

Selective Logging and Wildlife Conservation in Tropical Rain-Forest: Problems and Recommendations

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ABSTRACT

Exploited forests have frequently been regarded as being of little use in the conservation of animal species. While it is true that many species are adversely affected by selective logging and some are entirely unable to survive in disturbed forest, a large number of species are able to maintain viable populations. Logged forests may have an important rôle in the conservation of rain-forest animals as they will continue to occupy large land areas, whereas primary forest reserves will be increasingly restricted in size. Primary forests are of vital importance in supporting a full range of rain-forest species, but logged forests are able to support many animals, including some that cannot survive in small, isolated primary forest reserves.

INTRODUCTION

Tropical hardwood forests are an extremely valuable economic resource, representing a major (actual or potential) source of foreign currency for many tropical countries. Agencies concerned with the conservation of forests and wildlife are rarely given priority over governmental departments concerned with trade and the economy. Thus current forest exploitation rates are likely to increase, limited only by the extent and

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accessibility of the remaining forests. It is unrealistic to assume that owner countries will choose to conserve extensive areas of natural forest without sound and tangible economic reasons for doing so. Such sound economic reasons are not always easy to produce however, and even if obvious may not be heeded. Protection of mountain watersheds, for example, is frequently necessary to maintain water quality and to prevent downstream flooding, but such is rarely enforced (e.g. Robertson & Soetrisno, 1982).

Economic development is almost inevitably synonymous with disturbance or destruction of the natural habitat. Habitat destruction is assured where governmental or private agencies obtain maximum returns (at least in the short-term) by establishing cash-crop plantations or colonisation areas. The prospects for survival of rain-forest wildlife in such areas are bleak (Marsh *et al.*, in press). Where areas are set aside for long-term forestry, the prospects for wildlife may be far better. Some foresters have considered tropical rain-forests to be difficult to manage as a viable silviculture, and have recommended its replacement with single-species plantations (UNESCO, 1978). Fortunately for rain-forest wildlife, and to the relief of conservationists, established plantations have met with only limited success (see Kio, 1976). Far more effort has been devoted to maintaining rain-forest in an economically productive state: research has concentrated on developing effective silvicultural techniques to manage existing forest (UNESCO, 1978). Such techniques are based on the selective removal of economically valuable trees, allowing the residual forest to regenerate, with or without the implementation of management procedures.

Whether or not rain-forest wildlife can exist alongside the timber industry is a matter of some controversy. It is also of immediate importance in a world where undisturbed rain-forests are rapidly being reduce to small, isolated fragments. The long-term survival of many rain-forest animals may be correlated realistically with their ability to persist in logging areas and in regenerating logged forest.

Research into the ability of species to persist in logged forest with a view towards formulating conservation policy is a difficult exercise. Somewhat counter-productively, results demonstrating an ability of species to survive disturbance may be used by some to justify further disturbance of primary habitat. This problem has arisen particularly in South-east Asia, perhaps because studies of the effects of logging have concentrated on a few larger species, coincidentally successful ones, and opinions are

expressed accordingly (e.g. Wilson & Wilson, 1975; Wilson & Johns, 1982). Only in the consideration of the effects of disturbance on the rain-forest community as a whole can a realistic impression be achieved. Even then, results may be applicable only to the particular area involved. Results may, however, give an overall impression of the differing reactions of sub-sets of the fauna, and suggest why these differences occur.

This paper considers data from a recent study of the effects of selective logging on a rain-forest animal community in West Malaysia (Johns, 1983a). An analysis of ecological correlates of the responses shown by different animal species gives some support to theories of multiple-use management of rain-forest habitat.

WHAT IS SELECTIVE LOGGING?

Selective logging may be defined by a forester as 'the removal of mature, over-mature and defective trees in such a manner as to leave uninjured an adequate number and volume of healthy residuals of commercial species and other tree species, necessary to assure a future crop of timber and forest cover for the protection of soil and water' (Rapera, 1977). This involves the harvesting, by whatever means, of a certain proportion of commercially valuable trees from a forest. All too little attention may actually be paid to the environmental consequences of the logging practices: legislation designed to protect residual trees has proven almost universally ineffective (e.g. Liew, 1978).

