

Phylogenetic Age is Positively Correlated with Sensitivity to Timber Harvest in Bornean Mammals

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ABSTRACT

The reasons that forest vertebrates differ in their response to selective timber extraction in tropical forests remain poorly characterized. Understanding what determines response and sensitivity can indicate how forest management might yield greater conservation benefits, and help us identify which lesser-known species may be especially vulnerable. We assessed the response of 41 Bornean mammals to selective timber harvest and tested eight hypotheses regarding the correlation between those responses and a range of species characteristics. Multivariate analyses show that phylogenetic species age is a key variable determining sensitivity. Older species are less able to cope with the effects of selective timber harvest. Most of these species are endemic to insular southeast Asia, and do not occur on the Asian mainland. These species are more specialized, and appear less able to cope with habitat change. In contrast, species tolerant to logging evolved more recently. This group tends to be omnivorous or herbivorous, to use all vegetation strata, and to be regionally widespread. This finding allows the sensitivity to habitat disturbance of lesser-known species to be predicted, and therefore has important conservation implications. These new insights also help in the design of large-scale forest landscapes that combine sustainable forest management and species conservation requirements. We recognize that these functions can be compatible, but that some species still need completely protected areas for their survival.

Abstract in Indonesian is available at <http://www.blackwell-synergy.com/loi/btp>.

Key words: Borneo; conservation; dipterocarp forest; evolution; forestry; logging; palaeoenvironment; southeast Asia.

BORNEO'S FORESTS ARE BEING DEGRADED AND LOST (Fuller *et al.* 2003, Sodhi *et al.* 2004). Vertebrate species vary considerably in their response to various aspects of habitat alteration, but most appear able to persist in selectively logged forest areas, as long as threats such as hunting and forest fires are controlled (Meijaard *et al.* 2005). Forest management practices are becoming increasingly important, not only for the maintenance of natural forest cover and associated goods and services (*e.g.*, timber and nontimber forest products, provision of clean water), but also for landscape-scale biodiversity conservation (Fimbel *et al.* 1998, Pearce *et al.* 2003).

In Indonesia, effective management of timber concessions has the potential to make important contributions to biodiversity conservation. Of the 41 million ha in forest concessions, 43 percent is still pristine forest, and 27 percent of the logged forest is still considered in moderate to good condition (Sist *et al.* 2003). There is, however, much uncertainty about the compatibility between conservation and current forest exploitation practices, especially in southeast Asia (Bowles *et al.* 1998, Lugo 1999, Putz *et al.* 2000).

Meijaard *et al.* (2005) compiled an overview of the impact of timber harvesting on vertebrate species in Indonesian Borneo, which identified various ecological characteristics that appear to

make species vulnerable to selective timber harvest (hereafter 'logging'). For instance, among birds and mammals, specialized insectivores appear significantly more sensitive than other feeding guilds (Lambert & Collar 2002, Isaac & Cowlshaw 2004, Meijaard *et al.* 2005). Yet our understanding of what makes species vulnerable remains limited, as only a fraction of Borneo's wildlife has been studied, and almost all studies have limitations and caveats that undermine confidence in their general applicability.

Many Bornean vertebrates are threatened with extinction (Cardillo *et al.* 2006, IUCN 2006) and there is a need to identify which species require what kinds of intervention. In Borneo, however, studies that provide relevant ecological information to forest managers are scarce and those identifying species whose management would be most improved by ecological study are even scarcer (Meijaard & Sheil 2007). In this study, we investigate the biological characteristics that predict the responses of Bornean mammals to logging. Specifically, we aim to: (1) develop an empirical framework to examine the relative sensitivity of mammals to logging; and (2) predict which species should be targeted for special management in timber concessions.

We expect that species-level variation in sensitivity to forest logging is determined by a number of life-history, evolutionary, and ecological traits (Fisher & Owens 2004). Our goal is to identify which characteristics best explain variation between mammals in

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their sensitivity to logging. We expect that sensitivity to logging corresponds to an increased risk of extinction, a widely studied subject. We explore mechanisms most commonly proposed to explain the variation in extinction risk (e.g., Johns & Skorupa 1987, Purvis *et al.* 2000, Lambert & Collar 2002) through the analysis of eight species traits that are related to these mechanisms. We specifically tested a number of nonexclusive hypotheses about 41 species of Bornean rain forest mammals:

