No effect of small logging roads on the occupancy and movement of forest rats in Bornean logged forest

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ABSTRACT

Selective logging is driving the proliferation of roads throughout tropical rainforests, particularly narrow, unpaved logging roads. However, little is known about the extent of road edge effects, or their influence on movement of tropical understory animal species. Here, we used forest rats as a study taxon to address the following questions: (1) Does the occupancy of rats differ from road edges to forest interior within logged forests? (2) Do roads inhibit the movement of rats within these forests? We established trapping grids along a road edge-to-forest interior gradient at four roads and at three control sites within logged forest in Sabah, Malaysia. Captured rats were translocated across the road and recaptured on subsequent nights to quantify the probability of road crossing. In total, we caught 216 individuals from eight species in 3024 trap-nights. Occupancy did not differ across the road edge-to-interior gradient, and 48 percent of 105 translocated individuals returned from across the roads. This proportion was not significantly different from the proportion of rats returning from control sites (38 % of 60 individuals), suggesting that small roads were not acting as barriers to movement within logged forests. Sub-adults were significantly more likely to return from translocation than adults in both road and control sites. Our results represent good news for the ecology of small mammal communities in heavily-logged forests: small logging roads are unlikely to create an edge effect or influence habitat selection, nor do they restrict the movement of rats.

Key words

dispersal; linear openings; movement ecology; road barrier effects; small mammals; tropical forest
ROADS ARE A CATALYST OF FOREST FRAGMENTATION AND DEFORESTATION IN TROPICAL FORESTS GLOBALLY (Clements et al. 2014; Laurance et al. 2009). Generally created during logging operations, roads bisect forest and facilitate further anthropogenic activities such as hunting and resource exploitation. Road networks can be vast: in Sabah, Malaysian Borneo, there are already approximately 0.65 km of roads per km² (> 37,000km) (Gaveau et al. 2014). These networks, particularly those of small, unpaved roads, are rapidly proliferating, growing at > 7,000 km per year across Borneo (Gaveau et al. 2014) and more than 17,000 km per year in the Brazilian Amazon (Ahmed et al. 2013). Understanding the impact of these small logging roads on the biodiversity inhabiting logged tropical forests represents an urgent conservation priority, as species responses to roads are likely to mediate long-term persistence.

Logging roads are likely to affect biodiversity in two important ways. Firstly, they generate linear clearings that create forest edges, altering the habitat and abiotic conditions for rainforest species (Goosem 1997; Goosem 2000; Laurance 2002; Malcolm and Ray 2000; Pohlman et al. 2007). Logging roads can also act as movement barriers, which may induce changes in dispersal patterns to some species (Jaeger et al. 2005; Laurance 2002; Laurance et al. 2009; McGregor et al. 2008; Oxley et al. 1974). In large mammals, studies suggest that roads may negatively affect the abundance, movement and spatial distribution of animals (Fahrig & Rytwinski, 2009), with vulnerable species showing behavioral avoidance of traffic and associated disturbances such as noise and light (Fahrig & Rytwinski, 2009).

In small mammals, road ecology studies from temperate regions have produced contrasting findings, with some studies suggesting that roads have no effects on small mammal distribution,
densities and dispersal ability (Fuentes-Montemayor et al. 2009; Marques & Mira 2011; Rico et al. 2007), while others suggest that roads are barriers to movement (Jaeger et al. 2005; McGregor et al. 2008; Oxley et al. 1974). These studies have employed different methods to determine dispersal including mark-recapture, observational studies or radio tracking to discern general patterns, which are frequently confounded by varying physical attributes of the studied roads (Peter et al. 2013).

Only a few studies have examined road ecology of small mammals in the tropics (Burnett 1992; Goosem 2000; Goosem 2001; Goosem 2002; Malcolm and Ray 2000). Goosem (2002) found that crossing of narrow, dirt roads by small mammals was influenced by the presence of the road itself rather than traffic levels. Roads may exert edge effects, with forest specialist small mammals in particular more likely to be found further away from the roads, while generalist species were able to explore both edges and forest interiors (Goosem 2001). Goosem (2001) also observed that edge effects on forest specialist species were more pronounced in wide, dirt roads (> 20 m) due to a lack of canopy cover, which is similar to the observation of Burnett (1992) that small mammals were more likely to cross narrow logging roads. Malcolm and Ray (2000) found no effect of roads on the diversity of rodent communities, although community composition was influenced by how the roads were constructed: primary and secondary roads had the strongest impacts on mammal communities, while skid trails had the lowest impact.

