Kent Academic Repository

**Harris, Arianne, Hallett, Mathew T, Davis, Micah, Carter, Martin, Singh, Dwarka, Roopsind, Anand, Maharaj, Gyanpriya and Bicknell, Jake E. (2023)** ***Use of logging roads by terrestrial mammals in a responsibly managed neotropical rainforest in Guyana.*** **Forest Ecology and Management, 548 . ISSN 0378-1127.**

## Downloaded from
https://kar.kent.ac.uk/103014/ The University of Kent's Academic Repository KAR

## The version of record is available from
https://doi.org/10.1016/j.foreco.2023.121401

## This document version
Publisher pdf

## DOI for this version

## Licence for this version
UNSPECIFIED

## Additional information

## Versions of research works

### Versions of Record
If this version is the version of record, it is the same as the published version available on the publisher's web site. Cite as the published version.

### Author Accepted Manuscripts
If this document is identified as the Author Accepted Manuscript it is the version after peer review but before type setting, copy editing or publisher branding. Cite as Surname, Initial. (Year) 'Title of article'. To be published in ***Title of Journal*** , Volume and issue numbers [peer-reviewed accepted version]. Available at: DOI or URL (Accessed: date).

## Enquiries
If you have questions about this document contact ResearchSupport@kent.ac.uk. Please include the URL of the record in KAR. If you believe that your, or a third party's rights have been compromised through this document please see our Take Down policy (available from https://www.kent.ac.uk/guides/kar-the-kent-academic-repository#policies).

Forest Ecology and Management 548 (2023) 121401

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

# Use of logging roads by terrestrial mammals in a responsibly managed neotropical rainforest in Guyana

Arianne E. Harris[a,b,*], Matthew T. Hallett[c,d], Micah Davis[b], Martin Carter[b], Dwarka Singh[b], Anand Roopsind[e], Gyanpriya Maharaj[a], Jake E. Bicknell[f]

[a] *School of Graduate Studies and Research, University of Guyana, Turkeyen, Guyana*
[b] *Iwokrama International Centre for Rainforest Conservation and Development, Guyana*
[c] *Department of Wildlife Ecology & Conservation, University of Florida, Gainesville, United States*
[d] *Conservation Department, Jacksonville Zoo & Gardens, Jacksonville, United States*
[e] *Conservation International, Arlington, United States*
[f] *Durrell Institute of Conservation and Ecology (DICE), University of Kent, Canterbury, CT NR, UK*

ARTICLE INFO

*Keywords:*
Occupancy
Reduced-impact logging
Camera trap
Hunting
Management

ABSTRACT

Selective logging is the most widespread use of tropical forests. Building logging roads facilitates access to previously remote rainforests, and so proper management is essential for ensuring biodiversity retention in logged landscapes. Terrestrial mammals often directly use logging roads (via movement corridors, hunting or foraging), making them vulnerable to poorly managed roads. Here we explore how the presence, arrangement and use of logging roads influence terrestrial mammal occupancy and detection within a Forest Stewardship Council (FSC) certified logged forest in Guyana. We compared camera trap data from20 natural 'game' trails in an unlogged area, with camera trap data from 23 sites set near to or on logging roads within the Iwokrama forest. Our findings showed high occupancy within logged areas with no statistically significant difference to unlogged areas. Higher detections were noted along secondary and feeder roads compared to skid trails and the natural trails in control areas. Additionally, our data showed a negative correlation between occupancy and distance to village for a scatter hoarding rodent, most likely driven by subsistence hunting by local communities. Our results indicate that proper road management geared towards the monitoring and guarded access of logging roads, can have a positive effect on terrestrial mammal occurrence within responsibly managed rainforests.

## 1. Introduction

Logging is one of the most widespread drivers of land-use change in biodiverse and carbon- rich tropical forests such as South American rainforests (Asner et al., 2004; Wright, 2010). To reduce potential negative impacts, the promotion of sustainable logging has resulted in improved logging practices that can minimize rainforest damage and wildlife loss (Boltz et al., 2003; Medjibe & Putz, 2012). Terrestrial mammals play an essential role in maintaining mammal communities in selective logged and natural rainforests, with critical ecosystem services provided through species-specific seed dispersal (Carvalho Jr et al., 2021; Gardner et al., 2019; Stoner et al., 2007) and therefore the recruitment of some important timber trees (Brewer & Rejmánek, 1999; Camargo-Sanabria et al., 2015) as well as rich and diverse understory vegetation (Forget et al., 2001). Additionally, through acts of predation, large mammal predators help maintain populations of prey species by mitigating their herbivory pressure on seedlings, further helping to promote rainforest regeneration (Boltz et al., 2003; Medjibe & Putz, 2012). Among the issues inherent of all logging activities, is the prevalence of unguarded or poorly managed logging roads and their ability to increase access to forest interiors to facilitate deforestation, and hunting for wild meat (Bicknell et al., 2015; Corlett, 2007; Laurance et al., 2008; Pangau-Adam et al., 2012; Rosin, 2014).

Wild meat accounts for over 50% of the protein source for tropical rainforest inhabitants (Robinson & Bennett, 2004), with non-legalized commercial hunting generating monthly incomes of approximately US300 dollars in the Brazilian amazon region alone (Chaves Baía Júnior et al., 2010). Further, in non-certified forestry concessions, wild meat constitutes part of the diet of logging workers temporarily residing in the area (Bennett & Robinson, 2000; Robinson et al., 1999), resulting in

---

[*] Corresponding author at: School of Graduate Studies and Research, University of Guyana, Guyana.
*E-mail address:* arianne-elise.harris@my.uog.edu.gy (A.E. Harris).

https://doi.org/10.1016/j.foreco.2023.121401
Received 23 June 2023; Received in revised form 31 August 2023; Accepted 1 September 2023

additional pressure on game species regardless of whether the logging is sustainable or not. As a result of rising demand, wild meat hunting compounds the effects of logging activities and often results in lower densities, or local extinction of preferred species (Malhi et al., 2014). In addition to hunting via logging roads, there is the issue of unregulated management of logging roads whereby no clear guidelines exist to reduce vehicular activity and habitat loss introduced through unsupervised logging road use. The approach to construction and management of logging roads in selectively logged rainforests is at the discretion of the forest managers and governments in charge of the logging concessions (Kleinschroth & Healey, 2017; Lindenmayer et al., 2006; Putz et al., 2000). As such, each selectively logged rainforest may vary in limitations placed on road length and level of activity as well as the maximum number of logging roads allowed, crucially, whether they are closed between logging cycles (Bicknell et al. 2015). Management of logging roads impacts forest fragmentation, proliferation of swidden agriculture and soil nutrient changes (Kleinschroth et al., 2017; Sidle et al., 2004). These factors may work in conjunction with hunting to deter terrestrial mammals from these logged habitats thus reducing terrestrial mammal occurrence in selectively logged rainforests, thus hindering regeneration.

