. alvaresii</i>	FGI	x	-	-	-	-
<i>T. olax</i>	AF	x	-	-	-	-	<i>H. orealis</i>	FGI	x	-	-	-	-
<i>T. vernans</i>	AF	x	x	-	xx	xxx	ALCEDINIDAE						
<i>Ptilinopus jumbo</i>	AF	x	-	-	-	-	<i>Alcedo virens</i>	P	x	-	-	x	-
<i>Ducula badii</i>	AF	x	xxx	xxx	xxx	xxx	<i>Ceyx erithaca</i>	TI	x	x	-	-	-
<i>Streptopelia chinensis</i> *	TF	-	x	-	-	-	<i>Halyon concreta</i>	TI	x	-	-	-	-
<i>Chalcophaps indica</i>	TF	x	x	-	xxx	x	<i>Lacoia pulchella</i>	TI	x	x	-	-	-
PSITTACIDAE													
<i>Priniasia longicauda</i>	AF	-	x	-	-	-	MEROPIDAE						
<i>Ptilinopus cyanurus</i>	AF	xxx	xx	xxx	xxx	xxx	<i>Merops lezchenaulti</i> (Mig)	Sal	x	-	-	-	-
<i>Loriculus galgulus</i>	AF	xxx	x	xx	xx	xxx	<i>M. viridis</i> (Mig)	Sal	xxx	xxx	xxx	x	xxx
CUCULIDAE													
<i>Climacteris corniculata</i> (Mig)	AIF	-	x	-	-	-	<i>Nycternis amicus</i>	Sal	x	x	-	x	x
<i>Cazulius ussurus</i>	FGI	-	xx	-	-	-	CORACIIDAE						
<i>C. micropterus</i>	FGI	x	xx	-	-	xxx	<i>Eurystomus orientalis</i>	Sal	-	x	x	-	xx
<i>Cazemanus somerai</i>	FGI	x	x	-	-	-	BUCEROTIDAE						
<i>C. variolus</i>	FGI	x	-	-	-	-	<i>Berenicornis comatus</i>	FF	x	-	-	-	x
<i>Chrysocolaptes xanthorhynchus</i>	FGI	x	-	-	-	-	<i>Asorhinus galeritus</i>	FF	xxx	xxx	xxx	xxx	xxx
<i>Surniculus lagurus</i>	FGI	x	x	-	-	-	<i>Rhyticeros corrugatus</i>	FF	-	x	-	-	xxx
<i>Phaenophaeus thardi</i>	FGI	x	x	-	-	x	<i>R. undulatus</i>	FF	xxx	xxx	xx	xx	xx
<i>P. namoutanus</i>	AIF	x	-	-	-	-	<i>Anthracoeros malayanus</i>	FF	-	-	-	xx	xxx
<i>P. chlorophanus</i>	AIF	xx	xx	x	x	xx	<i>Buceros rhinoceros</i>	FF	xxx	xxx	xx	xxx	xx
<i>P. jerningii</i>	AIF	x	xx	x	x	xx	<i>B. bicornis</i>	FF	xxx	-	-	-	-
<i>P. curvirostris</i>	AIF	x	xx	x	xxx	xx	<i>Rhinoplax vigil</i>	FF	xxx	xxx	xx	xxx	xx
<i>Centropus rezusquius</i>	TI	x	x	-	-	-	CAPITONIDAE						
TYTONIDAE													
<i>Phodilus badius</i>	R	-	-	-	x	x	<i>Megalaima chrysoptera</i>	AIF	xx	xx	xx	x	x
STRIGIDAE													
<i>Onus rufescens</i>	R	x	-	-	-	-	<i>M. rafflesii</i>	AIF	x	-	-	-	-
<i>O. bakkamensis</i>	R	x	xx	x	xx	x	<i>M. myiactophanus</i>	AIF	x	xxx	x	xxx	xxx
							<i>M. henrici</i>	AIF	xx	xxx	-	xxx	xx
							<i>M. ussurialis</i>	AIF	xx	xxx	-	xx	-
							<i>Calamhamphus fuliginosus</i>	AIF	xxx	xxx	xxx	x	-