Roads divide forest landscapes into smaller fragments, exposing the margins to edge effects (Fuentes-Montemayor et al. 2009; Laurance et al. 2009). Edge-altered microclimate conditions persist for 25-30 m away from roads, characterized by significantly higher light penetration, higher temperature and lower humidity. The extent of these edge effects are dependent on the
physical attributes of roads, with wider roads creating larger openings and more severe edge
effects, and on the tolerance of small mammal species to these microclimatic changes. Species
strongly adapted to the dark, sheltered and cool rainforest understory may have lower tolerance
to microclimatic edge effects, triggering a shift in community structure (Pohlman et al. 2007).
This may be exacerbated by poor habitat quality at edges for some species (Bissonette & Rosa
2002), whereas other species show higher densities by road edges that are attributed to the dense
undergrowth which offers protection against predators and the availability of pioneer plant
species as food (Malcolm and Ray 2000; Schmid-Holmes & Drickamer 2001). Some studies
suggest that roads also influence social patterns in rats, with females favoring forest interior for
nest-building material (Wilder & Meikle 2006) while dispersive young males were more likely
to exploit edge habitats due to the need to establish their own territories (Fuentes-Montemayor et
al. 2009).

In addition to exerting edge effects, roads may form a dispersal barrier to small mammals, with
some studies suggesting small mammals are reluctant to cross roads (Fahrig & Rytwinski 2009;
Goosem 2001; Rico et al. 2007) or cross them infrequently depending on the physical features of
the road (Burnett 1992; McGregor et al. 2008; Oxley et al. 1974). A study in Canada found
significantly lower numbers of small mammals crossing roads than continuous forest habitat,
with no relationship between road crossing rates and traffic volume which implies that the
presence of the road itself was inhibiting movement (McGregor et al. 2008). This may be partly
due to increased predation risk (Wolf & Batzli 2004), with predators including civets
(Viverridae) and leopard cats (Prionailurus bengalensis) known to use roads as movement
corridors and to catch prey (Mohamed et al. 2013). However, several studies have also shown
that physical road attributes such as road width and substrate may also affect an individual’s willingness to cross, with small mammals more likely to cross narrow roads with higher canopy coverage (Laurance et al. 2009; Oxley et al. 1974), and more likely to cross unpaved than paved roads (Jaeger et al. 2005; Peter et al. 2013).

In this study, we examined the effect of small, unpaved logging roads on rats in Borneo, as this road type represents the majority of the road network in logged forests and road effects have been little-studied outside of primary forest. We focused on murid rodents (rats), the largest rodent family in the tropics (Wells & Bagchi 2005; Wells et al. 2006). Murids have a short life cycle, potentially responding and adapting faster to environmental changes than many understory vertebrate taxa (Bissonette & Rosa 2009; Peter et al. 2013; Steele et al. 1984). Murids are functionally important, forming a major prey source for predators including Sunda clouded leopards (Neofelis diardii), raptors and snakes (Nakayabashi et al. 2014). Forest rats also act as seed predators and dispersers, with the genus Maxomys responsible for a majority of the seed removal in tropical trees of the Fagaceae and Dipterocarpaceae (Lambert et al. 2014; Wells & Bagchi, 2005; Wells et al. 2007). We conducted the study in heavily logged tropical forests, which are rapidly becoming the norm in South-East Asia and are characterized by dense networks of logging roads (Gaveau et al. 2014). Bornean small mammals are more abundant in logged than in primary forest (Wearn et al. 2017), making it pertinent to understand the potential impact of roads on small mammal communities in these degraded forest habitats.

We aimed to answer the following questions: (1) Do small logging roads influence the occupancy patterns of forest rats in logged forests? and (2) Are these logging roads a barrier to the movement of rats in logged forests? If edge effects are pronounced (e.g. Goosem 2000), we
would expect reduced occupancy adjacent to roads. In particular, we hypothesized that forest specialist species such as the Red Spiny Rat (*Maxomys surifer*) (Cusack *et al.* 2015), should avoid road edges and be primarily restricted to the forest interior, while the generalist Whitehead’s Rat (*Maxomys whiteheadi*) would be found throughout the road edge-to-forest interior gradient. Assuming that murid behavioral responses to roads mirror those observed in temperate studies (Jaeger *et al.* 2005; McGregor *et al.* 2008), we hypothesized that roads will reduce frequency of rat movement.