There are two basic silvicultural techniques employed in tropical rain-forest. As defined by Whitmore (1984) these are:

- (a) Monocyclic systems, which remove all saleable trees in a single operation. The time that must elapse before re-logging can occur equals the rotation age of the trees.
- (b) Polycyclic systems, which are based on the repeated removal of selected trees in a continuing series of felling cycles, whose length is less than the rotation age of the trees.

Certain silvicultural systems employ both monocyclic and polycyclic techniques dependent on the local diversity of commercial species (e.g. the 'selective forest management system' employed in parts of West Malaysia: Canonizado, 1978; Whitmore, 1984).

The most important difference between the two techniques is that polycyclic systems rely on minimising damage caused to the residual stand, since it is the established adolescent trees which form the next crop. Thus the degree of habitat disturbance may be rather less under polycyclic systems, although felling and associated human disturbances occur more frequently. This is also dependent on the number of commercial trees extracted per unit area. Low densities of commercial species may promote polycyclic logging systems, very high densities are more efficiently logged by a monocyclic system with enrichment planting of commercial species on severely damaged land as appropriate (Whitmore, 1984).

WHERE IS SELECTIVE LOGGING OCCURRING?

Intensive selective logging for timber is a well-established industry in both South-east Asia and Africa. Most of the extant tropical forest in South-east Asia will have been logged by the beginning of the 21st century, although substantial tracts of primary forest will remain in central Africa (Myers, 1980). Intensive logging is a comparatively new phenomenon in South America, although it is becoming well-established in the coastal forest (Chocó) of Colombia and in north-east Brazil. In 1981, for the first time, timber was the main export of one of the Brazilian states (Pará, south of the lower Amazon river) (J. M. Ayres, pers. comm.).

Extensive logging, aimed at extracting rare but valuable trees from the forest, often by traditional means, is less of a problem than large-scale, mechanised logging and is discussed elsewhere (Johns, 1983*b*). It is worthy of note, however, that although large areas of forest will remain in Amazonia at the end of the 20th century (Myers, 1980), almost the entire lowland river system has already been penetrated by loggers in search of rare timbers (J. M. Ayres, pers. comm.).

EFFECTS OF SELECTIVE LOGGING ON RAIN-FOREST VEGETATION

Logging may selectively remove certain rare tree species from the forest where they are sought after as a valuable timber (Johns, 1983*b*). In conditions of large-scale, highly mechanised logging (where extraction rates equal or exceed 10 trees ha^{-1}), logging may, however, be largely

TABLE 1
 Predominant Tree Families in Hill Dipterocarp Forest Before and After Logging (Sungai Tekam: West Malaysia)
 (The majority of timber trees removed (84%) belonged to the families Dipterocarpaceae and Leguminosae. Most colonising trees were species of the Euphorbiaceae, the only other important genus being *Cassia* (Leguminosae).)

<i>Unlogged forest</i>			<i>Recently-logged forest</i>			<i>5-6 year-old logged forest</i>		
<i>Rank</i>	<i>Family</i>	<i>% sample</i>	<i>Rank</i>	<i>Family</i>	<i>% sample</i>	<i>Rank</i>	<i>Family</i>	<i>% sample</i>
1	Euphorbiaceae	27.0	1	Euphorbiaceae	28.2	1	Euphorbiaceae	37.5
2-5	Dipterocarpaceae	7.7	2	Dipterocarpaceae	7.5	2	Leguminosae	12.5
2-5	Leguminosae	7.7	3-5	Leguminosae	6.8	3	Burseraceae	7.4
4	Annonaceae	6.1	3-5	Annonaceae	6.8	4	Myristicaceae	6.6
5	Meliaceae	5.4	5	Meliaceae	5.4	5-5	Anacardiaceae	4.4
6	Sapindaceae	5.2	6	Myristicaceae	5.2	5-5	Dipterocarpaceae	4.4
7	Lauraceae	4.8	7	Sapidaceae	4.8	7	Moraceae	2.9
8	Myristicaceae	4.6	8	Lauraceae	4.6	9-5	Annonaceae	2.2
9	Burseraceae	4.1	9-5	Anacardiaceae	3.4	9-5	Melastomataceae	2.2
10	Anacardiaceae	3.2	9-5	Myrtaceae	3.4	9-5	Myrtaceae	2.2
						9-5	Sapindaceae	2.2
N		1 140			565			272

random in its effects. Overall damage is severe and certainly not limited to the commercially important trees.