1. *Phylogenetic age.* We hypothesized that species that are more sensitive to logging would be older (H1). In other studies a positive correlation between the age of a lineage and its vulnerability to extinction has been reported (Gaston & Blackburn 1997, global and New World avifaunas; Johnson *et al.* 2002, Australian marsupials). In insular southeast Asia, older lineages tend to be more specialized and less able to withstand alterations of their habitat than are younger, typically more generalist taxa. We expected that this pattern would be especially marked in insular southeast Asia due to the recent history of palaeoenvironmental changes in the region (Meijaard 2003b).
2. *Island occurrence.* We hypothesized that species found on many islands would be more resilient to logging than species found on few islands (H2). Many of the smaller islands in the Sundaic subregion were formed after the last glacial maximum when sea levels rose by 120 m, separating once contiguous mammal ranges into small fragments (Heaney 1984, Meijaard 2003a). The species that survived this habitat fragmentation are the hardy remnants of previously more extensive ecosystems (Balmford 1996). These survivors appear to be ecologically more adaptable than species that were absent from these islands or occurred on only very few (Meijaard 2003a).
3. *Body size.* We hypothesized that vulnerability to logging would be associated with body size (H3). Body size can affect a species' vulnerability in a range of ways (Blackburn *et al.* 1993, Onderdonk & Chapman 2000, Fagan *et al.* 2001, Henle *et al.* 2004). Some have proposed a positive relationship and larger-bodied species may respond better to habitat disturbance since their lower metabolic requirements and higher energy reserves allow them to survive periods of reduced food availability (Wheatley 1982, Lindstedt & Boyce 1985). In contrast, larger species are expected to have slower replacement rates and may be at greater risk from hunting (Jerozolinski & Peres 2003), so an inverse relationship may be expected. Empirical trends indicate that overall, large body size leads to higher extinction risk (Cardillo 2003; Cardillo *et al.* 2005).
4. *Taxonomy (species per genus, subspecies per species).* We hypothesized that a higher degree of taxonomic diversification would be associated with higher vulnerability to logging (H4). Taxonomic groups with many taxa are more likely to contain rare species than smaller taxonomic groups thus increasing the extinction risk of individual taxa within that group (Lozano & Schwartz 2005).
5. *Life-history.* We hypothesized that species susceptible to logging were more likely to have fewer young per litter, longer interbirth intervals, and to be older at the first reproduction when compared with more tolerant species (H5). In general, species with relatively fast life-histories may have a lower risk of extinction because they can recover more quickly from population declines (Purvis *et al.* 2000, Polishchuk 2002).
6. *Distribution.* We hypothesized that more widely distributed species would be less sensitive to logging (H6). In southeast Asia, species with larger distribution ranges cover a greater variety of environmental conditions and are better adapted to cope with changes in local environmental conditions. Larger geographical ranges also decrease extinction risk (Gaston & Blackburn 2000, Purvis *et al.* 2000), possibly because increased diversification rates buffer species from extinction (Cardillo *et al.* 2003).
7. *Feeding categories.* We hypothesized that species with higher-quality diets and higher degrees of specialization would be more negatively affected by logging (H7). The degree of feeding specialization has been linked to the extinction risk in a range of species (Harcourt *et al.* 2002, Davies *et al.* 2004, Safi & Kerth 2004, Charrette *et al.* 2006). More specifically, feeding specialization predicts the sensitivity of Sundaic bird species (Lambert & Collar 2002) and primates (Johns 1997) to the effects of logging.
8. *Habitat use/Feeding stratum.* We hypothesized that species that are more specialized in their use of forest environments would be more vulnerable to logging (H8). We were able to assess this using feeding strata. Canopy-dwelling species will be more susceptible to habitat disturbance because they are less able to cope with disruption to the forest canopy from tree felling (Marsh *et al.* 1987). Also, strictly terrestrial species are more sensitive to habitat disturbance than species that are able to use different vegetation strata (Lambert & Collar 2002).

The eight hypotheses and related factors are not independent. Therefore, following univariate exploration of the relationships between variables, we used multivariate and covariate analyses to test our hypotheses and to determine which factor best predicts the sensitivity of species to logging.

METHODS

We analyzed the relationship between ecology, distribution, phylogenetic age, and life-history characteristics of 41 of the most studied Bornean mammal species and their sensitivity to logging. Meijaard (2003b) compiled the information on species ages and palaeoenvironmental conditions in southeast Asia. Species ages were obtained from published molecular phylogenies in which data on pairwise genetic divergences between species were converted to approximate times since divergence. This approach followed the method used by Webb and Gaston (2000). Individual studies were checked for adequate sample size, analysis of lineage-specific molecular change, and appropriate use of calibration points from the fossil record. Additional data were provided by M. L. Patou and G. Veron (pers. comm.). The categorization of our principle analytical variables is shown in Table 1.