**METHODS**

**STUDY AREA** — We conducted fieldwork at the Stability of Altered Forest Ecosystems (SAFE) Project site at the Kalabakan Forest Reserve (4°42’N, 117°34’E) in Sabah, Malaysian Borneo between March and July 2016. The forests at SAFE have undergone two cycles of selective logging with an estimated 302.8 t ha⁻¹ above ground biomass removed (Pfeifer *et al.* 2016) and are crossed by a dense network of logging roads (Ewers *et al.* 2011). In total, we examined four logging roads and three logged forest control sites (Table S1). We selected logging roads (Fig. 1A) to meet the following criteria: (1) Road width ± 10 m, ensuring widths representative of the wider network of logging roads in Sabah; (2) Unpaved road surface (Fig. 1B); (3) Active roads in use by vehicles, ensuring we quantify the road effects when they are likely to be most severe; (4) Forest on both sides of the road extended a minimum distance of 420 m before another road edge was encountered (ensuring a minimum forest interior distance of 210 m); (5) Discontinuous canopy coverage over the road to ensure arboreal rats were not able to cross roads via the
canopy; (6) No vegetation or median strips on the roads, as this may influence road crossing 
(McLaren et al. 2011). We selected only roads that were >25 years old, being present during a 
logging cycle conducted during the 1990s (Fig. 1A). All roads were re-opened for active use in 
2015-16 when the study area underwent a new round of logging. We did not monitor traffic at 
our sites as forest rats are nocturnal (Yasuda & Miura 2000) and vehicles rarely used these roads 
in the evening. We established three control sites in comparable logged forest nearby, with each 
control site located 230 m from the nearest road edge.

LIVE TRAPPING — At each site, we established a trapping grid that consisted of eight rows of 
nine traps each. Trap points were separated along each row by 15 m, while the rows were 
separated by 30 m. We designed the spacing as a compromise between ensuring adequate 
independence between individuals caught at different distances from the edge, and ensuring that 
individuals returning from a translocation event were likely to be recaptured. A distance of 30 m 
exceeds two times the observed home range radius of *Maxomys whiteheadi*, comfortably the 
most commonly-encountered small mammal species in this study system (Chapman et al. 2018; 
Nakagawa et al. 2007; Wearn et al. 2017), and was therefore chosen as the spacing between 
rows. Within any given row it was more important that we had the highest possible likelihood of 
recapturing a returning individual, so we used a 15 m spacing that we have previously found to 
maximize the number of captures (PMC, pers. obs).

At the road sites, we established a trapping grid with the rows arranged parallel to the road, 
beginning at 0 m (i.e. immediately adjacent to the road edge), and finishing 210 m from the edge 
(forest interior). At control sites, we used an identical grid design located in the forest interior 
>230 m from any road edge. We placed one “Tomahawk style” steel cage trap (280 x 140 x 140
mm) within a 5 m radius of each grid point, and baited it with oil palm fruit (*Elaeis guineensis*).

We checked traps daily between 0830 h and 1100 h, for six consecutive nights at each site, replacing bait as necessary. We anesthetized all captured rats using diethyl ether administered using a fume box and injected them with a passive integrated transponder tag (Francis Scientific Instruments, Cambridge, UK). We identified individuals to species (according to Francis & Payne 2007) and recorded their weight, age and sex.

**TRANSLOCATION** — We ran traps at each grid for a total of six nights. Rats captured from the first five trap nights were translocated, with all individuals moved in a fixed direction perpendicularly across the road. We standardized the distance between capture and release, translocating all individuals 220 m (210 m of the trapping grid plus 10 m of road width).