In a West Malaysian logging area (Sungai Tekam Forestry Concession), an extraction level of 18 trees ha^{-1} (3.3% of the total trees present) resulted in an overall loss of 50.9% of trees (Johns, 1983a). The high level of incidental damage resulted in the overall effect of logging being statistically random: the proportional representation of trees of different height classes did not change significantly following logging, nor did the relative abundance of different tree families (Table 1). Basal area of the forest is reduced by approximately 50%, from an average of 25 $\text{m}^2 \text{ha}^{-1}$ in primary forest to between 10 and 18 $\text{m}^2 \text{ha}^{-1}$ in logged forest.

In this example, the initial effect of logging is thus the random deletion of half of the trees in the forest. Regeneration is rapid, however: stem density increases rapidly in recently logged forest as colonising trees become established. In older logged forest the proportion of trees of smaller height classes increases considerably. The proportional representation of tree families also changes (Table 1); most colonising trees are species of the Euphorbiaceae, although *Trema* spp. (Moraceae), *Dillenia* spp. (Dilleniaceae) and *Adimandra* spp. (Theaceae) may be important in some areas. Many of the commercially important trees, notably dipterocarps, require shade to regenerate successfully (Whitmore, 1978) and will not regenerate until a closed canopy is recreated.

No information is currently available on the extent to which selective logging affects other taxa of forest plants. Lianas are perhaps the most important of these, in terms of their contribution to total leaf area, and these may be heavily cut during logging to reduce the danger of falling trees pulling down their neighbours. Both vegetative and reproductive parts of many lianas are highly palatable to rain-forest animals, and their loss may potentially be an important limiting factor. The rate at which the liana flora regenerates in logged forest is unknown. Many species are photophilic, however, and may thus regenerate rapidly in the more open conditions of logged forest.

EFFECTS OF SELECTIVE LOGGING ON RAIN-FOREST ANIMALS

Distribution and abundance of food resources

It is unlikely that any single factor continuously limits the density of an animal population (Cant, 1980): different factors vary in their influence at

different population densities, for example. Food resource availability may, however, be ultimately limiting (Dittus, 1977). The distribution and abundance of food is frequently correlated with behaviour patterns of animal species (e.g. Dawson, 1979; Leighton, 1982).

In hill dipterocarp forest at Sungai Tekam, changes in the distribution and abundance of food sources occurring as a result of selective logging were interpreted to cause changes in the 'cost-efficiency' of feeding on certain foods (Johns, 1983a). Diurnal primate species adapted to the changed conditions by changing their ranging behaviour, with a reduction in the time spent travelling and subsequent localisation of activity, and by altering their diet. Two species were studied in detail, lar gibbons *Hylobates lar* and banded leaf monkeys *Presbytis melalophos*: both fed more on leaf material in logged forest (Table 2). This may be correlated with a lesser abundance of fruit and flowers following logging, but an increase in the production of new leaves by surviving trees. A similar response was observed amongst squirrel species (Sciuridae), which compensated for a loss of fruit sources by feeding largely on bark and sap in recently logged forest (Johns, 1983a).

An alteration in the pattern of food resource availability would be expected to have a severe effect on the species-rich rain-forest avifauna. Tropical forest avifaunas characteristically show a greater degree of dietary specialisation than temperate avifaunas (Pearson, 1977). Following habitat disturbance tropical forest avifaunas suffer a proportionally greater loss of species (Karr, 1971). Even at a high intensity of selective logging, temperate forest avifaunas show very little or no loss of species (Michael & Thornburgh, 1971; Webb *et al.*, 1977).