Of the more benign methods of selective logging is Reduced-impact logging (RIL) which is designed as a low-impact logging practice that involves, among others, careful logging road planning that requires logging roads of specified widths, minimized skidding distances and avoidance of streams and rivers as well as mandatory road closure following logging cessation. The overall objective of RIL is to minimize disturbance from timber harvesting (Keller & Berry, 2007; Pinard et al., 1995). Studies have reported little to no negative effects of harvesting using RIL on terrestrial mammal diversity and richness (Alveira et al., 2023; Azevedo-Ramos et al., 2006; Bicknell & Peres, 2010; Tobler et al., 2018) due to post-harvest landscape recovery but few studies have tried to understand the role that the management of logging roads plays in this recovery (Griscom et al., 2019; Laufer et al., 2015; Scalbert et al., 2023; Yamada et al., 2014), leaving a gap in the literature. Third-party certification such as Forest Stewardship Council (FSC), give economic incentives to forest managers to comply to its management measures and regular audits encourage corrective action against unregulated road use. Furthermore, continued unsupervised road use following audits can result in the withdrawal of the FSC label. These measures can affect forest wildlife, particularly terrestrial mammals which make up a valuable portion of long distance seed dispersers, prey species and endangered species in tropical rainforests (Sollmann et al., 2017; Tobler et al., 2018). Regulated road use can include (but is not limited to) gated entrances and exits in and out of logging concessions and an upper limit on the number of permanent roads allowed. In most RIL rainforests, logging roads either become permanent roads for transportation in and out of logging concessions, are maintained for monitoring and research for future harvesting, or they are abandoned after logging stops (Kleinschroth & Healey, 2017). This contributes to the narrative of well managed logged forests becoming important conservation sites for mammals (Meijaard & Sheil, 2007; Struebig et al., 2013), though it's conservation value may not be similar to primary forests (Gibson et al., 2011).

Contemporary research utilizing camera trapping has revealed that medium-large mammal occupancy in low-impact, selectively logged rainforests can be positively correlated with logging (Costa & Magnusson, 2003) if harvest intensity remains low and logging roads are closed after harvesting stops. However, logging roads can make mammals easier to detect, potentially inflating detectability and therefore some estimates of occupancy. For example, detection probabilities of medium to large mammals in RIL rainforests in Peru and Guatemala, were higher on active roads compared to old roads, and were lower off road (Tobler et al., 2018). Although this indicates that standard spacing and placement of camera traps in logged rainforests can offer better insight into terrestrial mammal movements, camera trap placement has no effect on occupancy (Fonteyn et al., 2021). Furthermore, studies from Guyana in a forest that operates RIL, found that large mammal communities were not greatly affected by logging operations (Bicknell & Peres, 2010), however there did exist a negative correlation between mammal occupancy and subsistence hunting within the same area (Roopsind et al., 2017). Subsistence hunting by indigenous people is recognized as an acceptable form of wildmeat consumption and is given socio-economic distinctions and legal protection under the "Amerindian Act" of Guyana (Van Vliet et al., 2019). Wildmeat/ traditional diets make up a small but important aspect of indigenous culture and socio-economic systems in Central and South America (Fragoso et al., 2016; Silvius et al., 2004). The presence of possible anthropogenic pressures outside of hunting in Iwokrama's logged rainforest may imply that the persistence of hunting (even in a certified RIL rainforest) still remains a concern for terrestrial mammal conservation in logged rainforests.

The question of whether sampling along logging roads inflate detections of mammals may, vary according to the type (i.e. primary logging roads, secondary logging roads or 'skid trails') or level of activity (closed or open roads) of logging roads, as well as how prevalent anthropogenic disturbances outside of logging (i.e hunting) is within the logged rainforest. Although logging road construction is a decision that lies with forest managers, little is done in practice to ensure biodiversity conservation of tropical, logged forest (Sheil & Van Heist, 2000). Thus, certified RIL operations that place greater restrictions on logging roads may positively influence how terrestrial mammals occupy rainforests by controlling how often terrestrial mammals utilize logging roads during and after logging, as well as ensuring medium-large mammal densities remain stable by limiting the amount of hunting. This leaves RIL-forest management in a stronger position to inform long-term sustainability whilst also showing the efficacy of guarded, certified RIL rainforests (Bicknell & Peres, 2010; Brodie et al., 2015; Keller & Berry, 2007; Kleinschroth & Healey, 2017; Roopsind et al., 2017; Yamada et al., 2014).

In this study, we assessed terrestrial mammal occupancy varies in response to the effects of different types of logging roads (based on size/ frequency of use of roads), status (open vs. closed), their summed length within a given buffer, as well as their proximity to an indigenous community in an FSC certified forestry concession located in the Iwokrama rainforest in central Guyana, South America. This area operates a strict system of closing logging roads after a management unit is harvested - a recommendation of FSC certification that is not always implemented. We applied hierarchical, multi-species occupancy models whilst accounting for imperfect detection (Royle et al., 2009) to estimate richness and community occupancy in response to logging roads. We report findings at the community level which includes notable lowland, neotropical mammal species found in logging areas such as peccaries (Tayassidae), lowland tapir (*Tapiris terrestris*), and brocket deer (*Mazama* sp.*)*, as well as large predators such as the jaguar (*Panthera onca)* and puma (*Puma concolor*).