Therefore, individuals trapped immediately adjacent to the road edge were released 210 m from the opposite road edge, whereas those trapped 210 m from the road were released immediately adjacent to the opposite road edge. Translocation at control sites was identical except for the absence of the road. These procedures follow established protocols in small mammal road ecology (e.g. Kozel & Fleharty 1979; McGregor et al. 2008; McLaren et al. 2011; Rico et al. 2007) and therefore provide data comparable to existing studies. Translocation may not be representative of normal small mammal movement behaviour, but it applies a standardized, repeatable stimulus to the homing behaviour of small mammals that increases the chance of collecting sufficient data (McGregor et al. 2008). We continued trapping at each site for one further night, to allow translocated rats to return to the trap grid, with recaptured individuals recorded as “road crossers”. Preliminary road translocation trials showed that the small, common species *Maxomys whiteheadi* was capable of returning from a 210 m translocation within 24 hours. Nevertheless, we note that this method provides a conservative estimate of the frequency
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of road crossing for two reasons: (1) individuals may have crossed after we had completed our trapping; and (2) individuals may have crossed but not been recaptured.

ANALYSIS — We conducted all analyses using package lme4 (Bates et al. 2015) in R v. 3.2.1 (R Core Team 2015). To evaluate whether distance from the road edge has an effect on rat occupancy (presence-absence, excluding recaptured individuals), we fitted binomial generalized linear mixed-effects models (GLMMs) with the logit link function. We tested whether the binary response variable of occupancy was predicted by the fixed effects of edge-to-interior distance; treatment (road versus control); age class (sub-adult or adult); sex; and two-way interactions between treatment and distance, age and sex. We included trap night nested within site as random effects to control for potential sources of variability. We fitted one model for all species combined, and then separate models for the two most common species: the forest specialist Maxomys surifer, and the habitat generalist M. whiteheadi. As we were interested in examining relative changes in occupancy along ecological gradients rather than expressly quantifying absolute occupancy at any given site, we did not control for detectability (Banks-Leite et al. 2014).

To evaluate which factors influence the probability of rats crossing roads, we fitted a binomial GLMM with a binary response variable representing whether or not the translocated individuals were successfully recaptured. We tested whether road crossing events were influenced by the fixed effects of treatment (road versus control), sex, age and their respective two-way interactions with treatment. We included three random effects in the model: release point (distance from the opposite road edge) and trap nights nested within sites. Again, we fitted the
model to all species combined, and then fitted separate models to *Maxomys surifer* and *M. whiteheadi*.

To assess the significance of fixed effects, likelihood ratio tests were used to compare the fit of models that included the fixed effects and interactions against simplified or null models that omitted those fixed effects.

**RESULTS**

In total, we captured 216 individuals in 3024 trap-nights: 142 individuals from the four road sites and 74 individuals from the three logged forest control sites. We recorded eight rat species, seven of which were found in both treatments, the exception being the Brown Spiny Rat (*Maxomys rajah*) for which just a single individual was captured at a road site. The Whitehead’s Rat (*Maxomys whiteheadi*) (n = 105) and Red Spiny Rat (*Maxomys surifer*) (n = 48) were the most commonly captured species.

**Occupancy** — There was no difference in the total rat occupancy between the road and control site treatments ($\chi^2 = 1.19$, df = 6, $P = 0.98$). We also detected no significant changes in occupancy with distance from the edge ($\chi^2 = 1.03$, df = 6, $P = 0.98$) and no interaction effect between treatment and distance ($\chi^2 = 0.69$, df = 7, $P = 0.99$; Fig. 2A) (Table S2). The sex ($\chi^2 = 0.98$, df = 4, $P = 0.91$) and age ($\chi^2 = 0.37$, df = 4, $P = 0.96$) of the rats were also found to have no significant effect on rat occupancy (Table S2). Similarly, the interaction between treatment-sex ($\chi^2 = 0.56$, df = 5, $P = 0.99$) and treatment-age ($\chi^2 = 0.19$, df = 5, $P = 0.99$) were also not significant (Table S2).
At the species level, treatment ($\chi^2 = 1.26$, df = 4, $P = 0.87$), distance ($\chi^2 = 1.12$, df = 2, $P = 0.57$) and their interaction ($\chi^2 = 0.09$, df = 1, $P = 0.76$; Fig 2B) was not significant on rat occupancy for the generalist species, *M. whiteheadi* (Table S3). There was also no significant effect of sex ($\chi^2 = 0.87$, df = 2, $P = 0.65$), age ($\chi^2 = 4.8$, df = 2, $P = 0.79$), the interaction between treatment and sex ($\chi^2 = 0.46$, df = 1, $P = 0.50$) or between treatment and age ($\chi^2 = 0.11$, df = 1, $P = 0.74$) on *M. whiteheadi* occupancy (Table S3). A similar trend was observed in the occupancy of the specialist species, *M. surifer*, with no significant effects of treatment ($\chi^2 = 7.71$, df = 4, $P = 0.10$), distance ($\chi^2 = 1.89$, df = 2, $P = 0.39$) and their interaction ($\chi^2 = 0.62$, df = 1, $P = 0.43$; Fig. 2C) (Table S4), although no individuals of the latter species were caught immediately adjacent to road edges (0 m). There was also no significant effect of sex ($\chi^2 = 8.62$, df = 2, $P = 0.13$), age ($\chi^2 = 4.29$, df = 2, $P = 0.12$), the interaction between treatment and sex ($\chi^2 = 0.004$, df = 1, $P = 0.95$) or between treatment and age ($\chi^2 = 0.73$, df = 1, $P = 0.39$) on *M. surifer* occupancy (Table S4).