TABLE 2

Differences in the Proportional Representation of Broad Food Categories in the Diets of *H. lar* and *P. melalophos* in Primary and Logged Forest at Sungai Tekam

Food type	% total			
	<i>H. lar</i>		<i>P. melalophos</i>	
	Primary forest	Recently logged forest	Primary forest	Recently logged forest
Leaf material	12	36	34	58
Flowers	8	0	4	0
Fruit, seeds	77	60	60	42
Others	2	4	1	0

Amongst complex avifaunas, those groups of species that are most highly diversified, such as insectivores, lose a higher proportion of species following logging and show the highest level of species replacement. Many frugivorous species are able to exploit the rapidly growing colonising plants that appear directly following logging and local extinctions may be fewer as a result (Table 3). Taxa with a higher

TABLE 3
Trophic Structure of Primary and Logged Forest Avifaunas in Two Areas of South-east Asia

Trophic group	No. species			
	Sungai Tekam		Sabah ^a	
	Primary	Logged	Primary	Logged
Frugivores	34	21	32	26
Insectivore frugivores	43	28	30	29
Insectivore nectarivores	10	8	10	8
Insectivores	91	55	79	65
Carnivores	17	10	10	9
N	195	122	161	137

^a Data from Payne & Davies (1982): results are pooled from surveys in several geographically isolated forests.

proportion of their members practising more generalist-oriented feeding strategies (e.g. frugivores feeding on a wide range of fruit sizes; frugivore insectivores) possess a higher proportion of species that are found in both primary and disturbed forests. This is also true of taxa other than birds: the biomass of generalist-oriented species of a variety of taxa all increased rapidly in logged forest at Sungai Tekam (Johns, 1983a).

Changes in feeding behaviour will often result in altered ranging behaviour amongst animal species. Energetic constraints resulting from feeding on less nutritious foods limit daily ranging amongst certain primate species (e.g. Milton, 1980; Raemaekers, 1980), whereas fragmentation of the habitat may force other species to travel further each day in search of necessary food sources (e.g. frugivorous birds: Johns, 1983a). Species not able to adjust their ranging patterns to cope with an

uneven distribution of food resources are placed at a competitive disadvantage in logged forest.

Nothing is known concerning the responses of invertebrate species, but it may be supposed that removal of a high proportion of food plants may severely affect specialised herbivores, since many have very limited dispersal abilities.

Microclimate

Logging is known to have a considerable effect on the forest microclimate (Chew, 1968): subcanopy levels of the forest are exposed to vastly-increased insolation, increased temperature and decreased humidity. This would be expected to affect ectothermic animals to a greater degree than endothermic species. Primary forest amphibians have been noted to survive poorly following logging; species that are intolerant of the changed conditions rapidly disappear (Johns, 1983*a*). Certain understorey bird species may also be intolerant of altered microclimatic conditions. The activity of some species may be severely limited by temperature fluctuations (Bell, 1982; Wong, 1982; Karr & Freemark, in press): certain understorey species, for example, are known never to cross sunlit patches (Bell, 1982).

An additional effect of the changed forest microclimate is to cause widespread drying and hardening of the soil. This may severely affect terrestrial birds such as partridges (Phasianidae) and pittas (Pittidae) which feed to a large extent on litter arthropods.

Breeding success

Amongst primate species, short-term reductions in food quality have been inferred to cause mortality within a population, and such mortality may be age/sex class specific (Struhsaker, 1973, 1976; Dittus, 1977, 1980). Amongst certain species, population parameters such as group size have been related to the overall density of food resources acting on juvenile mortality (e.g. Marsh, 1979). In one documented case, selective logging resulted in the initial mortality of large numbers of infants, although the actual causes of mortality were unclear (Johns, 1981). Primate groups in forest logged three or more years before appeared to contain normal numbers of juveniles and infants, however, although a gap in the age structure of the population corresponded to a loss of infants at the time of logging (Johns, 1983*a*).