## 2. Method and analysis

### 2.1. Study area

We conducted data collection on the terrestrial mammal community within the Iwokrama Forest (4.5°N, 59°W), managed by the Iwokrama International Centre for Rainforest Conservation & Development (hereafter 'Iwokrama'), in Region 8, central Guyana, South America. Iwokrama is a 371,681 ha, primarily lowland terra firme tropical rainforest that is divided into a sustainable utilization area (SUA: 184,506 ha) and a wilderness preserve (WP: 187,175 ha). Reduced-Impact logging (RIL) and ecotourism are allowed in the SUA, whereas only scientific research and biodiversity conservation are allowed in the WP. Hunting using traditional methods exclusively for subsistence purposes is allowed throughout the reserve only for residents of indigenous Makushi communities within and neighboring Iwokrama.

RIL in Iwokrama's SUA employs 60-year polycyclic, silvicultural harvesting of approximately 20 Neotropical tree species. Iwokrama's RIL operation involves, directional felling of target trees (minimum > 40 cm diameter) and removal of linked vines to avoid connected trees being pulled down along with harvested trees. Mean logging intensity in the Iwokrama rainforest is 3.2 trees ha$^{-1}$, representing 6.3% of trees above 40 cm diameter harvested on average (Bicknell et al., 2014). Timber operations are certified under the Forest Stewardship Council (FSC). Forest management includes a comprehensive pre-harvest inventory, planning, and pre-determination of logging road and skid trail length and width to allow access to harvest blocks while reducing the impact on the forest. "Logging roads" in this study were defined as any road constructed, used and maintained by the logging operators within Iwokrama and further categorized as either secondary roads, feeder roads, or skid trails. Secondary roads are connective, dirt roads built for logging equipment and vehicle access to harvest blocks from a primary road (Fig. 1). Feeder roads are extensions of secondary roads that "feed" extracted logs to loggers for transport out of the harvest blocks. Skid trails are narrow trails that connect to feeder roads and are used by skidders to retrieve felled logs from the felling site. The Georgetown-Lethem highway also passes through the study area but was not included in the study as logging is not the main purpose of the highway (Fig. 1). Feeder road and skid trails in Iwokrama remain open until logging in the harvest block they access has been completed. The duration of time these roads are left open is dependent on the logging duration, which is typically between a few weeks to one year (pers. comm, Iwokrama International Centre). Secondary roads in Iwokrama remain open for several years as they are designed to access multiple harvest blocks and connect to the primary road for travel and shipment (pers. comm, Iwokrama International Centre). All logging roads in Iwokrama are carefully planned to not dissect any creeks or streams and secondary roads end at the Burro-Burro river (Fig. 2). As such, road structuring in Iwokrama follows this hierarchy of activity: Primary > Secondary > Feeder > Skid trail.

### 2.2. Camera-trap surveys

Camera-trap surveys were conducted from June 2015 – June 2017. A total of 43 camera traps (Bushnell Trophy Cam #119447C, #119734C, #119736C, and #119837C; Bushnell®, KS, USA) were set within Iwokrama's SUA and WP zones to allow for comparisons between logged and unlogged areas (Fig. 1). Camera-trap locations outside of the SUA's logged area served as our control for the impact of RIL logging roads on terrestrial mammals. Control sites were chosen based on whether they were unlogged and had no existing logging roads. In these control sites, ten (10) camera traps were set at each location (20 total), predominantly along trails that appeared to be used by medium-large mammals (hereafter 'natural trails'). Within the SUA, 23 camera traps were set and periodically removed due to logging activity in nearby harvest blocks. To reduce possible disruptions from logging road activities in neighboring harvest blocks, cameras in the SUA did not follow a uniform placement and were set 2–3 km apart when possible, along, skid trails, secondary roads, and feeder logging roads. To maintain consistency, cameras in the control sites were set the same distance apart along game trails (Fig. 2). Cameras were not baited and were positioned at points of observed animal activity in an effort to increase likelihood of detection (Hallett et al, 2019). Each camera was fastened and stabilized to trees at a height of 40 cm and oriented to maximize capture range. Cameras used were equipped with passive infrared flash with a 1 s delay between photos and stored images in a 3-image sequence. Mammals captured between 30 min durations were deemed independent events (Burton et al., 2015).

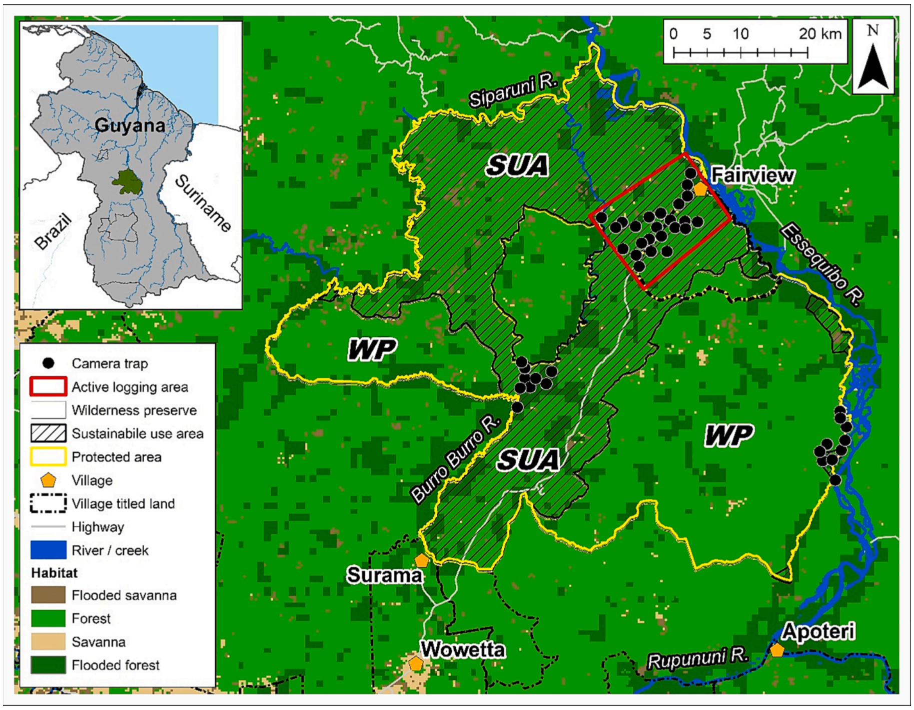

**Fig. 1.** Camera trap locations in Iwokrama's Sustainable Use Area (SUA) and Wilderness Preserve (WP). "Surama", "Wowetta" and "Apoteri" represent villages located outside of the Iwokrama protected area. "Fairview" represents the only indigenous village located within the Iwokrama protected area.