TABLE 1. Description of variables used in the analysis and the sources used.

| Name | Description | Statistical class | Source ¹ |
|----------------------------------|--|-------------------|---|
| Species per genus | Number of extant species per genus | Continuous | after Corbet and Hill (1992), unless more recent taxonomic reviews were available |
| Subspecies per species | Number of extant subspecies per species | Continuous | after Corbet and Hill (1992), unless more recent taxonomic reviews were available |
| Phylogenetic age of species | Age in millions of years of divergence from sister species | Continuous | (after Meijaard 2003b), with additional data from M. L. Patou and G. Veron. |
| Island occurrence | Number of small Sundaic islands on which species occurs | Continuous | (after Meijaard 2003a), with updates (Meijaard, pers. obs.) |
| Body weight | Mean weight of adult female (kg) | Continuous | as reported in the literature |
| Number of young per litter | Mean number per young per litter | Continuous | as reported in the literature |
| Group size | Mean number of animals in a group | Continuous | as reported in the literature |
| Distribution | (1) endemic to Borneo; (2) endemic to the Sundaic subregion; (3) occurring in both the Sundaic and Indochinese subregions | Nominal | Corbet and Hill (1992) |
| Diet categories | (1) >70% frugivorous; (2) fruits and leaves (animal matter < 10%) (3) omnivorous (no category > 40%); (4) fruit and animal matter (other plant parts < 10%); (5) > 70% insectivorous or carnivorous; (6) > 70% herbivorous | Nominal | as reported in the literature |
| Foraging stratum | (1) terrestrial; (2) ground-understory; (3) lower-middle strata; (4) ground canopy | Nominal | as reported in the literature |
| Interbirth interval | Mean number of days between successive births. | Continuous | Hayssen <i>et al.</i> (1993) |
| Female age at first reproduction | Mean female age in months at first live birth | Continuous | Hayssen <i>et al.</i> (1993) |

¹ The literature, including 47 books or book sections, 153 publications in peer-reviewed journals, and 80 unpublished reports or theses, is summarized in Meijaard *et al.* (2005).

Our dependent variable, sensitivity to logging, was obtained from 24 regional field studies on the study species (for an overview see Meijaard *et al.* 2005). Logging sensitivity was coded as follows (see Fig. 1 for our scoring of species-specific logging tolerance):

- Intolerant: Severely impacted by selective logging, *i.e.*, densities decline by more than 20 percent in the first year after logging, and do not recover within 5 yr after logging.
- Neutral: No recorded effects from selective logging, *i.e.*, no significant changes ($< \pm 20\%$) in densities have been reported following logging.
- Tolerant: Positive effect of logging, *i.e.*, densities increased by more than 20 percent within the first year after logging.

Compiling and reviewing the available studies, we summarized the percentage changes in each species density following logging. For each study, we also made judgments about study design and reliability and, if it could be determined, local hunting pressure. For each species, we generalized sensitivity by assessing density trends from a range of studies in relation to age of logging and the absence or presence of hunting (full data tables are given in Meijaard *et al.* 2005). The number of studies per species ranged from one to 11 (mean 2.85). The effects of logging on the densities of each of our

selected species were occasionally inconsistent across studies ($N = 13$ of 41 species), with some research showing increases following logging and others indicating decreases. When evaluating contradictory studies, we assessed the soundness and robustness of the various studies (*e.g.*, duration, replication, controls, confounding factors), and considered other factors such as hunting pressure and logging intensity. For instance, the Bornean gibbon *Hylobates muelleri* Martin was observed to decline following logging in six of 11 studies, with two (short-term) studies noting an increase. Though the majority of studies showed a decline, we considered the alternatives. The short-term studies were given less weight because short-term fluctuations in productivity are common in Borneo's forests. Also, the number of transects in the short-term study was much less than in the other studies. We therefore considered those studies indicating density reductions to be more accurate and therefore classified Bornean gibbons as intolerant to logging. We used such reasoning in 13 of 41 species and in all but two cases our determination agreed with the majority of published studies. The two exceptions were: plantain squirrel *Callosciurus notatus*: declined (number of studies, $N = 2$), increased ($N = 2$); we assigned it to the logging-tolerant group, based on our frequent observation of the species in all vegetation types, including urban environments; and long-tailed macaque