It is apparent that a combination of factors (e.g. reduced availability of certain food types, loss of suitable nest sites) limit the reproductive success of certain bird species even in forest logged 25 years previously (Wong, 1982). Hole-nesting bird species may be dependent on the presence of over-mature trees in logged forest; these include hornbills, Bucerotidae (McClure, 1968), Costa Rican parrots *Amazona vittatus* (F. H. Wadsworth, in Ewel & Conde, 1976), and a variety of Australian eucalypt forest species (Friend, 1982). Mammal species which rely on such holes for refuges may also be adversely affected if the abundance of these is reduced in logged forest (e.g. lion tamarins *Leontopithecus rosalia*: Coimbra-Filho, 1977). It is important to note, however, that this effect of logging may be controlled relatively easily: unless they are the target of forest management procedures, large over-mature trees are not selectively removed during logging. In West Malaysia, red giant flying squirrels *Petaurista petaurista* rely on such trees for refuges, and do not decrease in numbers following logging (Johns, 1983a; E. Barrett, pers. comm.), and hornbills were observed nesting in recently-logged forest (Johns, 1982). It may be suggested that logging creates suitable refuges where branches are torn from their neighbours by falling trees, or where boles of trees are snapped, and this compensates for the loss of established nesting and refuge sites during logging (although it may take some time for holes to rot out).

Predation

It has been speculated (J. P. Skorupa, pers. comm.) that fragmentation of the forest canopy following selective logging may increase the vulnerability of certain African monkeys to predation (particularly by crowned eagles *Stephanoaetus coronatus* and by chimpanzees *Pan troglodytes*). The same may be true of other taxa. In West Malaysia, both diurnal and nocturnal raptorial predators occurred at exceptionally high density in the vicinity of logging roads and cleared areas (Johns, 1983a). This may be correlated with a necessity for their prey species to cross such open areas in the course of their normal activities. Certain species may thus suffer increased predation as a direct effect of selective logging, whereas some predators benefit by an increased accessibility of prey.

Disease

Selective logging may influence the susceptibility of certain animal species to disease, brought about first by a lowering of general body condition,

and secondly by an alteration in the parasite and disease vectors present in the habitat and the probabilities of animals coming into contact with them (J. P. Skorupa, pers. comm.). A general lowering of bodily fitness may be induced by stresses associated with habitat disturbance (Rijksen, 1978). These aspects of the overall effects of selective logging have yet to be investigated.

Summary: Population dynamics in logged forest

Populations of many rain-forest animals may be limited in size by the occurrence of rare 'ecological crunches' (Wiens, 1977), when the availability of resources suddenly becomes critical. Such ecological crunches have rarely been recorded (e.g. Struhsaker, 1973, 1976; Cant, 1980; Dittus, 1982; Faaborg, 1982), but it may be assumed that reduction of certain food resources or other environmental effects of selective logging may equal or exceed the limiting conditions caused by an ecological crunch (at least for some species). Where such conditions are exceeded, critical reduction of species' populations and deletion of species from the community is likely to occur.

Only animal species with a very rapid reproduction rate will continually show a correlation between population size and resource abundance. Those species with larger body size and longer inter-birth intervals will, however, better withstand conditions of an ecological crunch due to a greater energy reserve. Species such as primates, which are highly *K*-selected (Pianka, 1970), are unlikely to show an immediate population decrease following the onset of an ecological crunch (although animals may begin to starve in time; Dittus, 1982; Foster, 1983).

Amongst primates, the likelihood of a species exhibiting a decrease in numbers may be broadly correlated with dietary features: specifically with their ability to adapt to a changed distribution and abundance of food in the *r*-environment of regenerating forest (Johns, 1983a). The most successful species are those that feed preferentially in disturbed forest areas even within primary forest (e.g. tamarins, *Saguinus* spp.: Mittermeier & Coimbra-Filho, 1977) or those that are able to exploit early successional tree species as a food source (e.g. *Colobus guereza*: Oates, 1977). Many of the animal species that increased in numbers following logging at Sungai Tekam (e.g. commensal rats, Muridae; colonising birds: bulbuls, prinias, white-eyes and munias) were also those species that were primarily adapted to exploiting treefall, edge or other

disturbed habitats (Johns, 1983a; see also Harrison, 1968; Payne & Davies, 1982). For such species, logging does not represent an ecological crunch, rather it increases the volume of their preferred *r*-environment.

