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The persistence and conservation of Borneo's mammals in lowland rain forests managed for timber: observations, overviews and opportunities

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Abstract Lowland rainforests on Borneo are being degraded and lost at an alarming rate. Studies on mammals report species responding in various ways to habitat changes that occur in commercial forestry concessions. Here we draw together information on the relationship between the ecological, evolutionary, and biogeographic characteristics of selected Bornean non-volant mammals, and their response to timber harvesting and related impacts. Only a minority of species show markedly reduced densities after timber harvesting. Nonetheless there are many grounds for concern as various processes can, and often do, reduce the viability of wildlife populations. Our review of what we know, and of current understanding, helps predict mammalian dynamics and subsequent mammal-induced ecosystem changes in logged forests. We identify groups of mammal species that, although largely unstudied, are unlikely to tolerate the impacts associated with timber harvesting. On a positive note we find and suggest many relatively simple and low-cost ways in which concession management practices might be modified so as to improve the value of managed forests for wildlife conservation. Improving forest management can play a vital role in maintaining the rich biodiversity of Borneo's tropical rain forests.

Keywords Asia · Certification · Ecology · Production forestry · Sustainable forestry · Wildlife conservation

Introduction

Tropical rainforests are the most species-rich terrestrial ecosystems on earth, but these forests are rapidly disappearing as land is cleared for timber, agriculture, development, and other uses. Biological diversity is being lost. Strictly protected areas in Indonesian Borneo cannot conserve the full biological diversity found within these tropical forests (Jepson et al. 2002). The fate of many species depends on what happens to forests outside protected areas. Further, recent data show that the forest cover of Indonesian Borneo is declining more rapidly within protected areas than outside (Curran et al. 2004; Fuller et al. 2003).

Forest areas used for environmentally sound and sustainably productive uses represent an opportunity for conserving biodiversity. Although not a substitute for protected areas, many species could be conserved within a forest estate that is carefully managed for ecological sustainability (Frumhoff 1995). Productive exploitation of natural forests (hereafter referred to as 'logging') generally involves some ecosystem modification, which can change the local flora and fauna. However, management choices and operational practices can greatly influence the nature and degree of these changes. Since most tropical forests are considered poorly managed, not just for biodiversity conservation but also for productive exploitation (Poore et al. 1989), there is considerable room for improvement (Hunter 1990; Johns 1997; Sheil and van Heist 2000).

This paper is based on the premise that sustaining biological diversity in production forests requires environmentally sound management practices that incorporate available scientific knowledge about species vulnerability into interventions. Ecologists often choose to emphasise how little is known about tropical forests. Obviously more research is needed, but 'lack of

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knowledge' is not an excuse for the prevalence of poor practices in forest management. Sheil and van Heist (2000) proposed that a considerable body of ecological information relevant to managing tropical forests already exists, even though it is little used in practice. They argued that improving the status quo would require pragmatic collaboration between ecologists and forest managers. A recent review and synthesis on logging impacts on Bornean vertebrates (Meijaard et al. 2005; Sheil and Meijaard 2005) is one component in trying to achieve this collaboration.

Based on their findings, Meijaard et al. (2005) provided recommendations to three main target audiences: timber concessionaires, government, and the scientific community. This paper more specifically addresses recommendations to timber concessionaires, especially how management changes can lead to maintaining high biodiversity values in logging concessions. In Indonesia, and also Malaysia, such information is timely. After several decades of over-exploitation of tropical forests, the economic role of the forestry industry is declining, while non-forest land uses, such as oil palm and timber plantations, agriculture, and mining are increasingly important. We need to show that sustainable forestry can make an important contribution to the conservation of forests and species. Our present review provides insights on what particular aspects of logging are most negatively affecting Borneo's mammals. For instance, the removal of very large trees has a disproportionally negative effect on particular species, as well forest regeneration. New insights help develop guidelines for species conservation in production forestry, which in the above example would be to set a maximum cutting diameter.

Although most of our research focused on East Kalimantan Province in Indonesian Borneo, the findings and recommendations presented in this paper are widely relevant to management in all Bornean and other SE Asian rainforests.

Predicting tolerance to logging

Determining the mechanisms by which forestry interventions affect wildlife is often difficult, particularly given the complex interactions and the difficulty in investigating most species (Bernard 2004). Yet, ecological studies help determine a range of actual and potential factors that may influence functional or taxonomic mammal groups under particular forest disturbance regimes. A clearly argued account of the various ecological details that might be addressed in good harvesting practices would help in developing more biodiversity-friendly logging guidelines. Current perceptions of supposed good management are preoccupied with silvicultural (timber production) practices and socio-cultural issues (e.g. FSC 2004). Yet, many ecological and taxa-centred studies, even when not addressing forest impacts directly, contain relevant information about the life history and habitat requirements of potentially vulnerable taxa. A growing body of ecological studies of individual species identifies possible changes in feeding, ranging or other behaviour following logging, and how these changes may affect population changes. Such information is useful for guiding forestry activities and further supplements studies examining logging impacts on density and distribution. However, because specific data are of limited value for generalised decisions and often not consistent over a larger range of species (e.g. Hill and Hamer 2004), categorisation and classification into larger groups with particular responses are crucial to incorporating ecological data into timber production.

Meijaard et al. (2005) compiled the available information on ecological, evolutionary, and life history variables of Bornean mammals. In that study, we, along with many colleagues, first reviewed the scientific literature for references to the ecology and natural history of a selected number of Borneo's best-known mammal species. We also compiled information on the factors that may determine vulnerability for each taxon. Some attributes that may help explain vulnerability—such as physiological tolerances—could not be determined due to lack of information. These compilations and syntheses, updated with a handful of more recent data, and bolstered by insights from studies in other regions of the world, allow us to draw general conclusions about logging and wildlife in Borneo.