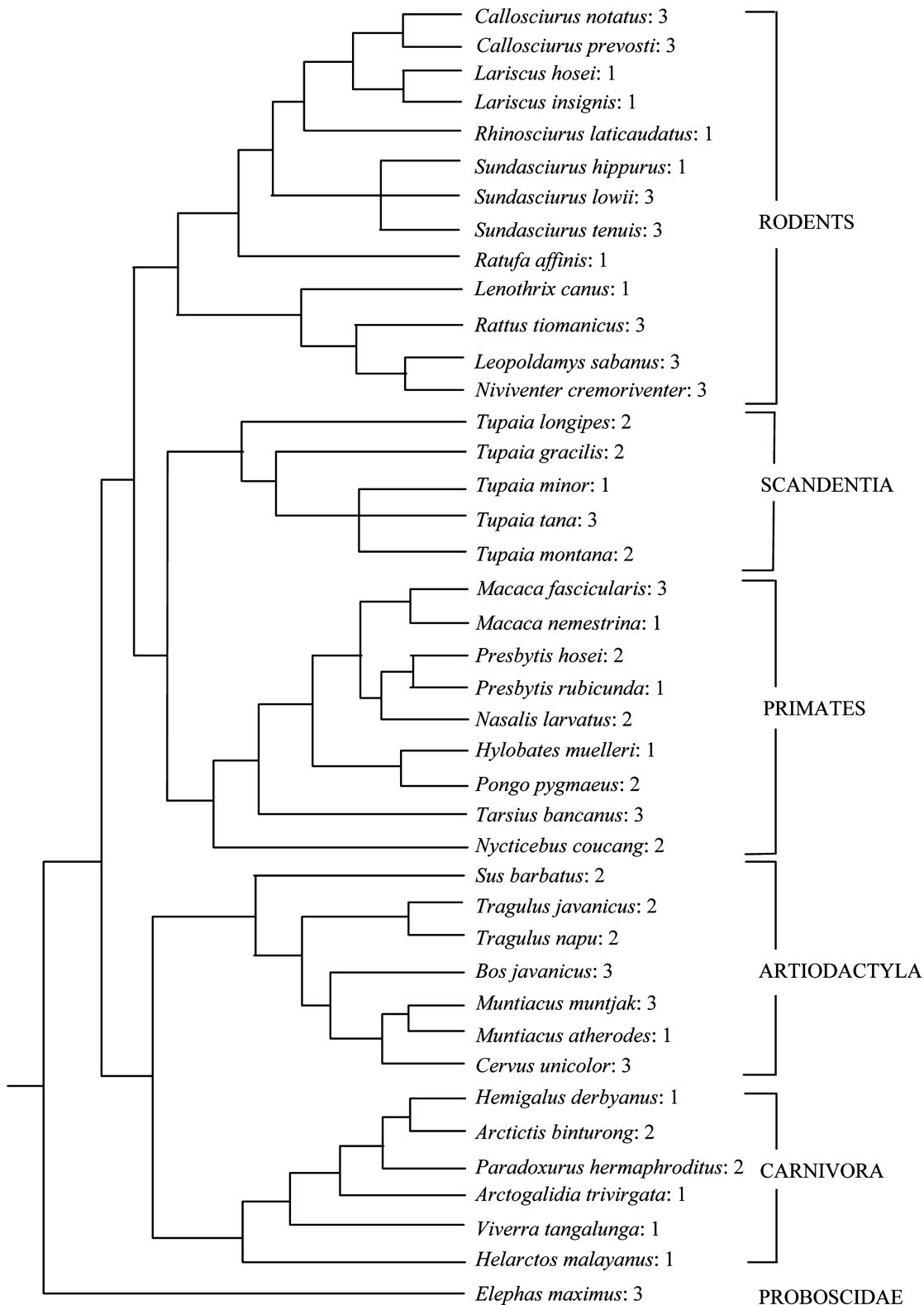


FIGURE 1. Phylogenetic relationships between test species (taxonomy following Wilson & Reeder 1993). Branch lengths not to scale. Numbers behind names represent tolerance levels to logging (1 = intolerant; 2 = neutral; 3 = tolerant). Phylogenetic relationships after Cronin *et al.* (1996), Bininda-Emonds *et al.* (1999), Bromham *et al.* (1999), Han *et al.* (2000), Schmitz *et al.* (2000), Veron and Heard (2000), Adkins *et al.* (2001), Amrine-Madsen *et al.* (2003), Mercer and Roth (2003), Meijaard and Groves (2004a, b), Pitra *et al.* (2004), Poux and Douzery (2004), and Lucchini *et al.* (2005). For species name authorities see Corbet and Hill (1992).

Macaca fascicularis: declined ($N = 1$), neutral ($N = 4$), increased ($N = 1$); we assigned it to the logging-tolerant group, because the four studies showing neutral responses were conducted in forest logged 12–45 yr previously, whereas between 2 and 10 yr following logging the species increased. In these two cases, the studies we viewed as ‘best designed’ were used in the analysis.

To create a single diet variable that could be entered into the regression analysis, we reduced data on the percentage of leaves, fruit, and animal matter in each species diet to a single continuous predictor diet quality (DQ) (Sailer *et al.* 1985, Leonard & Robertson 1994). We used the formula: $DQ = P + 2f + 3.5a$, where P = percent of diet from leaves, f = percent diet from fruit, and a = percent animal material. Thus, DQ varied from 100 (100% folivorous) to 350 (100% faunivorous). We also tested the percentage diet data for individual dietary components.

Species cannot be treated as independent statistical combinations of traits and behaviors because species may share ancestral states with similar traits and behaviors. When traits and behaviors are correlated among species, it is useful to distinguish adaptive explanations based on shared evolutionary pressures from the alternative that this merely reflects common ancestry. We tested for phylogenetic independence of logging tolerance among our test species using a phylogenetic regression technique (Grafen 1989). In this procedure, each phylogenetic branchpoint provides a single independent contrast with which an adaptive hypothesis can be assessed. We created a phylogeny for all selected species using published phylogenetic information as compiled in Meijaard’s (2003b) review (Fig. 1). Note that phylogeny enters our analysis in two distinct ways. Through the concept of phylogenetic age—the length of time a species has existed—and through the relationships among the species included in our analysis.