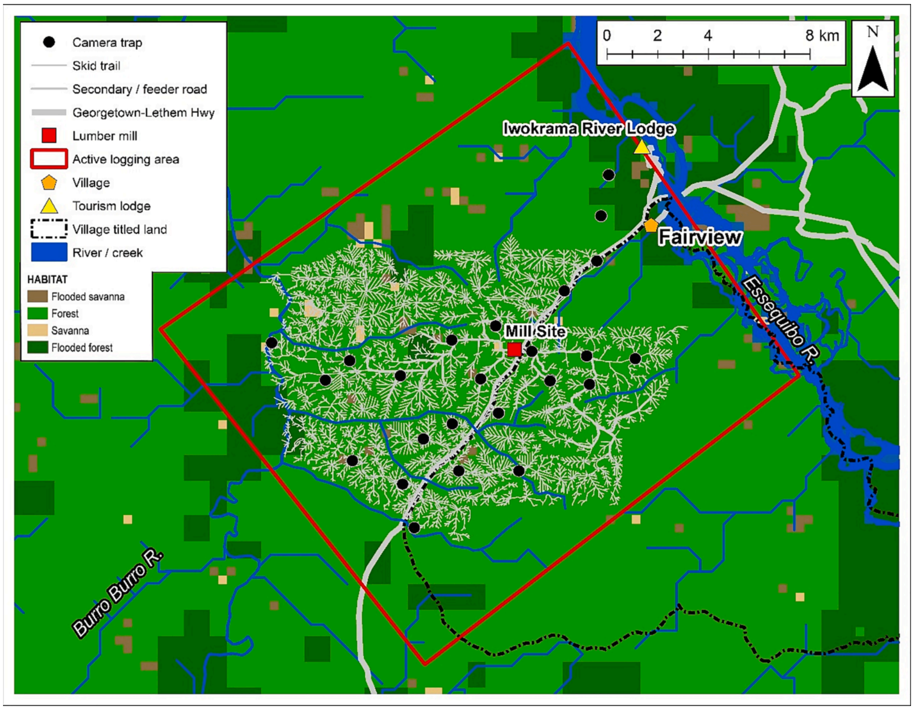

**Fig. 2.** Location of camera traps along logging road network within Iwokrama's active logging area. 'Millsite' represents the central logging mill. 'Fairview' represents the only indigenous village located within the Iwokrama protected area.

## 2.3. Data analysis

We employed Bayesian, multi-species, hierarchical occupancy analyses to model the relationship of occupancy against parameters of interest (Dorazio et al., 2006; Hallett et al., 2019). Multi-species occupancy modelling or community occupancy modelling, can be defined as studies focusing on state variable species richness in response to an environmental disturbance (MacKenzie et al., 2018). State variable species richness is defined as the sum of species found within a given area(MacKenzie et al., 2018). Due to camera failures, removal of cameras from active logging areas, and extended sampling at some sites, each camera had different start and end times over the 2-year period. To address this, we first categorized survey dates according to Guyana's wet (May-June, November- January) and dry seasons (February – April, October- November). Trapping effort was then standardized to 40 trap nights per season, thus fulfilling the closed season assumption (MacKenzie et al., 2002). Detection probability was then calculated based on consistent detection per species across all survey sites. Both species-level and community-level detection probability followed a Bernoulli distribution and were recorded as a binary response variable (1 = observed, 0 = not observed) per camera trap location. Independent events were calculated on binary detection of a species following a 30–60-minute interval. Number of images representing independent events of capture per species was compiled using r package CamTrap R (Niedballa et al., 2016)in R studio (R version 4.1.3, RStudio Team, 2020).

We removed all reptile and bird species to allow for analysis on mainly terrestrial mammal species, but also included one semi-arboreal and two arboreal mammals as well. Models were run using Markov chain Monte Carlo estimations in the r package JAGS (Just Another Gibbs Sampler; Kellner, 2019) in R studio (R version 4.1.3, RStudio Team, 2020). We used uniform, uninformative priors and ran each model in four chains of 6,000 iterations with a burn in of 1,000 samples.

Categorical variables used in this study were logged vs. control sites as well as two logging road status variables (open vs closed) and four road/trail types (secondary, feeder, skid trail, or natural trail). For analysis, buffers were placed around each camera trap at four levels to represent local (100 m and 200 m) and landscape (500 m and 1000 m) impacts of total road length in order to assess predictors of large mammal community occupancy. Our trial models found that 200 m local and 500 m landscape level buffers were zero at the community occupancy level, with non-overlapping, null credibility intervals. Therefore, we report findings utilizing 100 m and 1000 m buffers only. To assess community response to logging road presence, we measured the total length (in meters), of all roads within a given buffer and named this variable "total road length".

Lastly, to account for the effect of anthropogenic pressures on occupancy that are outside of logging and inclusive of hunting pressure, we modelled the Euclidean distance of each camera trap in both logged and control sites to the nearest village and named it "distance to village". All variables used in this study were spatially estimated in QGIS (QGIS version 3.24.3), with Iwokrama providing information on logging road type and status. Model checking and interpretation was done through the posterior distribution via visual checks of convergence from trace plots. Model covariates that lie within the 95% Bayesian credibility intervals (CrI) are considered statistically relevant explanations of community occupancy and detection (Dorazio, 2016). In an effort to standardize sampling effort across all sites and land use types, we analyzed data for 40 trap nights per location, keeping sampling season consistent.