Mammals in logged forest on Borneo—an overview

The effects of logging on Bornean mammals have been investigated for primates, non-volant small mammals such as tree shrews and rodents, small carnivores and ungulates, but the intensity and quality of the studies vary. Hence, the logging-induced differences in species density are incompletely known for most species, and we must focus on general trends. While some species are well investigated, data for others are only available from a few short-term studies. Of the mammal species used in our review, 41% have a well-known biology and ecology (for example, at least one long-term field study of more than 2 years), 38% can be considered moderately known (at least one short-term study, <2 years), and 21% are little known. The well-known species include five diurnal primates, two deer, one bear *Helarctos malayanus* (Raffles, 1821), one civet *Viverra tangalunga* (Gray, 1832), one cat *Prionailurus bengalensis* (Kerr, 1792), one pig *Sus barbatus* (Müller, 1838) and one squirrel *Ratufa affinis* (Raffles, 1821). Of these, one deer *Cervus unicolor* (Kerr, 1792) and the cat are known primarily from South Asia. The mouse-deer species (*Tragulus* spp.) are known primarily from one detailed ecological study, but research attention to the bear species has recently increased considerably (Augeri 2001; Fredriksson et al. 2006; Wong 2002; Wong et al. 2002, 2004). Primates are generally well-studied, but again, the ecology of one colobine *Presbytis hosei* (Thomas, 1889) is known primarily from just one PhD thesis (Mitchell 1994). The least known mammals include squirrels, tree shrews, rats and mice, and civets, many of which may play a significant role in dispersing seeds and regenerating forests.

Primates

The effects of logging on primates are fairly well studied compared to other Bornean mammals (Felton et al. 2003; Johns 1987, 1997; Morrogh-Bernard et al. 2003; Plumptre and Johns 2001; Rijksen 1978; Wilson and Wilson 1975). Our review indicates that, in particular, densities of *Hylobates muelleri* (Martin, 1841) and *Presbytis hosei* decrease following logging, whereas the information for other species such as *Macaca* spp. and *P. rubicunda* (Müller, 1838), is more ambiguous. It is unclear at this stage to what extent these patterns are explained by the ecological effects of logging or by other factors such as increased hunting pressure. Bornean orangutans *Pongo pygmaeus* (Linnaeus, 1760) appear to cope relatively well with logging, especially the eastern subspecies *P. p. morio* (Owen, 1837) (Ancrenaz et al. 2004).

In general, primates, especially the more generalist feeders, appear fairly adaptable to selective logging, changing their ranging patterns and diets to accommodate changes in forest structure and composition (Johns 1997). Johns and Skorupa (1987) noted that, generally, a primate species' degree of frugivory shows a significant negative correlation with its ability to persist in recently logged forests, as expressed by comparative population densities in unlogged and adjacent logged forests. Marsh et al. (1987) suggested its degree of terrestriality will also affect a primate's adaptability. Most Old World species capable of colonising secondary forest are at least semi-terrestrial in habits, which must facilitate survival in small patches. This behaviour, however, also predisposes them to crop raiding, making them more vulnerable to hunting.

Squirrels

Diets and the degree of terrestriality also appear to determine the sensitivity of squirrels (Sciuridae, Table 1). Many of these species feed on a large and overlapping variety of different arthropods, fruits and other plant material (Emmons 2000, K. Wells unpublished data; Langham 1983). Details of their diets are, however, sparse. Still, there appear to be some general trends to more carnivorous diets in terrestrial species (Emmons 1995). Similarly, vertical foraging activity and stratification patterns are roughly known, but the details of habitat partitioning and shifts in logged forests along vertical gradients still require investigation (Wells et al. 2004).

Among squirrels, the population density of some species appears to decline, notably *Ratufa bicolor* and *Lariscus insignis* (F. Cuvier, in Geoffroy and Cuvier, 1821), while others, such as *Callosciurus prevostii* (Desmarest, 1822), *C. notatus* (Boddaert, 1785), and *Sundasciurus tenuis* (Horsfield, 1823) show increases or no significant change (Bennett and Dahaban 1995; Dahaban et al. 1996; Johns 1997). Still, the effects are always not consistent between sites. For instance, Bennett and Dahaban (1995) and Dahaban et al. (1996) reported a higher density of small *Sundasciurus* squirrels *S. tenuis* and *S. lowii* (Thomas, 1892) in old shifting cultivation areas compared with primary forest, which suggests that these species benefit from conditions in these heavily disturbed forests. On the other hand, Wells (2005) caught twice as many *S. lowii* in primary forest than in secondary forest (31 vs. 14) with similar trapping efforts, while Yasuda et al. (2003) similarly recorded a decline in *S. lowii* following logging.

As suggested by Johns (1997), terrestrial, largely insectivorous squirrels seemed least able to adapt to conditions in logged forests. This would fit the observed decreases in *L. insignis* and *Rheithrosciurus laticaudatus* (Gray, 1867) (Yasuda et al. 2003), and *S. hippurus* (Geoffroy, 1831) (Dahaban et al. 1996, Laidlaw, 2000).

Tree shrews

In contrast to squirrels, which have mostly diversified in the canopy, tree shrew species are primarily terrestrial. Emmons (2000) compared tree shrew captures in logged and unlogged areas at different times of the year in Danum Valley, Sabah. Other data are provided by Stuebing and Gasis (1989) who studied tree shrew populations in logged forest and monocultural tree plantations. These two studies suggested that logging severely impacts the lesser tree shrew, *Tupaia minor* (Günther, 1876), and *Ptilocercus lowii* (Gray, 1848), the only arboreal tree shrew species (Emmons 2000), eliminating them from sites in which other species remained unaffected; their disappearance was probably a direct result of the forest canopy being destroyed. Conversely, Wells (2005) recorded *T. minor* as a common species for a logged site in Sabah (44 out of 320 captures). The persistence of other *Tupaia* species in logged areas and plantations appeared to depend primarily on understorey vegetation density.

In selective logged forest with dense understorey, *T. tana* (Raffles, 1821) increases significantly (Wells 2005). Emmons (2000) speculated that logging has little affect on the big terrestrial tree shrews that feed on invertebrates in litter and decomposing wood, as long as the understorey is dense, the ground surface litter layer is shady and moist, and arthropods are abundant near the surface. In plantations where there is little ground cover, the surface is drier, and arthropods and worms may descend deeper into the soil (Fragoso and Lavelle 1992). Moreover, such plantations may lack decomposing wood and the associated arthropod fauna as the plantations are generally burned before tree planting.