**TRANSLLOCATION** — In total, 165 individuals were translocated, of which 73 individuals were recaptured. We translocated 105 individuals across roads and 60 within the control logged forest sites. Out of these, 48 percent (n=50) of the individuals returned when translocated across the road, while 38 percent (n=23) of the individuals returned when translocated in the control sites. The probability of rats (all individuals) being recaptured did not significantly differ between treatments ($\chi^2 = 3.25$, df = 2, $P = 0.20$; Fig. 3A; Table S5). The recapture probability following translocation was significantly higher for sub-adults than for adults ($\chi^2 = 6.32$, df = 2, $P < 0.05$; Fig. 3B) but did not differ between males and females ($\chi^2 = 4.66$, df = 2, $P = 0.09$) (Table S5).

There were also no significant treatment-age interaction ($\chi^2 = 2.15$, df = 1, $P = 0.14$) or treatment-sex interaction ($\chi^2 = 2.62$, df = 1, $P = 0.27$) (Table S5). At species level, we did not detect any significant differences between treatments on the recapture probability of *Maxomys*...
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whiteheadi ($\chi^2 = 5.15$, df = 3, $P = 0.16$; Fig. 3C), on the age ($\chi^2 = 3.65$, df = 2, $P = 0.16$) or sex ($\chi^2 = 4.54$, df = 2, $P = 0.10$) of individuals, with no significant interactions between treatment and age ($\chi^2 = 3.46$, df = 1, $P = 0.06$) or between treatment and sex ($\chi^2 = 0.01$, df = 1, $P = 0.93$) (Table S6). The same was observed for Maxomys surifer, with no difference in recapture probability between treatments ($\chi^2 = 2.31$, df = 3, $P = 0.51$; Fig. 3D), the age ($\chi^2 = 0.46$, df = 2, $P = 0.59$) or sex ($\chi^2 = 0.09$, df = 2, $P = 0.95$) (Table S7). The interaction between treatment and sex ($\chi^2 = 0.04$, df = 1, $P = 0.85$) and between treatment and age ($\chi^2 = 0.22$, df = 1, $P = 0.64$) were also not significant (Table S7).

DISCUSSION

We found no effect of small, unpaved logging roads on the occupancy or movement behavior of rats, indicating such roads have no discernable impact on the dynamics of understory murid populations in heavily logged tropical forests of Borneo. This is contrary to our hypothesis, and represents welcome news from a conservation perspective given the ecological importance of this group and the widespread distribution of logging road networks. Nevertheless, we make no inference about the potential impact of the larger, wider paved roads constructed during the logging process. We also emphasize that rodent communities in heavily-logged forests may experience consistent, landscape-wide dispersal limitation (Isabirye-Basuta & Kasenene 1987; Struhsaker 1997).
Our results suggest that roads do not influence rat occupancy across the road edge-to-forest interior gradient, and do not support our hypothesis of lower occupancy closer to edges than at forest interior sites. While these results contradict the patterns of reduced abundance at edges reported by Goosem (2000) and Wolf & Batzli (2002), our results are not unique. Several other studies did not detect altered occupancy patterns across an edge gradient for a range of small mammal species (e.g. Desert Woodrats *Neotoma lepida*, Bissonette & Rosa 2009; Cozumel Harvest Mice *Reithrodonomys spectabilis*, Fuentes-Montemayor *et al.* 2009; and White-footed Mice *Peromyscus leucopus*, McGregor *et al.* 2008).