We undertook two models (‘Model1′ & ‘Model2′). Model1 assessed community level occupancy against potential covariates (logging road status, logging road type, total road length and distance to village). Model2 also assessed community level occupancy against all covariates, but additionally detection probability at the community and species levels against road type and road status. We undertook Model2 to explore the potential effect of detection probability being higher in logged sites due to the logging roads – as literature has shown that terrestrial mammals do not avoid logging roads and may be more easily detected as such (Scalbert et al. 2023). Effort was accounted for in all models. Final model equations are provided below whereby $\psi$ = occupancy probability and $\alpha_{i,j}$ = detection probability of $i^{th}$ species at $j^{th}$ site. Detection probability and occupancy in control sites are represented as

$\alpha_0$ and $\beta_0$ respectively:

$$\text{Model1}: \text{logit}(\psi_{\text{community}}) = \alpha_0 + \beta_0 + \beta_1 * \text{ LOGGING STATUS} + \beta_2 * \text{DISTANCETOVILLAGE} + \beta_3 * \text{TOTALROADLENGTH} + \beta_4 * \text{ROADTYPE} + \beta_5 * \text{ROADSTATUS} + \alpha_{i,j} * \text{effort}$$

$$\text{Model2}: \text{logit}(\psi_{\text{community+species}}) = \alpha_0 + \beta_{\mathbf{0}} + \beta_1 * \text{LOGGING STATUS} + \beta_2 * \text{DISTANCETOVILLAGE} + \beta_3 * \text{TOTALROADLENGTH} + \beta 4 * \text{ROADTYPE} + \beta 5 * \text{ROADSTATUS} + \alpha_{i,j} * \text{ROADTYPE} + \alpha_{i,j} * \text{ROADSTATUS} + \alpha_{i,j} * \text{effort}$$

## 3. Results

A total of 9,456 images were recorded between 2015 and 2017 across 27,477 trap nights. Of the total images, 5,699 were mammals, 3,726 were birds and 31 were reptiles. Once birds and reptiles were removed and trap nights were standardized to 40 nights, 2,589 independent events representing 27 mammal species (24 terrestrial, 1 semi-arboreal and 2 arboreal) belonging to eight orders, were recorded over 1,720 trap nights (Table S1). Twenty-three species occurred in both logged and unlogged sites, with the brown capuchin (*Sapajus apella*) and long-nosed armadillo (*Dasypus kappleri*) recorded only in unlogged sites and the bush dog (*Speothos venaticus*) and mouse opossum (*Marmosa murina*) only recorded in logged sites. Species richness in the logged sites was highest for omnivores, frugivores, and carnivores whereas herbivore richness was higher in the control sites (Table 1).

### 3.1. Logging status and distance to nearest village

Logging status appeared to have no impact on occupancy. Community-level occupancy in logged sites was higher than in the control sites, with estimates varying between 1.3 and 2.6 individuals per species occurring within logged sites (Model1*:* $\beta_{\text{logged}} = 2.603$, CrI: −3.90, 7.53; Model2: $\beta_{\text{logged}} = 1.377$, CrI: −0.68, 3.42; Table S2 & S3), but there was not a statistically significant difference (Model1: $\beta_0$: 0.895, CrI: −1.12, 3.03; Model2: $\beta_0$: 0.696, CrI: −1.36, 2.60). Notable species that increased in occupancy in logged areas were the red-rumped agouti (*Dasyprocta leporina*) ($\beta_{\text{logged}} = 2.607$, CrI: −0.91, 6.35), the lowland Paca (*Cuniculus paca*) ($\beta_{\text{logged}} = 2.347$, CrI: −0.80, 5.76), lowland tapir (*Tapirus terrestris*) ($\beta_{\text{logged}} = 2.011$, CrI: −0.92, 4.93) and red-brocket deer (*Mazama americana*) ($\beta_{\text{logged}} = 1.244$, CrI: −1.11, 3.67), as well as all four carnivorous cats - Jaguar (*Panthera onca*): $\beta_{\text{logged}} = 3.109$, CrI: −0.30, 6.64; Puma (*Puma concolor*): $\beta_{\text{logged}} = 2.461$, CrI: −0.94, 6.15; Ocelot (*Leopardus pardalis*): $\beta_{\text{logged}} = 2.203$, CrI: −1.16, 5.79; Margay (*Leopardus wiedii*): $\beta_{\text{logged}} = 2.092$, CrI: −1.35, 5.77). No species showed a statistically significant increase in occupancy in logged areas compared to the control (Table S6).

When testing the relationship with distance to village, there was a non-significant (Model1*:* $\beta_{\text{village}}$: 0.013, CrI: −0.08, 0.11; Model2*:* $\beta_{\text{village}} = 0.016$, CrI: −0.07, 0.11; Fig. 3) increase in community-level occupancy as distance to village increased (Table S2 & S3). At the species

**Table 1**
Species recorded during the survey period 2015–2017 within the Iwokrama logged and unlogged zones *- Homo sapiens represent loggers, tour guides/tourists and hunters recorded during the survey period.