To many species of rain-forest wildlife, selective logging may represent a disruption of resource availability to a level beyond the extreme of natural fluctuations. A number of animals appear to be particularly susceptible to the effects of habitat disturbance, and in many cases this can be tentatively correlated with particular facets of the species' ecology (see above). The degree of disturbance is obviously extremely important. For example, extreme drought conditions in a Puerto Rican rain-forest severely reduced the availability of food (particularly of fruit and seeds) and caused severe decreases in the populations of many bird species, but did not delete a single species from the community (Laaborg, 1982; see also Foster, 1983). Selective logging has been observed to cause loss of species of many rain-forest taxa (Payne & Davies, 1982; Johns, 1983a), although many species may be expected to reappear in older logged forest if areas exist from which recolonisation can occur (Wilcox, 1980).

From a consideration of results generated from model ecosystems, Pimm (1979) has indicated that large perturbations affecting complex systems (such as rain-forests) will most often result in reduced numbers rather than deletion of species. There will, however, be a level of population reduction beyond which species cannot effectively recover: the number of species whose populations are critically reduced will be a reflection of the extent of the perturbation. Further, the loss of each species results in a 'ripple effect' (Gilbert, 1980) through the entire system. Repercussions will be most severe where an affected species itself provides essential support to a variety of other organisms within a system. A reduction in the numbers of such 'keystone mutualists' (see Gilbert, 1980) may result in alteration of a variety of interactive webs within a community, the effects of which may not be immediately obvious. Predator/prey or pollinator/disperser interactions, or a reliance on commensalism may all be a cause of gradual deletion of a species from a disturbed community (Terborgh & Winter, 1980).

SELECTIVE LOGGING AND CONSERVATION

The potential value of logged forest

The results of a long-term study at Sungai Tekam (Johns, 1983a) indicate a surprising degree of community stability under certain defined

conditions of selective logging, but nevertheless show certain changes in species composition. It is unlikely that an area of selectively logged forest will support all species formerly present, although it may support an equally high diversity of species. Most importantly, a large area of logged forest may support species that would be deleted from isolated refuge areas of primary forest.

The feeding guilds most prone to extinction as a result of insularisation have been indicated for a rain-forest fauna by Karr (in press): his main observation is that species dependent on patchy and/or variable resources are most susceptible. For example, nectarivorous species such as hummingbirds, Trochilidae, are required to range widely in search of suitable food resources: their numbers at any given site will vary drastically over time (Feinsinger, 1976). The same is true of macaws, *Ara* spp. (Terborgh & Winter, 1980), hornbills, Bucerotidae (Medway & Wells, 1971), and many large mammal species (e.g. Indian elephants *Elephas maximus*: Olivier, 1978). Results presented by Johns (1983a) indicate that those species dependent on resources that are either rare and patchily distributed or unpredictable in their availability are, to a certain extent, pre-adapted (*sensu* Wilson, 1975) to survive following selective logging (providing that overall food availability is not critically reduced). Thus, many species that are prone to extinction in isolated primary forest refugia are those species that may survive well in logged forests (Table 4).

The implications of these findings to conservation are clear. It will always be necessary to maintain primary forest reserves, since many species cannot survive in altered conditions of microclimate and food supply following logging. Logged forests, however, may support populations of many rain-forest species. There is no reason to suppose that large areas of logged forest will not support more species than small areas of primary forest. Although the species-area curve may rise more slowly for logged forest, the larger the area the greater the microhabitat diversity that may be expected, and the greater the number of species that may be supported (Fig. 1). The potential value of logged forest lies in the preservation of otherwise vulnerable species.

Small isolated refugia are of limited use in the conservation of animal species: such refugia inevitably suffer a gradual loss of species—the phenomenon termed ‘faunal relaxation’ or ‘faunal collapse’ (see Wilcox, 1980). While partially dependent on the degree of isolation, the loss rate from an isolated reserve will be in proportion to its area (Soulé *et al.*, 1979; Terborgh & Winter, 1980; Struhsaker, 1981). Large tracts of logged

TABLE 4
Comparative Survival Ability in Logged Forest of Taxa Listed as Vulnerable to Extinction in Isolated Refugia