We used a correspondence analysis to investigate the relationships among the different nominal variables (Table 1). We investigated the relationships among the different numerical variables (Table 1) using logging tolerance as the dependent variable. We performed Mann–Whitney U and Kruskal–Wallis tests to assess whether our numerical variables were distributed differently among the logging-tolerance categories. In addition, we conducted simple logistic regressions in two ways, using a binary (intolerant or not) and ordinal response variable (intolerant, neutral, tolerant). We used Nagelkerke’s R^2 to measure the strength of associations (Nagelkerke 1991) and Akaike’s information criterion (AIC) to compare goodness of model fit (Akaike 1974). To identify and test for relationships between variables that could have confounded our results, we examined plots of all variables plotted against all others. This procedure identified several correlated variables and reassured us that these relationships were principally monotonic in nature (*i.e.*, no unimodal or peaked relationships). The independent effects of predictor variables that were correlated with each other were determined through multiple logistic regression (*i.e.*, generalized linear models based on a logit link function), which examined the effects of each variable while others were held constant. As above, we did this for binomial and ordinal responses. To allow confidence to be assessed under alternative assumptions we quote full P values (Day & Quinn 1989, Stewart-Oaten 1995) without Bonferroni correction procedures (see Nakagawa 2004). Analyses were done in

a specialized analytical package ‘*phylo8.glm*’ (Grafen 1989), JMP 5.0.1.2 (JMP 2003), and SPSS 11.5.0 (SPSS 2002).

RESULTS

Based on our literature review, we categorized 15 species as intolerant, 12 as neutral, and 14 as tolerant to logging. For some tests the sample sizes differed from these numbers due to limited data on some ecological and life-history traits.

CORRESPONDENCE ANALYSIS.—Species distribution ranges appear to be correlated with logging tolerance (H6). Thirteen of 15 (87%) species that were negatively affected by logging were Bornean or Sundaland endemics. None of the eight Bornean endemics were tolerant to logging; seven of 14 tolerant species (50%) occurred throughout southeast Asia (Fig. 1). Other potentially interesting relationships were those between diet and foraging strata and logging tolerance (H7). Six of 10 (60%) frugivores were intolerant to logging, and only two were tolerant. Only one of nine (11%) insectivores and carnivores was tolerant to logging. Of the species that were logging tolerant, 87 percent were omnivores. Foraging strata were poorly correlated to logging tolerance (H8). Seven of the 15 (47%) intolerant species were terrestrial, and eight of 16 (50%) species that occurred both in lower vegetation strata and on the ground were tolerant to logging.

BIVARIATE ANALYSIS.—Initially, we tested our data without accounting for phylogeny. Among 12 different continuous variables, phylogenetic age (H1) and the number of subspecies per species (H4) differed significantly between the three sensitivity groups (intolerant, neutral, tolerant; Table 2). Because we were primarily interested in the species that are intolerant to logging, we combined the neutral and tolerant groups, containing 14 and 12 species, respectively. *Rattus tiomanicus* was identified as an outlier because the genus *Rattus* contains 56 species, and therefore dominated the relationship between number of species per genus and logging sensitivity. Removal of this species weakened the relationship with logging sensitivity ($P = 0.11$). Additional bivariate tests of the effects of interbirth interval and female age at the first reproduction (H5) (but sample sizes were small), distribution (H6), diet (H7), and foraging strata (H8) showed these variables had no consistent effects on the interspecific pattern of variation of response to logging. Although nonsignificant, there was a consistent trend for tolerant species to be smaller (H3), have lower quality diets (H7), and perhaps have ‘faster’ life-histories (H5). The following independent variables were highly correlated with each other and were controlled for in the subsequent multivariate analyses: (1) diet and phylogenetic age, specifically, young species had low-quality diets (*i.e.*, more folivorous); (2) diet and body size, with larger species having lower quality diets; and (3) number of subspecies per species and number of islands inhabited. Other variables were not strongly correlated, except body size versus home range, and group size versus home range.