| Scientific name | Order | Common name | Feeding Guild | IUCN status | Detection probability (α0) | Naïve SE | Occupancy (β0) | Naïve SE2 |
|---|---|---|---|---|---|---|---|---|
| *Mazama americana* | Artiodactyla | Red-brocket deer | Herbivore | Data Deficient | −1.757 (±0.17) | 0.002 | 1.146 (±1.29) | 0.017 |
| *Pecari tajacu* | Artiodactyla | Collared peccary | Herbivore | Least Concern | −2.931 (±0.37) | 0.005 | 0.119 (±1.27) | 0.016 |
| *Mazama nemorivaga* | Artiodactyla | Brown-brocket deer | Herbivore | Least Concern | −2.349 (±0.37) | 0.005 | 0.894 (±1.35) | 0.017 |
| *Puma concolor* | Carnivora | Puma | Carnivore | Least Concern | −2.517 (±0.27) | 0.003 | 1.058 (±1.67) | 0.022 |
| *Eira barbara* | Carnivora | Tayra | Omnivore | Least Concern | −3.319 (±0.37) | 0.005 | 0.631 (±1.49) | 0.019 |
| *Leopardus pardalis* | Carnivora | Ocelot | Carnivore | Least Concern | −3.221 (±0.32) | 0.004 | 1.298 (±1.50) | 0.019 |
| *Herpailurus yagouaroundi* | Carnivora | Jaguarundi | Carnivore | Least Concern | −4.85 (±0.68) | 0.009 | 0.953 (±1.59) | 0.02 |
| *Nasua nasua* | Carnivora | Coati | Omnivore | Least Concern | −4.39 (±1.023) | 0.013 | 0.826 (±1.59) | 0.021 |
| *Leopardus wiedii* | Carnivora | Margay | Carnivore | Near threatened | −4.461 (±0.73) | 0.009 | 1.001 (±1.52) | 0.02 |
| *Speothos venaticus* | Carnivora | Bush dog | Carnivore | Near threatened | −4.712 (±1.38) | 0.018 | 0.575 (±1.51) | 0.02 |
| *Panthera onca* | Carnivora | Jaguar | Carnivore | Vulnerable | −2.123 (±0.39) | 0.005 | 0.723 (±1.51) | 0.019 |
| *Dasypus* sp. | Cingulata | Long-nosed armadillo sp. | – | – | −2.481 (±0.30) | 0.004 | 0.471 (±1.17) | 0.015 |
| *Priodontes maximus* | Cingulata | Giant armadillo | Insectivore | Vulnerable | −3.083 (0.72) | 0.009 | −0.006 (±1.33) | 0.017 |
| *Dasypus novemcinctus* | Cingulata | Nine-banded armadillo | Insectivore | Least Concern | −3.44 (±0.37) | 0.005 | 0.322 (±1.39) | 0.018 |
| *Dasypus kappleri* | Cingulata | Greater long-nosed armadillo | Frugivore/ Insectivore | Least Concern | −5.01 (±1.14) | 0.015 | 0.408 (±1.71) | 0.022 |
| *Didelphis marsupialis* | Didelphimorphia | Common opossum | Omnivore | Least Concern | −2.205 (±0.21) | 0.003 | 0.596 (±1.39) | 0.018 |
| *Philander opossum* | Didelphimorphia | Grey-four eyed opossum | Omnivore | Least Concern | −2.854 (±0.42) | 0.005 | 0.127 (±1.26) | 0.016 |
| *Marmosa murina* | Didelphimorphia | Mouse opossum | Insectivore | Least Concern | −3.944 (±1.077) | 0.014 | 0.637 (±1.44) | 0.019 |
| *Tapirus terrestris* | Perissodactyla | Lowland tapir | Herbivore | Vulnerable | −1.644 (±0.23) | 0.003 | 0.307 (±1.27) | 0.016 |
| *Myrmecophaga tridactyla* | Pilosa | Giant anteater | Insectivore | Vulnerable | −2.673 (±0.41) | 0.005 | 0.883 (±1.35) | 0.018 |
| *Tamandua tetradactyla* | Pilosa | Tamandua | Insectivore | Least Concern | −4.44 (±0.59) | 0.008 | 0.598 (±1.49) | 0.019 |
| *Cebus olivaceus* | Primates | Wedge-capped capuchin | Omnivore | Least Concern | −4.924 (±0.97) | 0.013 | 0.697 (±1.60) | 0.021 |
| *Sapajus apella* | Primates | Brown capuchin | Omnivore | Least Concern | −4.686 (±1.24) | 0.016 | 0.532 (±1.49) | 0.019 |
| *Homo sapien** | Primates | Human | Omnivore | Least Concern | −3.885 (±0.78) | 0.01 | 1.063 (±1.61) | 0.021 |
| *Cuniculus paca* | Rodentia | Lowland paca | Frugivore | Least Concern | −1.214 (±0.15) | 0.002 | 1.47 (±1.55) | 0.02 |
| *Rattus* sp. | Rodentia | Spiny rat sp. | Herbivore | – | −1.608 (±0.19) | 0.002 | 0.045 (±1.22) | 0.016 |
| *Dasyprocta leporina* | Rodentia | Red-rumped agouti | Frugivore/ Insectivore | Least Concern | −0.325 (±0.11) | 0.001 | 1.464 (±1.69) | 0.022 |

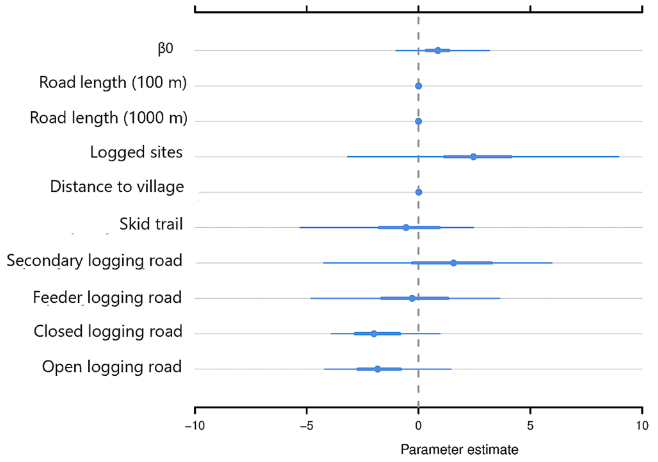

**Fig. 3.** MCMC intervals of parameter effects on community-level occupancy. “β0” = Occupancy probability in control sites.

level (Table S6) only the red-rumped agouti showed a statistically significant increase in occupancy further away from the nearest village ($\beta_{\text{village}}$ = 0.191, CrI: 0.00, 0.44). Referencing our posterior sample, distance to the nearest village showed a lower probability of influence on occupancy (61%) when compared to logging status (90%).

### 3.2. *Logging road type, status, and summed length*

Exploring associations with roads, community-level occupancy showed a non-significant decline closer to skid trails and feeder roads compared to secondary roads, with a further decline noted closer to closed roads and open roads (Fig. 3). However, neither the effect of road type nor road status was a statistically significant predictor of community occupancy but it was a significant predictor for detection probability (Fig. 4).

Model2 (Table S3) revealed that community-level detection probability was highest closer to secondary roads, and feeder roads and lowest along skid trails. At the species level (Table S4), both the red-brocket deer and amazonian brown-brocket deer (*Mazama nemorivaga*) had higher detection probabilities along secondary and feeder roads compared to skid trails. The Jaguar, puma, and ocelot all showed higher detection probabilities closer to feeder roads only. Red-rumped agouti, collared peccary (*Pecari tajacu*), gray four-eyed opossum (*Philander opossum*), jaguarundi (*Puma yagouaroundi*), and Linnaeus’s mouse opossum (*Marmosa murina*) showed higher detection probabilities closer to secondary roads only (Fig. 5).

Road status appeared to impact occupancy, though these findings were less conclusive. Community-level detection probability had a statistically significant decline closer to closed roads, but did not decrease significantly along open roads (Fig. 4). Only the red-rumped agouti ($\alpha_{\text{open}}$ = -2.446, CrI: −4.33, −0.07) had a statistically significant decrease in detection probability closer to open roads only whereas the lowland tapir ($\alpha_{\text{open}}$ = -2.936, CrI: −4.33, −0.07; $\alpha_{\text{closed}}$ = -2.808, CrI: −4.55, −0.33), and lowland paca ($\alpha_{\text{open}}$ = -3.523, CrI: −5.96, −0.89; $\alpha_{\text{closed}}$ = -2.682, CrI: −4.29, −0.17) showed statistically significant decreases along both open and closed logging roads (Table S5).