<i>Taxa with a high proportion of species susceptible to deletion in isolated refugia^a</i>	<i>Status in logged forests</i>
Raptors (Accipitridae)	Populations of most species little reduced
Falcons (Falconidae)	Populations maintained or increase as open conditions increase ease of access of prey species
Pheasants and partridges (Phasianidae)	Decrease as foraging substrate badly affected by logging (soil and litter dried out)
Woodpeckers (Picidae)	Populations of larger species little affected or increase. Populations of some smaller species decrease as foraging substrate badly affected (abundance of bark insects reduced by bark scorch)
Tinamous (Tinamidae)	? (Occur in logged forest but species array considerably reduced)
Guans and curassows (Cuculidae)	? (Occur in logged forest, in the absence of hunting, but in reduced numbers)
Hornbills (Bucerotidae)	Populations of larger species reduced in recently logged forest, but recover rapidly. Smaller species may be more abundant in logged forest.
Toucans (Ramphastidae)	? (Appear to show similar responses to hornbills)
Parrots and macaws (Psittacidae)	Populations of most species little reduced
Cotingids (Cotingidae)	? (Primary forest species appear to be replaced by species specialised to secondary habitats)
Babblers (Timaliidae)	Decrease as intolerant of changed conditions of environment and food supply
Hummingbirds (Trochilidae)	Populations of most species little reduced
Sunbirds (Nectariniidae)	Populations of most species little reduced
Top carnivores (e.g. <i>Panthera</i> spp.)	Populations appear to be maintained in logged forest (in the absence of hunting)
Myrmecophages (e.g. anteaters, Myrmecophagidae)	? (Smaller species appear little affected by logging)

^a After Willis (1979), Eisenberg (1980), Terborgh & Winter (1980). ? denotes preliminary results.

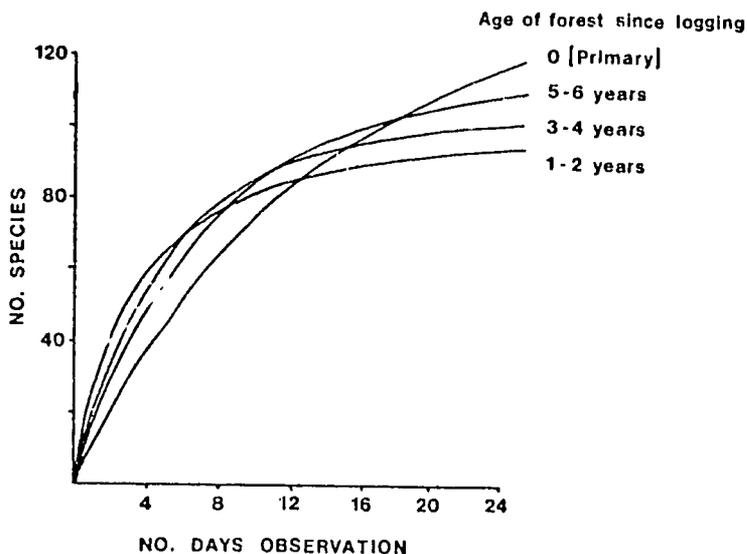


Fig. 1. Cumulative abundance of bird species in unlogged and logged forest at Sungai Tekam, West Malaysia.

forest, although supporting a lower species diversity than primary forest areas of equal size, are less likely to show faunal relaxation than small isolated reserves.

Possibilities for multiple-use land management

It is a maxim of practical conservation that areas of disturbed habitat are rarely considered as useful in maintaining populations of animals (Foster, 1980; Johns, 1983a). Disturbed areas are generally only considered in management plans where undisturbed habitat is critically reduced or non-existent (e.g. Whitten *et al.*, 1979; Payne & Davies, 1982). The general feeling that disturbed habitat is of little value is based on very little empirical evidence. The overall picture is all too often complicated by problems of secondary disturbance following logging: increased hunting or the encroachment of shifting agriculture may limit the ability of species to survive in disturbed habitat (Struhsaker, 1981; Johns, 1983c). The point is made by Frankel & Soulé (1981) that multiple-use management of tropical rain-forest is potentially compatible with conservation of wildlife only where hunting is absent or carefully controlled.