Table 1 Non-flying squirrels, and their response to logging

Species	Body size (kg)	Ecological stratification	Density trend after logging	References
Ratufa affinis	0.9–1.5	Canopy. Feeds on seeds	↑	Johns (1997)
			↓	Dahaban et al. (1996)
			↓	Bennett and Dahaban (1995)
Ratufa bicolor	0.9–1.5	Canopy. Feeds on fruits and nuts	↓	Johns (1997)
Callosciurus notatus	0.15–0.28	Middle of canopy. Feeds on fruits and insects	↑	Johns (1997)
			↑	Dahaban et al. (1996)
			↓	Syakirah et al. (2000)
			↓	Yasuda et al. (2003)
Callosciurus prevostii	0.25–0.50	Canopy. Feeds on fruits and insects	↑	Johns (1997)
Callosciurus caniceps	0.25–0.50	Middle of canopy. Feeds on fruits and insects	↑	Laidlaw (2000)
Callosciurus nigrovittatus	0.15–0.40	Middle of canopy. Feeds on fruits and insects	–	Laidlaw (2000)
Rhinosciurus laticaudatus	0.18–0.26	Terrestrial. Feeds mostly on insects	↓	Laidlaw (2000)
			↓	Yasuda et al. (2003)
Lariscus hosei	0.15–0.22	Terrestrial. Feeds on fruits and roots.	↓	Dahaban et al. (1996)
Lariscus insignis	0.12–0.23	Terrestrial. Mixed diet of bark, fruits, leaves, and insects	↓	Johns (1997)
			↓	Yasuda et al. (2003)
Sundasciurus hippurus	0.30–0.42	Mostly terrestrial, but uses middle canopy. Diet of mostly fruits, some seeds and insects	↑	Wells (2002)
			↓	Laidlaw (2000)
			↓	Rijksen (1978)
			↓	Dahaban et al. (1996)
Sundasciurus lowii	0.06–0.12	Mainly small trees and terrestrial. Feeds on fruits, insects and fungi	↑	Wells (2002)
			↑	Bennett and Dahaban (1995)
			↓	Yasuda et al. (2003)
Sundasciurus tenuis	0.06–0.1	Mainly small trees and terrestrial. Feeds on fruits and seeds	↑	Johns (1997)
			↑	Bennett and Dahaban (1995)
			↓	Rijksen (1978)

↑ Increase in density after logging, ↓ decrease in density or absent from recently logged areas, – no difference. Information on ecological stratification was obtained from Lekagul and McNeely (1977) and Payne et al. (1985)

Murid rodents

Several studies have examined how logging affects densities of rats and mice in SE Asia, but the patterns are not conclusive. For example, two studies from peninsular Malaysia found a significantly higher density of *Leopoldamys sabanus* (Jentink, 1879)—an omnivorous species living in ground and lower vegetation levels with occasional forays to the canopy—in regenerating forest compared to primary forest (Yasuda et al. 2003; Zubaid and Ariffin 1997). Conversely, out of 175 individuals of *L. sabanus* caught by Wells (2005), 103 originated from primary forest, and the remainder from secondary forest with no differences in abundance if only single trapping sessions were compared. Similarly, Yasuda et al. (2003) found that two *Maxomys* species, *M. whiteheadi* (Thomas, 1894) and *M. rajah* (Thomas, 1894)—both terrestrial and insectivorous, but the latter with more fruit in the diet—were significantly more common in primary forest. For *M. rajah* this was confirmed by Zubaid and Arrifin (1997), but *M. whiteheadi* appeared to be slightly more common in disturbed forest (difference not statistically significant). Wells (2005) found no significant differences between catching results in primary and secondary forest for the three most common species of *Maxomys*: *M. rajah* (29 specimens in primary forest vs. 47 in secondary forest); *M. surifer* (Miller, 1900) (21 vs. 29); and *M. whiteheadi* (48 vs. 25). So, it appears that for every study providing a particular finding, there is another suggesting the opposite. The underlying reason may be that ecological factors other than those related to logging, for instance interspecific competition, determine the density of these rodents.

Civets

Civets (Viverridae) form a diverse group. Borneo alone has nine species (Payne et al. 1985). Some civets feed almost exclusively on fruit, generally favouring the more sugar-rich and soft-pulped ones, other species have more carnivorous or insectivorous diets (Colón 1999; Heydon and Bulloh 1996; Rabinowitz 1991). In Sabah, Heydon and Bulloh (1996) recorded a marked decrease in civet density in logged forests, with predominantly carnivorous species declining more than fruit-eating ones. In peninsular Malaysia, however, Johns (1983) recorded civets as being extremely scarce in unlogged forest. Immediately after logging began, several additional civet species moved into the area. A similar result was reported by Syakirah et al. (2000), who recorded the Malay civet, *Viverra tangalunga*, only in recently logged forest, but not in forest regenerated after logging in the 1970s, while Stuebing and Gasis (1989) found *Paradoxurus hermaphroditus* (Pallas, in Schreber, 1777) exclusively in plantation areas and not in logged forest. In a 2-year study, Colón (1999) in contrast found that densities of *V. tangalunga* were 57% higher in an unlogged site than in a logged one; also, fruit comprised a larger proportion of the diet in unlogged forest compared to logged forest. The small-toothed palm civet, *Arctogalidia trivirgata* (Gray, 1832), was only found in regenerated and unlogged forest, but not in recently logged forest (Syakirah et al. 2000).

From our own observations in timber concessions in Borneo, species such as *V. tangalunga*, *P. hermaphroditus*, and *Paguma larvata* (Smith, 1827) are seen almost every night during surveys on logging roads, probably more so in the less disturbed forest than in the recently logged, heavily disturbed areas (E. Meijaard, unpubl. data). The largely arboreal *A. trivirgata* and *Arctictis binturong* (Raffles, 1821) are rarely encountered, and the effects of logging on these species remain unclear. Overall the data are probably insufficient to generalise about how logging affects civets. Logging likely affects all the investigated civets negatively, either through primary or secondary effects, but this might also depend on local habitat conditions: a plantation, for example, might be favourable for civets if sufficiently large forest refugia are accessible nearby.