When we incorporated phylogenetic relationships into our analysis using independent contrasts and two ‘sensitivity’ groups as our classification scheme, three factors were correlated with the

TABLE 2. Comparison of 12 predictor variables in relation to species' sensitivity to logging, expressed in either of the three categories (intolerant, neutral, and tolerant). Trend: + indicates variable makes species less susceptible to logging, – indicates makes species more susceptible to logging; signs in parentheses denote nonsignificant, but potentially biologically meaningful trends. Phylogenetic relationships were not taken into account.

| Variable | Intolerant | | | Neutral | | | Tolerant | | | Trend | Ordinal response (Kruskal–Wallis) | | Nominal response (Mann–Whitney) | |
|---------------------------|------------|------|----|---------|------|----|----------|-------|----|-------|--------------------------------------|------|------------------------------------|------|
| | mean | SD | N | mean | SD | N | mean | SD | N | | H | P | U | P |
| Species age (mya) | 6.1 | 3.4 | 10 | 4.6 | 2.6 | 8 | 2.6 | 2.1 | 12 | – | 7.69 | 0.02 | 49 | 0.02 |
| Subspp. per species | 3.9 | 3.4 | 15 | 8.6 | 11.6 | 11 | 11.1 | 11.9 | 14 | + | 7.39 | 0.03 | 116 | 0.04 |
| Island number | 7.1 | 8.0 | 15 | 15.5 | 16.8 | 11 | 15.9 | 14.8 | 14 | (+) | 3.43 | 0.18 | 124 | 0.08 |
| Spp. per genus | 5.7 | 4.4 | 15 | 6.8 | 4.4 | 12 | 12.6 | 13.2 | 14 | (+) | 5.56 | 0.06 | 131 | 0.08 |
| Young per litter | 1.6 | 0.7 | 14 | 1.9 | 1.4 | 10 | 2.1 | 1.0 | 14 | ns | 1.86 | 0.40 | 141 | 0.41 |
| Interbirth interval | 750 | 487 | 2 | 927 | 1279 | 4 | 523 | 450 | 6 | ns | 0.42 | 0.82 | 7 | 0.52 |
| Age at first reproduction | 67 | 75 | 2 | 66 | 77 | 4 | 58 | 62 | 5 | ns | 0.04 | 0.98 | 9 | 0.99 |
| Body weight (kg) | 6.5 | 12.7 | 15 | 21.5 | 44.9 | 12 | 180.4 | 534.6 | 14 | ns | 0.94 | 0.63 | 194 | 0.98 |
| Diet quality | 233 | 70 | 15 | 218 | 79 | 12 | 207 | 80 | 14 | ns | 0.64 | 0.73 | 169 | 0.48 |
| Percent plants in diet | 19.7 | 17.8 | 15 | 28.3 | 31.7 | 12 | 40.7 | 31.7 | 14 | ns | 3.57 | 0.17 | 146 | 0.19 |
| Percent fruit in diet | 45.2 | 27.5 | 15 | 42.9 | 31.3 | 12 | 29.5 | 21.3 | 14 | ns | 2.58 | 0.28 | 155 | 0.28 |
| Percent animals in diet | 35.1 | 37.3 | 15 | 29.6 | 37.1 | 12 | 30.5 | 21.3 | 14 | ns | 0.26 | 0.88 | 183 | 0.75 |

differences among species: (1) number of subspecies per species; (2) number of small islands on which species occur; and (3) species age ($P < 0.05$) (Table 3). The similarity of results determined with and without controlling for phylogeny in this instance indicates that 'shared ancestral states' do not significantly confound the patterns we observe. Thus, in our subsequent analyses we consider only nonphylogenetically controlled results.

Binary logistic regression analysis (species intolerant or not) showed that species logging sensitivity was related to phylogenetic age (H1; older species were more sensitive, $N = 30$, $R^2 = 0.24$, $P = 0.019$, AIC = 33.9); number of subspecies per species (H4; species with more subspecies were less sensitive, $N = 40$, $R^2 = 0.18$, $P = 0.051$, AIC = 49.7); and number of islands on which species occur (H2; less sensitive species were found on more islands, $N = 40$, $R^2 = 0.15$, $P = 0.050$, AIC = 52.1). The best-fit model (indicated by lowest value for AIC) was the model including only phylogenetic age. Ordinal regression analysis (species intolerant,

neutral, or tolerant) showed that logging sensitivity of species was related to: phylogenetic age (H1; $N = 30$, $R^2 = 0.29$, $P = 0.003$, AIC = 55.8); number of subspecies per species (H4; $N = 40$, $R^2 = 0.11$, $P = 0.045$, AIC = 82.5); bodysize (H3; $N = 41$, $R^2 = 0.11$, $P = 0.040$, AIC = 91.2); and number of species per genus (H4; $N = 41$, $R^2 = 0.17$, $P = 0.010$, AIC = 85.1). As with the binary logistic models, the one incorporating only phylogenetic age was the best fit to the data. *Rattus tiomanicus* (with 56 species in the genus *Rattus*) dominated the relationship between the number of species per genus and logging sensitivity in the ordinal regression analysis. When this taxon was removed, the number of species per genus regression was less significant ($P = 0.03$). Removal of *R. tiomanicus* did not alter any other patterns uncovered by our binary or ordinal simple logistic regressions.