One of the most often suggested designs for rain-forest reserves proposes an inviolate core of primary forest, surrounded by areas of forest which may be logged but which may not be cultivated or penetrated by hunters (this design has been proposed for Biosphere Reserves in UNESCO's Man and Biosphere programme: Whitmore, 1980). This design provides a source of colonisers to replace any species that are unable to survive in recently logged forest but may recolonise a later successional stage. A variation of this idea is the 'corridor' design, where unlogged corridors of forest are left along watercourses extending through logged forest areas. These corridors have the additional advantage of protecting water quality, adding economically sound justification to the scheme, and are being recommended in conservation strategies currently being developed in West Malaysia (Shelton, in press). Of course, such designs are only as effective as the ability of local conservation agencies to protect the integrity of the conserved areas.

Multiple-use of rain-forest may be of great potential importance in the conservation of animal species, but should not be regarded as an alternative to maintaining primary forest areas. Only primary forest may be expected to support a full diversity of animal species. It has been argued that a limited amount of forest management may optimise the habitat for certain species (e.g. selective cutting of palms increases the growth rate of food plants exploited by Javan rhinoceros *Rhinoceros sondaicus*: Schenkel *et al.*, 1978; similarly, a limited amount of tree-felling creates a mosaic habitat type favoured by mountain gorillas *Gorilla gorilla beringei*: Murnyak, 1981). In South-east Asian forests, similar arguments have resulted in the experimental practice of 'liberation thinning', a procedure designed to increase the density of food sources and hence increase the carrying capacity of the environment for certain frugivorous mammals (Proud & Hutchinson, 1980). However, in forest management procedures aimed at increasing the proportional representation of certain species, be it fruit trees or timber trees, there is a danger of altering the species composition of other taxa of the rain-forest community (Leighton & Whitten, in press).

Clearly, conservation methods are most useful where they consider general trends of land use and attempt to integrate principles of conservation into management regimes (Roche, 1979). Where rain-forests are a desirable economic resource, management practices are unlikely to be adhered to if they demand exclusive rights to large areas of productive primary forest. One reservation that is frequently expressed, however, is

that the extent to which disturbed forests are able to advance to the species richness of primary forest is largely unknown. It is suggested, for example, that opening up of the forest canopy severely affects soil mycorrhizae, the role of which is crucial to the eventual rehabilitation of primary forest (N. Myers, pers. comm.). Roche (1982) points out, however, that recent historical remains of human settlements have been discovered under what was assumed to be primary tropical forest. There is thus some evidence that rain-forests are able to regenerate successfully, although their ability to regenerate under conditions of multiple-use management will also be a factor of the extent of damage caused by each disturbance cycle (see Skorupa & Kasenene, in press).

Undoubtedly logged forest is less pleasing aesthetically than primary forest and may be of little use as a recreational amenity, but it is of great potential value in the long-term conservation of rain-forest animal species. In West Malaysia, for example, 41 000 km² of forest have the status of permanent forest reserve (these areas are left to regenerate and re-logged as appropriate), whereas only 16 000 km² have the status of National Parks or equivalent reserves (Leong, 1977). Further to this, few National Parks may be regarded as totally inviolate. Although they can never be regarded as a substitute for primary forest reserves, management of exploited forests with a view towards wildlife conservation may be the last hope of many rain-forest species.

ACKNOWLEDGEMENTS

Original research on which this paper is based was carried out in West Malaysia with the permission of the Socio-economic Research and Planning Unit of the Prime Minister's Department. I am grateful to all who assisted with the research project, particularly Drs M. Kavanagh and D. J. Chivers, and to Syarikat Jengka Sdn. Bhd. for permission to work at Sungai Tekam. Financial support was primarily through Contract no. NOI-CO-85409, US National Institute of Health, with the University of Cambridge. A full list of acknowledgements is given in Johns (1983a).

I am grateful to the following for comments on various drafts of this manuscript: E. Barrett, Ms E. L. Bennett, Dr J. O. Caldecott, Dr D. J. Chivers, A. G. Davies, Dr M. Kavanagh, Dr N. Myers, J. P. Skorupa and Dr A. J. Whitten.

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