Malayan sun bear

Apart from a few small investigations, four significant field research studies focused on wild sun bears, *Helarctos malayanus*, in different forest and plantation types on Borneo (Augeri 2001; Nomura 2003; Wong 2002; Wong et al. 2002, 2004). Another study looked into the sun bear trade (Meijaard 1999, 2001) and found correlations between the timber trade and illegal trade in sun bear gallbladders, suggesting a negative, but indirect impact of logging on these bears.

Fruit availability and diversity are highly important for *H. malayanus'* nutritional stability. Wong (2002) suggested that the poor physical condition and mortality of some bears observed in his study resulted from a prolonged fruit scarcity. Where alternative food is available, such as near an oil palm plantation and in large contiguous primary forests, bears are generally in good condition even during food shortages (Augeri 2002; Nomura 2003). When little fruit is available, species like *H. malayanus* will turn to other food sources, especially in small forests where key foods may be less diverse or abundant, obliging bears to forage outside the forest boundary (Augeri 2004, S. Wulfraat pers. comm.). Fredriksson (2001), Wong (2002) and Augeri (2002, 2003) note that alternative foods such as aboveground termite colonies, beetles, bee hives, and ants are important foraging resources for sun bears.

Augeri (2003) noted a significantly higher degree of bear habitat use in older, more heterogeneous primary forests. Overall, he found significant positive relationships between bear habitat use and higher levels of forage diversity, canopy cover, ground cover, escape cover, and the predominance of large, mature fruiting trees. More research is needed, but current data indicate that various logging practices affect sun bear habitat use, foraging patterns and persistence, particularly in small or isolated forest patches and reserves. Forest clearing can play an important, and sometimes, dominant role in the ecological dynamics of interior forest and edge communities, particularly in small forest "island" reserves and those with a substantial edge–area ratio. This can affect sun bears by (1) preventing access to productive forage areas, (2) reducing the diversity and abundance of key resources, (3) intensifying or creating drought effects and altering local and regional fruit productivity, availability, and distribution, and (4) increasing access for hunters.

Ungulates

Ungulates are generally much sought-after by hunters, and studies into logging impacts need to consider to what extent changes in hunting pressure change ungulate density. Such information is, however, not always considered, making data interpretation difficult. Overall it appears that the herbivores among these ungulates benefit from post-logging conditions, whereas frugivores are negatively affected (Table 2).

Mouse-deer (*Tragulus* spp.) selectively feed upon fallen fruit from a wide range of species, remaining in one vegetation type and in one small home range throughout the year. Both *Tragulus* species frequently feed on fruit falling from figs (*Ficus* spp.) (Heydon and Bulloh 1997), although they also feed on other foods (see Matsubayashi et al. 2003). Ecological characteristics and distribution ranges suggest that *T. kanchil* (Raffles, 1821) is an ecologically more adaptable species than *T. napu* (Chasen, 1940), with the former species occurring in drier, more open forests in Thailand, Cambodia, and Vietnam, while the latter is restricted to the wet tropics (Meijaard and Groves 2004). Heydon and Bulloh's (1997) and Davies et al.'s (2001) data seem to support this, with a reported 55–66% decrease in *T. javanicus* (= *T. kanchil*) densities and a 71–90% density decrease in *T. napu* in selectively logged forest, compared with unlogged forest.

Heydon (1994) suggested that the obligate frugivory of mouse-deer limited their ability to compensate by browsing. However, in peninsular Malaysia, Johns (1997) observed a larger adaptability to modified sites by mouse-deer and found *Tragulus* spp. to be more common in logged forests than in mature forests. Also, Laidlaw (2000) regularly encountered *Tragulus* spp. in tree plantations and bush land in peninsular Malaysia. The use of disturbed habitats by *T. javanicus* (= *T. kanchil*) was confirmed by Matsubayashi et al. (2003), who found that in Sabah, mouse-deer primarily feed in crown-gap areas dominated by bamboo stands, probably because they prefer fruits and the soft leaves of pioneer plants with lower concentrations of secondary metabolites. For frugivorous animals, these crown gap areas are good foraging sites because many pioneer plants in gap areas produce fruit several times a year, whereas most climax species in mature forest produce fruit once a year or less (Whitmore and Burslem 1998).

Table 2 Changes in cervid and tragulid densities after selective logging

Species	Body size (kg)	Ecological stratification	Density trend after logging	References
Cervus unicolor	100	Terrestrial, herbivorous	↑↑	After Heydon (1994) in Davies et al. (2001)
			–	Rijksen (1978)
Muntiacus atherodes	15	Terrestrial, mainly frugivorous	↓	After Heydon (1994) in Davies et al. (2001)
Muntiacus muntjakx	20	Terrestrial, mainly frugivorous	↑↑	After Heydon (1994) in Davies et al. (2001)
			↑ ?	Duff et al. (1984)
Tragulus napu	4	Terrestrial, mainly frugivorous	↓↓	After Heydon (1994) in Davies et al. (2001)
Tragulus kanchil	2	Terrestrial, mainly frugivorous	↓↓	After Heydon (1994) in Davies et al. (2001)
Sus barbatus	125	Omnivorous	–	Davies et al. (2001)
			–	Linkie and Sadikin (2003)
			↓[a]	Wilson and Johns (1982)

– < 20% difference between mean density in logged and primary forests; ↑/↓ increase/decrease of 20–60% between logged and primary forests; ↑↑/↓↓ increase/decrease of > 60% between logged and primary forests

[a] Effect ascribed to hunting

The two species of muntjac (*Muntiacus* spp.) feed primarily on fruits and browse, being selective for plant parts, and remain within one or a few vegetation types throughout the year. *M. atherodes* (Groves and Grubb, 1982) appears to predominate in lowlands and *M. muntjak* (Zimmermann, 1780) in upland habitats (E. Meijaard, unpubl. data), although no robust quantitative data exist to support this. Duff et al. (1984) and Heydon (1994) reported an increase in the frequency of *M. muntjak* sightings in logged forests compared with unlogged forests, and the latter author reported a concurrent decrease in *M. atherodes*. *M. muntjak* appears to include a higher proportion of browse within its diet than the two mouse deer species and *M. atherodes* (Barrette 1977). This may explain *M. muntjak*'s better competitive ability in logged forests, assuming that logging does not generally have a negative effect on grazers (Davies et al. 2001). This mirrors the situation in *Tragulus* spp. where the most logging-intolerant species has the smallest distribution range and is restricted to the tropics; *M. atherodes* is a Bornean endemic, whereas *M. muntjak* occurs throughout SE Asia with habitats ranging from dry open woodland savanna to dense wet forest.