Road edges may not affect rat occupancy for several reasons. First, the dense undergrowth dominated by pioneer plant species such as ferns (particularly *Dicranopteris linearis*) and ginger (*Zingiberaceae* spp.), and the abundance of coarse woody debris (logs and fallen branches) from logging operations may provide adequate shade, protection from predators, and fulfill foraging niche requirements for small, terrestrial murids (Cusack *et al.* 2015; Loveridge *et al.* 2016; Yamada *et al.* 2016). Second, regenerating vegetation along road edges may be a resource-rich environment, supplying rats with an abundance of seedling and invertebrate food (Fahrig & Rytwinski 2009; Fuentes-Montemayor *et al.* 2009; Wilder & Meikle 2006). Third, as nocturnal endotherms with greater capacity to thermoregulate (Yasuda & Miura 2000), rats may be less sensitive than other taxa such as frogs or leaf litter invertebrates to altered microclimatic conditions at road edges (Delgado *et al.* 2013; Wells *et al.* 2007). Lastly, our study area has been subjected to repeated heavy logging, creating a heterogeneous, patchy forest structure with many canopy gaps throughout the landscape (Pfeifer *et al.* 2016). Together, roads and logging canopy gaps may lead to widespread, additive edge effects and dispersal limitation across the study area (Isabirye-Basuta & Kasenene 1987; Struhsaker 1997). If this is the case, the roads we studied
may not significantly impede movement or exert additional edge effects beyond those found in
the wider landscape, including in our control sites. Nevertheless, all captured species persist at
increased abundances in our study area than they do in nearby primary forest (Chapman et al.
2018; Wearn et al. 2017), suggesting that any such broad-scale dispersal limitation, if it occurs,
has limited impact on local population sizes.

Modelling all species combined, we found no differences between male and female murids in
their patterns of occupancy or road-crossing behaviour, echoing the findings of previous studies
(e.g. Fuentes-Montemayor et al. 2009; Kozakiewicz 1993). Similarly, we also found no sex
specific road impacts on either the generalist or habitat specialist murid species in our study.
Bornean small mammals probably form monogamous pairs and may have relatively minor
differences in parental investment between sexes (Nakagawa et al. 2007), so it is possible that
sex has minimal impact on patterns of habitat selection and risk-taking behaviour. This
interpretation is consistent with our results, but is limited by the small number of species that we
examined and should not be generalized to the wider murid community.

In this study, we found no evidence to support our prediction that the forest specialist *M. surifer*
avoided road edges, although our results support the hypothesis that the generalist *M. whiteheadi*
is found throughout the gradient. Although *M. surifer* is a forest interior species, Wells et al. (2008)
found that it was also common in logged forests. Our results appear to contradict the findings of
Cusack et al. (2015), who suggested that *M. surifer* avoids even natural forest gaps, although we
note that we captured no *M. surifer* immediately adjacent (0 m distance) to roads, perhaps
suggesting that edge avoidance occurs only at scales less than the 30 m spatial grain of our
sampling design.
This study represents one of only a handful to examine small mammal movement across narrow, unpaved tropical forest logging roads. As with many small mammal studies, catching sufficient individuals to obtain robust sample sizes represents a limiting factor. The study area was affected by an El Niño Southern Oscillation (ENSO) event with a prolonged dry period during our study, which may have caused a decline in rat populations (Nakagawa et al. 2007) and was potentially reflected in a lower than usual catch rate for this study area (cf. Chapman et al. 2018; Cusack et al. 2015). Nonetheless, our sample size (n = 165 translocated individuals) remains considerably larger than previous studies which did find significant inhibition of small mammal movement: Goosem (2002) (Rattus spp., n = 110, P < 0.001, Cohen’s d = 0.50) and McGregor et al. (2008) (n = 91, P < 0.05, Cohen’s d = 0.50) on narrow, dirt roads and wide, paved roads respectively. Overall, therefore, we suggest that our sample size was adequate to detect any similar effects if present.