MULTIVARIATE ANALYSES.—As several factors were correlated with sensitivity to logging, and since some of these factors were correlated with each other, we conducted a multivariate analysis to determine the relative importance of each factor. We ran multiple logistic regressions of the independent effects of phylogenetic age against the other variables that were correlated with logging sensitivity in the bivariate analyses. In models with a binary response variable, phylogenetic age of the species was the only significant predictor in any of the multivariate models. When we reran the analyses for the ordinal response, patterns were the same, but R^2 values tended to be higher and P values lower, due to the increased power associated with having an ordered response rather than a binary one. These models consistently showed that phylogenetic age was the strongest and most significant predictor of sensitivity to logging (H1), and that once it is controlled for, other variables became insignificant: logging sensitivity versus phylogenetic age and number of species per genus (whole model $R^2 = 0.35$, $P = 0.004$; phylogenetic age:

TABLE 3. Phylogenetically controlled comparison (using the method of Grafen 1989) of six predictor variables in relation to species' sensitivity to logging, expressed in two categories (intolerant and neutral + tolerant). See Table 2 for means, sample sizes, and standard deviations.

| | Kruskal–Wallis (two categories) |
|----------------------------|---------------------------------|
| Species age | $F(1, 20) = 4.42$, $P = 0.05$ |
| Island number | $F(1, 29) = 5.26$, $P = 0.03$ |
| Species per genus | $F(1, 31) = 2.68$, $P = 0.11$ |
| Subspecies per species | $F(1, 35) = 4.85$, $P = 0.03$ |
| Number of young per litter | $F(1, 21) = 1.39$, $P = 0.25$ |
| Body weight | $F(1, 36) = 0.22$, $P = 0.65$ |

$\beta = 0.388$, $P = 0.015$; number of species per genus: $\beta = -0.09$, $P = 0.227$; AIC = 56.7); logging sensitivity versus phylogenetic age and number of islands where species occurs (whole model $R^2 = 0.41$, $P = 0.001$; phylogenetic age: $\beta = 0.412$, $P = 0.007$; number of islands: $\beta = -0.07$, $P = 0.081$; AIC = 54.6); logging sensitivity versus phylogenetic age and body size (whole model $R^2 = 0.32$, $P = 0.007$; phylogenetic age: $\beta = 0.361$, $P = 0.023$, bodysize: $\beta = -0.02$, $P = 0.62$; AIC = 55.8). The only model in which a second variable (in addition to phylogenetic age) was significant was logging sensitivity versus phylogenetic age and number of subspecies per species (whole model $R^2 = 0.56$, $P < 0.0001$; phylogenetic age: $\beta = 0.375$, $P = 0.013$; number of subspecies per species: $\beta = -0.387$, $P = 0.032$; AIC = 49.6). Comparison of AIC values indicated that these multivariate models (*i.e.*, multiple logistic regressions) did not fit the data as well as the simple logistic regression including only phylogenetic age.

DISCUSSION

Our results link sensitivity to logging with (a) relatively old phylogenetic age (and thus implied genetic distinctiveness) (H1) and suggest that this is associated with (b) restricted distribution and thus degree of endemism (H6), and (c) dietary specialization (H7). These additional traits have previously been associated with heightened extinction risk in a general context (Gaston & Blackburn 1997, Purvis *et al.* 2000, Harcourt *et al.* 2002, Johnson *et al.* 2002, O'Grady *et al.* 2004, Pavoine *et al.* 2005, Redding & Mooers 2006). Well-managed, sustainable logging affects relatively few species, but our findings imply that the most negatively affected species are likely to be those that are also vulnerable to extinction—local and global risks are thus associated.

Logging-intolerant and logging-tolerant species in Borneo were separated into two groups, although we recognize that there are intermediate cases. The former are primarily species that evolved during the Miocene or Early Pliocene. These species show little geographical variation in morphology (*i.e.*, few subspecies) and seldom occur on small islands. They tend to have narrow ecological niches, with strictly frugivorous, carnivorous, or insectivorous feeding habits. Some are restricted to feeding on the ground although others fed on trees and in bushes. In contrast, species tolerant to logging were younger, originating during the Late Pliocene or Pleistocene. They are common on small islands and often occur throughout southeast Asia, where they typically exhibit significant morphological variation (many subspecies). Most of the logging-tolerant mammals are herbivorous or omnivorous. Many of these species 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 artifacts of common ancestry.