Sambar deer (*Cervus unicolor*) are generalist grazers and browsers that feed on a range of grasses and plant parts. They prefer forest edges, riverbanks, grassy clearings, secondary scrub, and open farmlands (Nowak 1999), but they also occur in dense interior forest. Sambar deer use logging roads apparently as alternative forage areas and as corridors between favourable forest sites, including logged areas. Heydon (1994) notes that their numbers may be positively correlated with the area of severely degraded forest and negatively associated with climax stage forest (Heydon 1994).

Little is known about how timber extraction affects the remaining Bornean ungulates, bearded pig *Sus barbatus* and banteng *Bos javanicus* (d' Alton, 1832), although Davies et al. (2001) reported declining pig numbers following logging in their study sites. Based on what is known of bearded pig ecology it can be inferred that logging impacts on major fruiting crops can affect their migratory patterns, distributions, and possibly densities, thereby influencing dispersal and regeneration of other fruiting species (e.g., Meijaard 2003a). Interviews with hunters in Borneo suggest that pigs are leaner in logged areas (E. Meijaard, unpubl. data). Pigs fatten up during mass-fruiting of dipterocarps and other seed-bearing trees (Caldecott 1988); removing such timber trees is likely to reduce food availability. It is unclear how this will affect the population ecology and life history of *Sus barbatus*.

Hoogerwerf (1938 in Brookfield 1997) suggested that *B. javanicus* favours grasslands, savannas, and secondary forests over rainforest. Banks (1931) reported the same, as did Wharton (1968) who claimed that *B. javanicus* depends on forest areas cleared for agriculture, as they feed in secondary forest and on fields, and have little use for dense forest areas. Because *B. javanicus* is often found near fields and forest gardens, where they destroy crops, they are hunted as pests. It is therefore expected that the species benefits from forest clearing, except when hunting pressure keeps populations low. All ungulate species can suffer from the increased hunting that often accompanies the opening of forests for timber extraction (Bennett and Dahaban 1995; Bennett and Gumal 2001).

General patterns of sensitivity to logging

Although mammal species vary in their ecological requirements, the available information allows some common factors to be identified and used to predict how logging will affect mammal assemblages. Our analysis identified patterns among species with different logging tolerance levels. Intolerant mammals tend to have narrow ecological niches, and many have strictly frugivorous, carnivorous, or insectivorous feeding habits. They appear to be specialised at using particular forest strata, especially ground or upper canopy levels, rather than ranging through all levels. In contrast, logging-tolerant mammals are herbivorous or more omnivorous. Many of these species live in the lower vegetation strata, although some are found at all levels. We recognise that these are generalisations and that the distribution and density of Bornean mammals is strongly influenced by conditions such as soil, altitude, climate and vegetation type (Bernard 2004; Wells 2005). Still, there is enough information to suggest some consistency in how logging affects particular Bornean mammals. These generalisations are important because they provide the basis for recommending specific management changes in production forestry. Knowing which species are likely to be negatively affected allows concession holders to develop specific actions to minimise impacts. Also, relatively few Bornean mammals have been studied, and so understanding some species allows the logging tolerance of ecologically similar species to be predicted.

Meijaard et al.'s (2007) statistical analysis of the traits of 44 mammal species indicated that a species' phylogenetic age best predicts its sensitivity to logging. Other factors that could plausibly be argued to be true causal variables and not merely correlated with phylogenetic age, such as body size, diet and life history, are not as good predictors. Phylogenetic age appears to capture a diverse bundle of co-varying life history characteristics relevant to logging sensitivity.

The study by Meijaard et al. found that logging-intolerant and logging-tolerant species in Borneo separate into two groups with different evolutionary backgrounds, although intermediate cases were also recognised. The logging-intolerant are primarily species that started to evolve during the Miocene or Early Pliocene. These species show little geographical variation in morphology (few subspecies) and are generally rare on small islands. They tend to occupy narrow ecological niches, with strictly frugivorous, carnivorous, or insectivorous feeding habits. Some are restricted to terrestrial feeding strata although others also occur higher up in trees and bushes. In contrast, logging-tolerant species appear to be younger, originating during the Late Pliocene or Pleistocene. They are common on small islands and across SE Asia, where they typically exhibit significant morphological variation (many subspecies). Most logging-tolerant mammals are herbivorous or omnivorous. Many live in the lower vegetation strata or on the ground. Our phylogenetic analyses show that these outcomes represent adaptations based on shared evolutionary pressures, rather than artefacts of common ancestry.

Using the phylogenetic age of several poorly known species, Meijaard et al. (2007) predicted several species expected to cope poorly with the effects of timber extraction (Table 3).

The data generally suggest that species with wider ecological niches are more tolerant to logging. Ecological specialisation is thought to increase susceptibility to decline and extinction when environmental conditions are changing (Harcourt et al. 2002; Owens and Bennett 2000). A species' ability to switch between dietary components likely allows it to compensate when logging directly reduces the availability of certain foods. It is unclear why terrestrial or canopy species with specialised feeding strategies are intolerant of logging; perhaps logging simply removes the particular food items that these species rely on. Or possibly, by opening up the canopy and slashing ground vegetation, logging has a significant micro-climatic effect on lower vegetation strata, which especially impacts invertebrate abundance. This has been proven for termites, which decline significantly in species richness and abundance after primary forests are logged in Sumatra (Jones et al. 2003); in Sabah, however, there was no obvious decline between primary forest and two selectively logged forest types (Eggleton et al. 1997). Jones and colleagues (2003) argued that the forest was more disturbed in Sumatra than in Sabah, and thus logging affected the termite population more.