PICIDAE													
							<i>Sasia abnormis</i>	BGI	x	-	-	-	-

Family and species	Feeding guild	C13C (P)	C13C (L)	C5A	C1A	C2	Family and species	Feeding guild	C13C (P)	C13C (L)	C5A	C1A	C2
<i>Celaus brachyurus</i>	BGI	x	-	-	-	-	<i>S. nigricollis</i>	FGI	xx	-	-	xxx	-
<i>Picus puniceus</i>	BGI	xxx	xx	xx	x	x	<i>S. mindanensis</i>	FGI	xx	-	-	x	-
<i>P. montalis</i>	BGI	x	x	-	x	-	<i>S. erythroptera</i>	FGI	xxx	xx	x	xxx	xx
<i>P. minor</i>	BGI	x	-	-	-	-	<i>Macronus gularis</i>	FGI	xx	xxx	x	xxx	xxx
<i>Dinopium rafflesii</i>	BGI	x	-	-	-	-	<i>M. pilosus</i>	FGI	x	-	-	-	-
<i>Megalyptes sukhi</i>	BGI	x	x	-	xx	-	<i>Aloupe brunneicauda</i>	FGI	x	xxx	x	xxx	-
<i>Mulleripicus pulverulentus</i>	BGI	-	-	xx	-	x	<i>Yuhina cantholoea</i>	FGI	xxx	xx	x	xx	-
<i>Dryocopus javensis</i>	BGI	-	-	-	-	xxx	TURDIDAE						
<i>Picoides canicapillus</i>	BGI	x	-	-	-	-	<i>Eritrichus cyane</i> (Mig)	TI	x	-	-	-	-
<i>Hemicircus concretus</i>	FGI	xx	xx	x	xx	xx	<i>Corychus saularis</i> *	FGI	xx	xx	xxx	xxx	xx
<i>Myiophobus rubiginosus</i>	BGI	xx	x	x	x	x	<i>C. malabaricus</i>	FGI	xxx	xxx	x	xxx	x
<i>Reinwardtipicus validus</i>	BGI	x	x	x	-	-	<i>C. pyropygus</i>	FGI	x	x	-	-	-
EURYLAIMIDAE													
<i>Ceylon sumatranus</i>	FGI	-	x	x	-	x	<i>Bnicurus ruficapillus</i>	TI	xx	-	-	-	-
<i>Gymbrichynchus macrorhynchus</i>	FGI	-	-	-	-	x	<i>E. leschenaulti</i>	TI	x	-	-	-	-
<i>E. schwaneri</i>	FGI	x	-	-	-	-	<i>Turdus obscurus</i> (Mig)	TI	x	-	-	-	-
<i>Calyptonna viridis</i>	AF	xx	x	-	-	-	<i>Zosteria citrina</i>	TI	x	-	-	-	-
PITTIDAE													
<i>Pitta granatina</i>	TI	x	-	-	-	-	SVLVIDAE						
HIRUNDINIDAE													
<i>Hirundo rustica</i> (Mig)	SwI	p	p	p	-	p	<i>Gerygone sulphurea</i>	FGI	x	-	-	-	-
CAMPUPHAGIDAE													
<i>Hemipus pinnatus</i>	Sal	x	x	-	-	-	<i>Phylloscopus inornatus</i> (Mig)	FGI	x	-	-	-	-
<i>H. hirundinaceus</i>	Sal	xx	x	-	-	-	<i>P. borealis</i> (Mig)	FGI	x	-	-	-	-
<i>Tephrodornis virgatus</i>	FGI	xxx	xx	x	-	-	<i>P. coronatus</i> (Mig)	FGI	xxx	xxx	x	-	-
<i>Corvus formicivorus</i>	AIF	-	-	-	-	-	<i>Abrosopus superciliosus</i>	FGI	-	x	-	-	-
<i>Parus caeruleus</i> (Mig)	FGI	x	-	-	-	xxx	<i>Orthotomus sepius</i>	FGI	xx	x	x	x	
<i>P. cinereus</i>	FGI	xx	-	-	-	-	<i>O. atrogularis</i>	FGI	xxx	xx	xx	xxx	xxx