Our translocation results indicated that movement of rats was uninhibited by small logging roads, with translocated individuals recaptured at the same rate at road and control sites. These results contradict the findings of McGregor et al. (2008), but although that study examined roads of a similar width (6-14 m), all roads were paved. Our results are consistent with other studies that suggested small mammals are more likely to cross unpaved, narrow (<20 m wide) roads than wider, paved roads (Burnett 1992; Goosem 2000; Jaeger et al. 2005; Mader 1984; Oxley et al. 1974; Peter et al. 2013; Rico et al. 2007). Narrow roads are more likely to have a higher density of canopy coverage from adjacent tall trees (Goosem 2001; Laurance et al. 2009), providing enhanced shade during the day and reducing visibility (and thus predation risk) on moonlit nights (Goosem 2002).
We recaptured a higher proportion of sub-adult rats than adult rats following translocation, at both the road and control sites. The higher frequency of sub-adults returning may possibly be explained by their competitive inability to exploit novel habitat areas, as adult rats defend established home ranges, displacing newly-arrived sub-adults and forcing them to return to their point of origin (Fuentes-Montemayor et al. 2009; McLaren et al. 2011; Nakagawa et al. 2007). Sub-adult rats of both sexes may be more willing to take risks such as crossing roads than adults as they have a strong need to disperse and establish territories in vacant areas (Burnett 1992; Van Dyck & Baguette, 2005). Conversely, adults tend to be inherently more risk-averse through learned behaviour and experience (Prevedello et al. 2010). However, further work is required to separate these hypotheses, in particular to understand how risk perception varies with age class and life history.

In summary, we found little evidence that forest rats in Bornean logged forests avoid road edge habitats. Indeed, this functionally important group can exploit most of the forest area in heavily logged forest landscapes, and are not restricted in mobility by the presence of small, unpaved logging roads. This contrasts with strong edge avoidance behavior and dispersal limitation found by previous studies of other taxa, and underlines the high resilience of small mammals to logging (Chapman et al. 2018; Wearn et al. 2017). By 2050, it is projected that 25 million kilometers of new roads will be built in developing nations, where most tropical rainforests are located (Laurance et al. 2009). As the large-scale construction of wildlife crossing passages or other mitigation measures are not a financially viable option in many countries, our results represent a positive outcome for biodiversity conservation in heavily logged tropical rainforests.
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DATA AVAILABILITY STATEMENT

Data used in this paper are freely available from the SAFE Project website (https://www.safeproject.net/datasets/view_dataset?id=25; DOI: 10.5281/zenodo.1198569).

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FIGURE CAPTIONS
FIGURE 1. (A) The sampled sites and network of logging roads that was present in the 1990s (obtained from Gaveau et al. (2014)). Inset shows the location of the study area in Sabah, Malaysia. (B) An example of a narrow, unpaved logging road site examined in the study area.

FIGURE 2. Mean probability ($\pm$ S.E) of rat occupancy across road edge-to-forest interior gradients (dark shading) in comparison to rat occupancy in logged forest control sites (light shading) for (A) all individuals, (B) *Maxomys whiteheadi* and (C) *Maxomys surifer*.

FIGURE 3. Mean probability of rats ($\pm$ S.E) returning from translocation in road (dark shading) versus logged forest control sites (light shading) for (A) all translocated individuals, (B) by age class, (C) *Maxomys whiteheadi* and (D) *Maxomys surifer*. 
SUPPLEMENTARY INFORMATION

TABLE S1. Information on the sampling sites in the Kalabakan Forest Reserve, Sabah.

TABLE S2. Effects of treatment (roads versus control), distance, their interaction (treatment-distance), age, sex, the interaction of treatment-age and treatment-sex on the probability of rat occupancy.

TABLE S3. Effects of treatment (roads versus control), distance, age, sex and the interactions: treatment-distance, treatment-age and treatment-sex on the probability of occupancy for *Maxomys whiteheadi*.

TABLE S4. Effects of treatment (roads versus control), distance, age, sex and the interactions: treatment-distance, treatment-age and treatment-sex on the probability of occupancy for *Maxomys surifer*.

TABLE S5. The effects of treatment (road versus control), age, sex, the interactions of treatment-age and treatment-sex on the probability of rats returning following translocation. Significant effects are highlighted in bold.
TABLE S6. The effects of treatment, age, sex and the interaction of treatment-age and treatment-sex and on the probability of *Maxomys whiteheadi* returning from translocation.

TABLE S7. The effects of treatment, age, sex, interaction of treatment-age and treatment-sex on the probability of *Maxomys surifer* returning from translocation.
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A. All individuals

B. M. whiteheadi

C. M. surifer
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A. All translocated individuals

B. Age class

C. M. whiteheadi

D. M. surifer