Other groups of Bornean invertebrates affected by logging include butterflies (Cleary 2004), beetles (Chung et al. 2000), and geometrid moths (Beck et al. 2002). We note here that within the Indonesian selective cutting and replanting system (Tebang Pilih Tanaman Indonesia = TPTI) regulations, concession-holders are legally required to repeatedly slash all undergrowth and climbers for several years after felling to reduce aggressive 'weeds' and encourage regeneration. In practice, this

Table 3 Species in Borneo with an expected sensitivity to logging effects because of a phylogenetic age of more than 5 million years. Information on species age compiled by Meijaard (2003b)

Common name	Scientific name	Authority
Moonrat	*Echninosorex gymnurus*	Raffles, 1821
Western tarsier	*Tarsius bancanus*	Horsfield, 1821
Pen-tailed tree-shrew	*Ptilocercus lowii*	Gray, 1848
Clouded leopard	*Neofelis nebulosa*	Griffith, 1821
Bornean bay cat	*Catopuma badia*	Gray, 1847
Marbled cat	*Pardofelis marmorata*	Martin, 1837
Horsfield's flying squirrel	*Iomys horsfieldi*	Waterhouse, 1838
Banded linsang	*Prionodon linsang*	Hardwicke, 1821
Stink badger	*Mydaus javanensis*	Lechenault, in Desmarest, 1818
Grey tree rat	*Lenothrix canus*	Miller, 1903
Wooly tree rat	*Pithecheirops otion*	Emmons, 1993
Long-tailed porcupine	*Trychis fasciculata*	Shaw, 1801
Sumatran rhinoceros	*Dicerorhinus sumatrensis*	Fischer, 1814

has a deleterious effect on many species, including rattan and timber seedlings (see Sheil and Burslem 2003) and many terrestrial vertebrates and invertebrates.

Small mammals' tolerance to forest disturbance may also be reflected by the size of their distribution range. Meijaard et al. (2007) found that Bornean endemics were more sensitive to logging than more widely-spread species. Wells' data (2005) support this, with the Bornean endemic squirrels *Lariscus hosei* and *Sundasciurus brookei* (Thomas, 1892) and the endemic rats *Chiropodomys major* (Thomas, 1893) and *Maxomys ochraceiventer* (Thomas, 1894) only recorded in undisturbed forest. Many Bornean endemics are restricted to mountainous habitats where commercial timber exploitation is expensive; generally these species are relatively safe from the impacts of logging. We predict, however, that Bornean lowland endemics face high threats from logging (for examples in addition to those mentioned above, see Table 4). This is substantiated by research on primates that shows that small geographic range and high ecological specialisation—both characteristic of Bornean endemics—are positively correlated with extinction risk (Eeley and Foley 1999; Harcourt et al. 2002).

The most obvious change in forest composition that results from timber harvesting is the removal of large timber species. Does this selective effect have consequences for wildlife? Logging in Borneo primarily targets dipterocarps, and so vertebrates that depend on these trees and other commercial timber species (e.g., *Agathis* spp.) would likely be disproportionately affected. No study suggests that any vertebrates depend on the leaves of timber trees to any significant extent. The relation with seeds and fruits is more complex. Seed eaters such as bearded pigs (*Sus barbatus*), murids such as *Maxomys* and *Leopoldamys* (Wells and Bagchi 2005), and certain squirrels eat these seeds in large numbers, at least during fruiting seasons—however these resources are very seasonal so all these species are also generalists that feed on various other resources. Still, general declines in pig fatness have been observed (but not substantiated) by indigenous hunters working in logged forest where mast-fruiting species have been largely removed (E, Meijaard, pers. obs.). The massive pulse of seeds that occurs during supra-annual masting events may be a significant factor in the reproductive success and longer-term population dynamics of various mammals—this is a topic deserving further study.

Larger-stemmed trees also provide hollows for many species to nest and store food. Little information exists about the distribution and determinants of tree hollows. They appear more likely in larger-stemmed, heartwood-forming species with relatively light timber. Initially, after limited timber removal, large and damaged trees may provide ample cavity-forming opportunities, but this may change if larger trees are ultimately removed, perhaps over several cutting cycles. Trees in regenerating forest stands may not contain much heart rot and may not develop large cavities. Not all tropical trees produce metabolically inert heartwood, although the subject is little studied (Ng 1986). In addition, the shape and architecture of cavities, and whether they collect water is likely to be influenced by the characteristic angle that branches make with the main trunk, the details of self-pruning, and active and passive responses to stem damage (e.g., Loehle 1988)—topics that all remain poorly researched.

Besides hollows, many mammal species also depend on other structural features for foraging, breeding or resting. We know little about the physical habitat structure required by most species. Maintaining a dense and moist understorey as well as continuous aerial pathways seems to be particularly important for many species. Also maintaining connectivity between forest patches appears important, as is protecting fruit trees such as figs and retaining dead wood. Logging affects the three-dimensional layout of a forest in many different ways, although it is difficult to generalise about the effects on any particular species. Creating gaps will affect energy requirements to move through the vegetation, with species that do not glide or jump worse affected. We expect, for instance, that flying lemurs, *Cynocephalus variegatus* (Audebert, 1799), and flying squirrels will be relatively unaffected by timber extraction. Some species will benefit from gaps being created, such as deer; others will fail to find food in gaps, such as interior forest bats like *Hipposideros* spp. and *Rhinolophus* spp. (Kingston 2004). Some species benefit from the cluttered structure of lower vegetation levels following logging (many small rodents). Again, the more adaptable a species is in its behaviour, the more likely it will cope well with the effects of logging.