Further analysis of our road buffers in both models found that total road length around the camera traps had no statistically significant effect on community level occupancy at the local (100 m buffer) or landscape (1000 m buffer) scales (Fig. 3). Overall, there was a 72% chance of a non-negligible effect of secondary roads on community-level occupancy, when compared to skid trails and feeder roads.

## 4. Discussion

Our study revealed that terrestrial mammal occupancy was similar between the logged and control sites, indicating a minimal impact of RIL on mammals. We did however detect a small impact from anthropogenic pressure (as measured by distance to village) on the red-rumped agouti, consistent with previous research from the same area (Roopsind et al. 2017). Notably the amount of logging road available locally and in the landscape had no effect on occupancy, however the type of logging road did have an effect on detection probability. As such we found secondary roads had higher detection probability compared with feeder (smaller) roads, skid trails and the natural trails in the control areas. This suggests that such secondary roads may have structural advantages in addition to less human traffic, which contributed to less avoidance by terrestrial mammals.

Limiting access to logging roads via security checkpoints or closing roads after logging is complete, in addition to limited vehicular activity during and after logging, is crucial to ensuring terrestrial mammals remain in logged forests. Enforcing these policies at strategic points

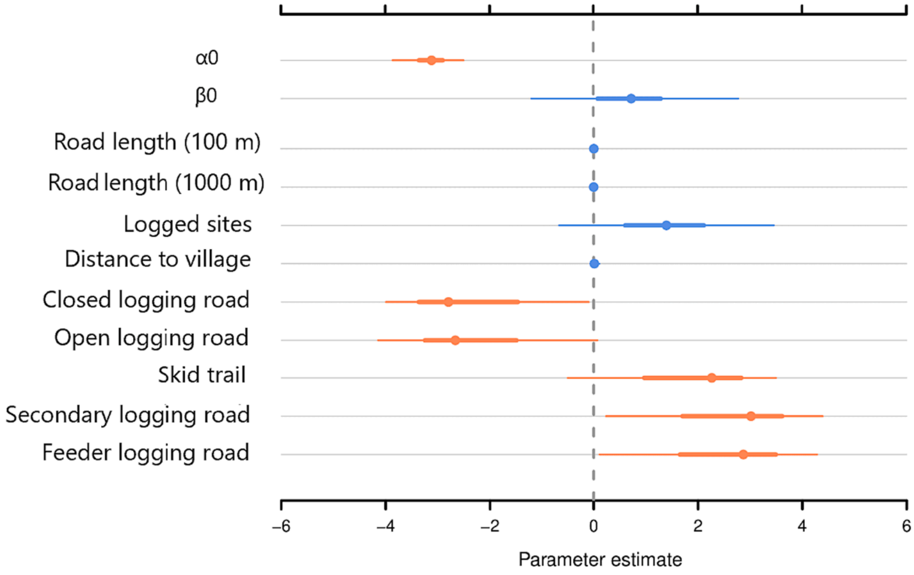

**Fig. 4.** MCMC intervals of parameter effects on community-level detection probability (orange) and community- level occupancy (blue). “α0” = Detection probability in control sites and “β0” = Occupancy probability in control sites.

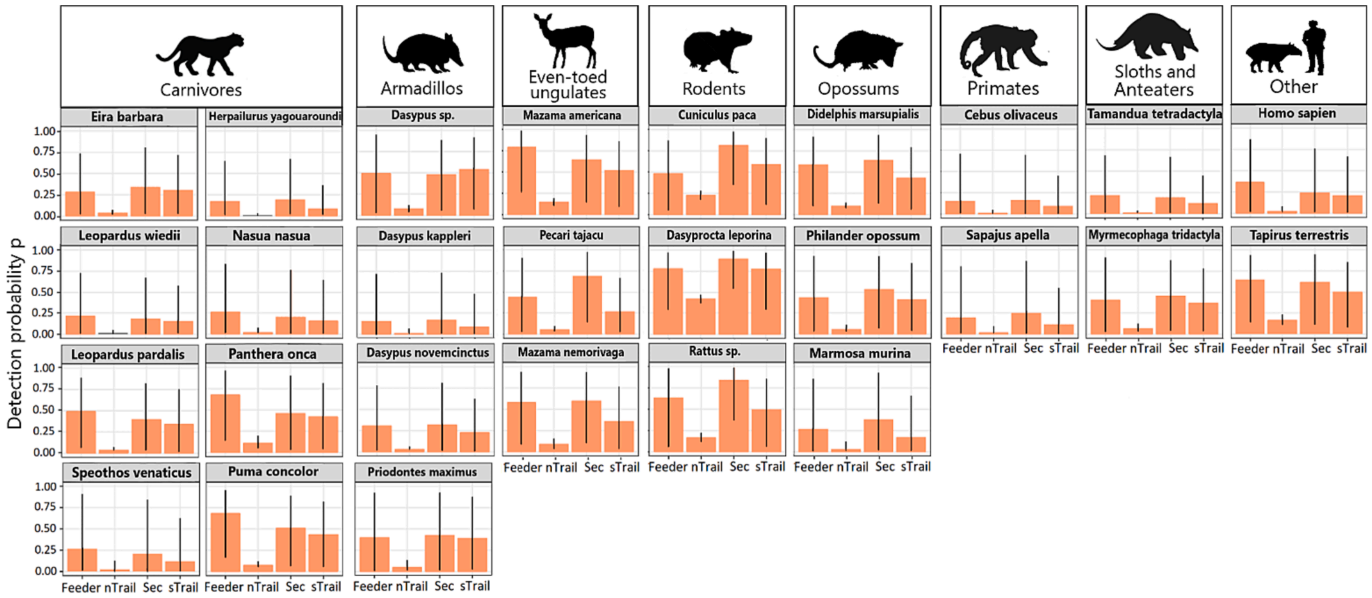

**Fig. 5.** Effects of road type on species-level detection probability. "nTrail" = natural trail found in control sites, "sTrail" = Skid trail found in logged sites. "Sec" = Secondary roads found in logged sites. "Feeder" = Feeder roads found in logged sites.

within the road network, can limit interior rainforest access and accidental killing via road traffic in addition to reducing hunter access (Bicknell et al., 2015; Mason & Putz, 2001). Our findings support this approach because most terrestrial mammal species were found within the sampled logged areas, and both occupancy and detection probabilities were influenced by some logging roads.