<i>P. flammatus</i>	FGI	xxx	xxx	xx	x	xxx	<i>O. ruficeps</i>	FGI	-	-	-	-	-
ASCITHINIDAE													
<i>Agathis viridissima</i>	FGI	x	x	x	xxx	x	MUSCICAPIDAE						
<i>A. lafrenoyi</i>	AIF	x	x	-	-	-	<i>Rhinomyias umbrinus</i>	Sal	x	x	-	-	-
<i>Chloropsis cyanopogon</i>	AIF	x	x	xxx	x	x	<i>Muscicapa strobila</i> (Mig)	Sal	x	-	-	-	-
<i>C. somerai</i>	AIF	xx	xx	xxx	-	-	<i>M. latirostris</i>	Sal	xx	xxx	x	-	x
<i>C. cochinchinensis</i>	AIF	xx	xxx	xx	xxx	xxx	<i>M. williamsoni</i> (Mig)	Sal	x	-	-	-	-
<i>Irena puella</i>	AF	xxx	xxx	xxx	xxx	x	<i>M. ferruginea</i> (Mig)	Sal	-	-	-	-	-
PYCNONOTIDAE													
<i>Pycnonotus melanoleucus</i>	AIF	x	-	-	-	-	<i>Bumyia thalassina</i>	Sal	x	x	-	-	-
<i>P. atriceps</i>	AIF	x	-	xxx	-	-	<i>Ficedula mugimabi</i> (Mig)	Sal	x	-	-	-	-
<i>P. ignipectus</i>	AIF	x	x	xxx	-	-	<i>F. solitaria</i> (Mont)	Sal	-	-	-	-	-
<i>P. cyaniventris</i>	AIF	x	x	xxx	x	xxx	<i>F. dumetoria</i>	Sal	x	-	-	-	-
<i>P. eutilinus</i>	AIF	x	-	-	-	-	<i>Cyanopitta cyanomelana</i> (Mig)	Sal	x	-	-	-	-
<i>P. goiavesis</i> *	AIF	-	x	xxx	-	-	<i>Cyornis sinensis</i>	Sal	x	-	-	-	-
<i>P. simplex</i>	AIF	xx	xx	xxx	xxx	xxx	<i>Caliopteryx zeylanensis</i>	Sal	xx	x	-	-	-
<i>P. brunneus</i>	AIF	xx	xxx	xxx	xxx	xxx	<i>Rhipidura perita</i>	Sal	xxx	xx	-	-	-
<i>P. erythrocephalus</i>	AIF	x	x	-	xxx	xx	<i>Sasia abnormis</i>	Sal	xxx	x	-	x	x
<i>Crimmer finchii</i>	AIF	x	-	-	-	-	<i>Philonota velatum</i>	Sal	x	x	x	x	-
<i>C. ochraceus</i>	AIF	xxx	x	x	-	-	<i>P. pyrhoptrum</i>	Sal	xx	x	x	x	-
<i>C. bres</i>	AIF	xx	x	xx	-	xx	<i>Terpsiphona paradiisi</i>	Sal	xx	-	-	xx	xx
<i>C. phaeocephalus</i>	AIF	xxx	x	x	xxx	xx	MOTACILLIDAE						
<i>Hypotaenidia crinita</i>	AIF	-	-	-	-	-	<i>Motacilla cinerea</i> *	TI	x	x	xx	-	x
<i>H. charlottae</i>	AIF	-	-	-	-	-	<i>Dendronanthus indicus</i>	TI	x	-	-	-	-
<i>H. malaccensis</i>	AIF	xxx	xx	xx	xxx	-	LANIIDAE						
DICRUPTIDAE													
<i>Dicrurus simplex</i>	IN	xx	x	x	xx	-	<i>Lanius cristatus</i> (Mig)	FGI	-	-	-	x	-
<i>D. aeneus</i>	FGI	xx	xx	x	xxx	xxx	<i>L. tigrinus</i> (Mig)*	FGI	x	x	x	-	x
<i>D. paradisi</i>	FGI	xxx	xxx	xx	xxx	xx	STURNIDAE						
OROLIIDAE													
<i>Oriolus chinensis</i>	FGI	xx	x										