Table 4 Some Bornean endemics restricted to lowland forests and likely to be logging-intolerant

Common name	Scientific name	Authority
Bornean bay cat	*Catopuma badia*	Gray, 1847
Grey tree rat	*Lenothrix canus*	Miller, 1903
Wooly tree rat	*Pithecheirops otion*	Emmons, 1993
Lesser ranee mouse	*Haeromys pusillus*	Thomas, 1893
Lesser pygmy flying squirrel	*Petaurillus emiliae*	Thomas, 1908
Hose's pygmy flying squirrel	*Petaurillus hosei*	Thomas, 1900
Tufted ground squirrel	*Rheithrosciurus macrotis*	Gray, 1856
Ear-spot squirrel	*Callosciurus adamsi*	Kloss, 1921

Hunting often affects species much more than logging itself in many parts of Borneo (Bennett and Gumal 2001; Bennett et al. 2000; Meijaard et al. 2005). The threat posed by hunting is especially great in Borneo's tropical forests because edible wildlife is relatively rare (Bennett et al. 2002; Meijaard 2004; Payne 1990). Hunting is likely to lead to changes in wildlife densities, distribution, and demography, which can then lead to shifts in seed dispersal, browsing, competition, predation, and other community dynamics. How all these factors relate to each other remains unclear, but the overall result is that most larger vertebrates in Borneo and some specifically targeted species such as the Sumatran rhinoceros *Dicerorhinus sumatrensis* (Fischer, 1814), turtles, crocodiles, ungulates, and certain birds have in many areas been hunted or collected to extirpation (Bennett and Gumal 2001; Bennett et al. 2002; Bradley-Martin 1989; Meijaard 1996; Robinson and Bodmer 1999; Robinson et al. 1999). Also, logging directly and indirectly facilitates hunting pressures by increasing access via roads and trails, and clearing, as well as increasing human settlements with subsequent increases in market economies and consumption (Bennett and Gumal 2001).

Recommendations for production forestry in Borneo

Having approximated how logging affects some vertebrate species, we would like to highlight possible changes in concession management that could significantly boost wildlife survival. First, it is important to realise that, according to Act No. 5 of 1990 of the Government of Indonesia, concession managers are obliged to prevent any activities detrimental to the survival of protected species (Ministry of Forestry 1990). This legal requirement has generally been ignored in the past, and in many cases forests have been logged and clear-cut regardless of protected species in the area. Clearly, improved legislation and law enforcement and increased accountability are needed.

The most threatening activities must also be identified. As pointed out above, hunting poses one of the greatest threats to certain species targeted for consumption or trade, and its regulation should be a top priority in well-managed logging concessions. In Borneo, low forest productivity for wild animals limits how much exploitation and habitat modification can be done sustainably. Bennett and Robinson (2000) and Fimbel et al. (2001) provided detailed recommendations on how to curtail hunting in forest concessions. The most important of these focus on access and enforcement. Closing of logging roads as soon as operations are complete reduces the opportunities for hunting as well as illegal re-entry logging. The concession needs to develop clear rules on hunting (which species cannot be hunted, commercial vs. subsistence hunting, setting sustainable harvest levels, and monitoring implementation). Monitoring the effect of such measures requires the development of simple survey methods that can be implemented by concession managers.

Habitat heterogeneity and structural diversity are among the most important factors determining species-rich communities in natural forest settings, and maintaining these factors is important. Interventions may also be directed towards conserving specific resources or features (food trees, lianas, salt licks, caves, clean rivers) that are important for certain taxa. Measures relevant within harvesting zones should be adopted in addition to identifying larger areas to exclude from any harvesting. Our recommendations concerning this are outlined below.

Reduce incidental damage to forests during harvesting. In particular, the area of severely damaged forest must be limited, such as along tractor skid trails and log-loading areas where vegetation and topsoil are most often removed. These areas are usually colonised first by vines and later by pioneer tree species. Areas dominated by such trees and vines are in effect food deserts to many frugivores, although some species thrive in these conditions. Reducing the area of heavily disturbed forest should benefit frugivores by limiting the growth of pioneers. Also, minimising the frequency of gaps in the canopy should reduce the impact on the movement of non-volant, arboreal animals (Putz et al. 2001).

Damage and invasion by pioneers could be reduced with specific measures such as mapping important food or habitat trees and special sites such wallows, riparian areas and salt springs; planning placement of skidder roads; and using light-weight, narrow, and wheeled rather than caterpillar skidders. Practices can be improved if skidders are used; examples include driving with the blade up, reversing out of skid trails, and exploring extraction routes on foot rather than from the cab. Such changes require education, training and modified incentive schemes—but should lower operating costs as well as reduce damage. Other low-impact extraction methods should be explored, including extraction by draught animals, lighter machinery, machinery with broad rubber tires, helicopters and skyline cables. These can considerably reduce soil compaction and erosion, and damage to non-harvested trees and vegetation in general.

Preserve canopy and mid-canopy fig trees. Regarded as a keystone food resource for many tropical frugivores, fig trees (*Ficus* spp.) have special significance in preserving fauna. Figs are especially important for wildlife as they provide fruit throughout the year and fulfil vital nutritional needs, such as the calcium needed by vertebrates living on otherwise mineral-poor diets (see O'Brien et al. 1998). Strangling figs also provide important refuge habitat for many mammal taxa. Because of the canopy germination habit of many figs, protecting larger mature individuals appears to be the only viable conservation measure during felling (Johns

1992); however, given the extended length of time to maturity, efforts should be made to conserve as many figs as possible, regardless of age. In collaboration with research institutions, concessions could develop survey methods to study the effect of protecting such fruit trees on local wildlife densities.

Better protect interior forest conditions. Many vertebrates, especially amphibians, reptiles and forest interior birds, require moist, relatively shady conditions, and many forest-dependent species need relatively high degrees of ground cover for hiding. By maintaining as much cover and canopy as possible, lower levels of the forest will not be subject to the drying influences of intense sunlight, and some species will retain a higher degree of security. Preserving the forest canopy will also aid in preserving leaf litter habitat. Roads and trails should be planned carefully and constructed in a way that minimises canopy damage. They should be kept short and narrow (a maximum overall width of 4 m is recommended by DFID 1999) and, if possible, overhead canopy contact should be maintained. The impact of roads on faunal dispersal remains largely unstudied on Borneo and requires the development of new survey techniques that are suitable for use in timber concessions. A simple road monitoring program is presently being implemented in a concession in East Kalimantan Province (E. Meijaard, unpubl. data; Gordon and Stewart, unpubl. data), which provides important information on road use and crossing by a range of species. Finally, the area compacted by machinery should be minimised; this is more effective for revegetation than attempting to rehabilitate these areas following logging (Pinard et al. 2000; Pinard and Putz 1996).