The relationships between phylogeny, ecological specialization, distribution range, and occurrence on small islands are complex. A review of the historical biogeography of southeast Asian mammals (Meijaard 2003b) indicated that the onset of glacial/interglacial cycles during the Late Pliocene (*ca* 2.8–2.4 mya) coincided with

rapid differentiation of species that were primarily adapted to more open vegetation types or forest edge habitats. This included several species of deer (*Cervus* spp.; Pitra *et al.* 2004), bovids (Ritz *et al.* 2000), and macaques (*Macaca* spp., Ziegler *et al.* 2007). Speciation in these groups was caused by the rapidly changing sea levels and concomitant break up of the land mass in what is now referred to as the Sundaic subregion (Corbet & Hill 1992). Species groups that were primarily adapted to more fragmented forests (our 'tolerant' species) migrated from the Asian mainland and displaced older ('intolerant') species. Many of these older species are now either restricted to the periphery of the Sundaic subregion, for example, northeast Borneo or the Mentawai Islands west of Sumatra—or in specific habitat types such as montane forests. This mirrors the findings of a review of 106 bird species that showed that with increasing species age, geographic ranges increased to a maximum after *ca* 2 million years (my), after which they contracted (Webb & Gaston 2000). Range contraction may lead to a reduced dietary niche breadth, as found among 51 African primate species (Eeley & Foley 1999).

We suggest that in southeast Asia, mammalian evolution during the Late Pliocene and Pleistocene shaped the species groups identified in this study: older, ecologically specialized species with small geographic ranges ('intolerant species' endemic to Borneo or the Sundaic subregion), and newer, ecological generalists with larger ranges ('tolerant species'). Because of their greater ecological adaptability, the latter group was more likely to survive on the many Sundaic islands that emerged following the last glacial maximum. These islands are small and most of them lack the environmental gradients typical of larger islands like Borneo. Ecological specialists would thus be disadvantaged compared to generalists when climatic fluctuations reduced specific resources.

Although phylogenetic age (and the life-history characteristics that covary with it) differs systematically between species in the different logging-tolerance categories, we found some notable exceptions. All species in the logging-tolerant group are less than 5-my old, with the exception of the tarsier *Tarsius bancanus*, Horsfield 1821, which diverged from its sister taxon 7.5 my ago. Most species of this phylogenetic age are intolerant to logging, but tarsier population densities appear to respond positively to logging. This seemingly contradictory result is readily explained when one considers that the tarsier's primary habitat, pole forests along rivers, is an area of high natural disturbance. In addition, light disturbance from gaps either created naturally or by selective logging, is likely to lead to increases in the density of insects and small vertebrates that comprise the tarsier's diet. Three other species diverged from the general trends reported here. Bornean gibbons *H. muelleri*, red leaf monkeys *Presbytis rubicunda*, Müller 1838, and sun bears *Helarctos malayanus*, Raffles 1821, are all relatively young (< 5 mya) species that appear to be intolerant to logging. The most likely explanation is that these species all eat highly frugivorous (or graminivorous in the case of *P. rubicunda*) diets and therefore likely experience disproportionate declines in food availability in logged forests. These species are also targeted by hunters, especially in newly opened timber concessions (Bennett & Gumal 2001). Thus, these exceptions to our overall patterns can be explained in light of their

ecology and do not reduce confidence in the general patterns we have identified.

In general, conservation is well served by considering evolutionary histories (Redding & Mooers 2006, Forest *et al.* 2007). Environments are now changing in large part due to increased human activities, and associated effects on climate and natural cycles. A species' evolutionary history can be predictive of its response to anthropogenic change, but this idea has not been sufficiently examined and exploited. Life-history theory can help us understand how different animals will respond to changes induced by human activities. Our analyses demonstrate that some species are intolerant to logging and associated impacts, whereas other species can tolerate some habitat disturbance. By being able to predict which species fall into which category we can better define guidelines and targets for species conservation, especially in the context of production forestry in the region.

The ecology of most Bornean forest mammals remains little known. In many cases, however, their phylogenetic age is reasonably well established or has been estimated. This offers hope for predicting which of the lesser known species (not in our original data set) are sensitive to logging (see Table S1). These sensitive species are rarely seen and their low densities and presumed sensitivity to forest disturbance increase their likelihood of extinction. Sighting or track records of these 'potentially vulnerable' species should be therefore kept by timber concessionaires. Areas in which vulnerable species are concentrated should be protected from disturbance. Such protected areas are requested in most forest management plans and in most forest certification schemes, including the Forest Stewardship Council's High Conservation Value Forests (HCVF) concept (FSC 2000).

The fact that a species declines after logging does not mean that it is lost. This is important if we compare wildlife presence in logged forest versus presence in alternative land uses such as oil palm or acacia plantation (see Duff *et al.* 1984, Stuebing & Gasis 1989). We envisage larger multifunctional landscapes that integrate production areas with strictly protected areas set aside for conservation and other purposes such as hydrology. We therefore encourage extractive forest management that provides real conservation benefits by maintaining connectivity of larger forest landscapes. We believe that timber companies in Borneo have the capacity and finances to implement forest management that encourages these values even for the sensitive species. Such well-managed concessions can contribute to wildlife conservation by complementing but not substituting strictly protected areas.

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SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article online at: www.blackwell-synergy.com/loi/btpp

Table S1. *Species in Borneo that are expected to be sensitive to the effects of logging*

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