Leave dead or partially dead trees standing or intact. Many mammals depend on large, old and hollow trees, including bears, civets, squirrels, arboreal murids, and porcupines. Losing large stems can have long-term influences (Gordon et al. 1990) and, although not well documented, potentially causes otherwise inexplicable decline or failure in forest regeneration in various parts of the world. The loss of mycorrhizal fungi possibly slows down recolonisation in clear-fells. Setting a maximum felling diameter might retain many large trees, but its impact on forest ecology and forestry economics requires testing. Trees infected by heart-rot should be retained wherever possible as these provide hollows for vertebrates for breeding, nesting, and storing food.

Reduce slashing. Slashing undergrowth and climbers for several years to reduce aggressive 'weeds' and encourage regeneration has a deleterious effect on many species, including rattan and timber seedlings. In parts of Borneo, compartments slated for logging are often incompletely accessed due to extreme gradients and rugged difficult terrain. Thus more than half a logged compartment commonly remains unlogged after harvesting is complete. In contrast, slashing is applied on foot and no areas are omitted, making it a much more general and obvious impact on 'logged areas' (D. Sheil, pers. obs. 1998–2003). Even if applied properly, the technique's silvicultural benefits appear limited, while the impacts on biodiversity and communities are considerable (while the impacts of slashing on wildlife are not closely assessed, the understorey is clearly greatly affected (Sheil et al. 2006)]. Slashing undergrowth and climbers may be as damaging as harvesting itself, and we suggest that the policy be reviewed.

Prevent streams from silting up. Species like the otter civet, *Cynogale bennettii* (Gray, 1837), depend on clear water for breeding and feeding. Proper drainage systems that feed into vegetated areas and well-constructed and well-maintained bridges and culverts are important in keeping streams clear, which is also very important for local human communities. Furthermore, the law requires logging exclusion zones around streams and waterways. Proper implementation of these laws will significantly benefit aquatic ecosystems in timber concessions.

Maintain interior forest connectivity. Maintaining contiguous undisturbed forests as well as corridors of interior forest benefits vertebrate fauna (Marcot et al. 2001). Preserving an array of adjacent undisturbed forests for refuges, core and supplemental habitats, and sources for recolonising populations is important, particularly for more sensitive forest-dependent species. Habitat corridors connect patches of undisturbed forest, thus assisting animals that will not enter open areas to disperse.

Ensure adequate recovery periods. When practical there will be benefits if annual felling coupes can be organised with some degree of dispersal to facilitate regeneration and migration of wildlife disturbed by logging (DFID 1999). If possible, this should involve closing some roads temporarily so that animals can migrate undisturbed and hunting pressure is reduced. This means dismantling river crossings (culverts) or installing gates and permanently closing roads when they are no longer in use (Mason and Putz 2001).

Ensure legal requirements are enforced. Means of enforcement should be built into guidelines. Since government authorities control logging and the concession controls security, self-policing should be combined with check-ups by forest police and other designated government representatives. Opportunities for involvement and verification should be given to other major stakeholders (community representatives, NGOs etc.) and to agreed third parties. Forestry certification audits, if applicable, provide one means to gauge success.

If carried out in areas selected for logging, these recommendations should help considerably in protecting vertebrate populations in tropical forests. However, these recommendations will not be successful without an overall plan for sustainable management and appropriate implementation of enforcement measures. Blockhus et al. (1992) proposed such a plan, which included the following:

- Creating a protected system linked by natural forest corridors
- Establishing monitoring programs to ensure effective implementation
- Implementing remedial action before changes are irreversible

Finally, long-term goals should balance economic benefits with environmental costs to conserve all components of biodiversity, including vertebrates.

Discussion

It is true that logging has had a bad press from conservationists in the past. Why should conservationists now invest in better logging and better forest management practices? Firstly, as we have argued, production forests, if well managed, retain habitat for most forest species. Secondly, considering that the majority of Borneo's remaining forests are under timber concessions (over 100,000 km^2 in Indonesian Borneo), working with production forests currently offers the only realistic way to maintain large-scale forest landscapes in Borneo. Only a small fraction of the forest landscape is strictly and effectively protected, but the remainder will be increasingly under pressure—as politicians and others seek revenues and development—for conversion to commercial land-use such as the large-scale oil-palm cultivation. Timber concessions offer opportunities for revenues and employment while maintaining forest cover. Our grander vision is that a zoned multiple use forest cover can provide large-scale forest landscapes. These landscapes can provide connectivity, support the persistence of wide-ranging species, and provide a management presence able to protect theses forests and the species sites and species they contain against the threats to which they will be subjected.

Another relevant question is whether our vision can be achieved and should therefore be supported. Concessions in Indonesia vary in their ability and in their willingness to improve. Many of the best companies have been pursuing certification for some time, and many more already spend considerable amounts on fulfilling environmental regulations and guidelines. These concessions envisage long-term involvement in the forestry industry, and they anticipate strict international conditions of timber trade and an increasingly restricted (Western) market demanding ecological and social justification. The costs of certification are low for large companies (around US$100/km^2, compared with US$500–5,000/km^2 in profits, averaged across several Borneo-based timber concessions), and can be recovered by improved access to premium markets and increased efficiency of timber operations. Other incentives for seeking certification are a 'green image', access to other markets, and publicity, while certification may also allow innovative managers to push through management changes that increase productivity and efficiency. There are still challenges. For example governments could do more to provide incentives, such as allowing tax-relief on areas set aside by concessions for protection. Also, implementation and control issues that are presently problematic need to be resolved.

Another argument why it might work and why we should try lies with the people of Borneo themselves. The people in Borneo do not want to lose their forests and wildlife. A recent interview-based study in one district in Indonesian Borneo found that all respondents (villagers, townspeople and civil servants) support some form of forest conservation for biodiversity conservation and also agree that logging companies need to be better controlled (Padmanaba and Sheil 2007).

Conclusion

Although logging in Borneo has not yet incorporated many of the measures required to reduce the impact of logging on mammals, our analysis indicates that well-managed selective logging can be compatible with conserving most forest mammal species. There is currently, however, much room for improvement. We suggest a number of changes in concession management and legal matters to improve the survival chances of vertebrates in Bornean production forests.

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