Detection probability at the community level was highest for cameras set closer to secondary and feeder roads compared to skid trails in the logged sites, and the natural 'game' trails in the control. These relationships indicate that RIL-managed logging roads do not pose a long-term negative affect on terrestrial mammal occurrence in logged habitats and highlights that greater detection success in logged areas is partially due to how often terrestrial mammals make use of logging roads. Additionally, the statistically significant detections along secondary and feeder roads compared to skid trails may imply a possible logging road preference, and warrants further in-depth testing (e.g. comparison of widths and level of traffic).

Distribution and abundance of food resources are correlated to foraging behaviours in all animal species (Leighton & Leighton, 1982) and an increase in detection along specific logging roads reiterates that carefully constructed road networks have the ability to support terrestrial mammal community richness due to the resource blooms and mobility benefits offered (Laurance et al., 2009). This becomes especially true in RIL rainforests where lesser disturbed rainforest bordering logged areas are maintained. As such, the combination of improved mobility via these logging roads and the presence of adjacent unlogged forests may be beneficial to logged areas. Furthermore, RIL road networks create canopy openings that are small and confined to where harvesting occurs due to careful road construction and pre-harvest vine clearing. This leads to an increase in more palatable understory vegetation (i.e. grasses), enticing forest herbivores to remain within logged zones (Tobler et al., 2018). Forest ungulates such as collared peccary, red brocket deer, Amazonian brown brocket deer as well as the red-rumped agouti showed higher detections closer to secondary roads. These species exhibit herbivorous, frugivorous, granivorous and grazing behaviours in the amazon regions (Barcelos et al., 2013; Prado, 2013; Silvius & Fragoso, 2003). As such, they would typically feed on shrubby, understory vegetation, or fleshy seeds/fruit. The correlation between forest herbivore/frugivores and logging roads, suggests that successional growth along logging roads can increase herbivore density in early regeneration stages. However, we found no statistically significant effect on community level occupancy or detection in correlation to open or closed logging roads. Alternatively, the statistically significant correlation of detection to secondary and feeder roads, compared to skid trails and the control's natural trails highlights again, a road type preference that may be indicative of how that logging road is managed. Overall, this pattern of response is not uncommon in papers addressing selective logging impacts and the changes in ungulate densities. The persistence of herbivorous and frugivorous mammals in selectively logged forests should be encouraged due to the ecological benefit of efficient seed dispersal that contributes to the longevity and genetic heterogeneity of forest plant communities (Houngbégnon et al., 2023). Considering that selectively logged forests should be managed for long-term sustainability, ungulate presence is an important aspect of successful selective logging practices and shouldn't be overlooked.

In Iwokrama's RIL operations, secondary and feeder roads are closed (by felling trees at the entrance to the road) once harvesting is complete. Secondary roads however, can remain open for connecting to nearby harvest blocks for future logging (pers. comm, Iwokrama International Centre). Thus, increases in detection probability closer to secondary and feeder roads in Iwokrama's RIL rainforest can likely be attributed to reduced road activity post-RIL. When compared to the non-significant community-occupancy response to open and closed roads, this community-level response may be indicative of how often these roads are used and supervised by logging and forestry workers. The Iwokrama logging concession maintains a network of roads that has only one exit and entry point from the Highway. Access via this exit/entry point is protected by a guarded gate that allows only logging operators or Iwokrama research staff entry into the logged rainforest. Although we did not estimate the number of vehicles that move in and out of Iwokrama's SUA, traffic remains low in the Iwokrama RIL area. This case therefore further highlights the benefits of carefully managed roads in logged rainforests.

A rise in prey species along, or in proximity to, logging roads can also correlate to increased animal predation due to the accessibility offered by roads (Johns, 1985; Scalbert et al., 2023). Detection probabilities were generally high for large predators such as jaguars, pumas and ocelot within Iwokrama's logged sites, with significantly higher detections of jaguars and pumas, along feeder roads. Alterations to predator–prey dynamics caused by the presence of logging roads may push prey species to avoid logged habitats and opt for unlogged rainforest, thus resulting in the non-significant difference in occupancy between logged vs. control sites. These results may also indicate that predation is higher in the logged sites due to it being easier to hunt for prey along logging roads though we remain cautious with this interpretation. The observation of a higher predator presence may be part of a natural cycle whereby predator densities increase in response to higher prey densities in logged areas. Furthermore, large cats possess large home ranges and their preference for logging roads depends upon the level of access/connectivity to rainforest interiors the road provides (Gordon & Stewart, 2007; Harmsen et al., 2010), which has also been found to explain their higher detections within logged rainforests (Tobler et al., 2018).

Our results show that community occupancy increased as distance to village increased, but was not significantly higher in unlogged areas (control) compared to logged areas. This finding suggests that while there may exist a small anthropogenic pressures such as hunting within the area, this pressure did not lead to significant declines or the extirpation of the mammal species. Though increased levels of human presence often coincide with easy access to forest interiors via logging roads (Poulsen et al., 2011; Rist et al., 2012), distance to village showed only a weak, positive effect on community-level occupancy, with a near zero credibility interval (Figs. 2 & 3). These findings echo that of Brodie et al, (2015) and Roopsind et al, (2017), whereby there was little increased negative effect caused by the combination of logging and subsistence hunting, however this may also be attributed to the low intensity of timber harvesting and subsistence hunting combined with reduced access from closing roads. Hunting pressure in the area is subsistence only (Guyana Bill No.7, 1995) and these communities depend more on freshwater fish than wild game species to meet their daily protein requirements (Harris et al., 2022; Watkins et al., 2004). In Iwokrama, Roopsind et al., (2017) recorded approximately 210 spatially independent kill sites in the logged zones. Additionally, Iwokrama enforces wildlife monitoring at it's ranger stations which requires village hunters and fishermen to log all wildmeat and fish caught during their time in the reserve. However, in their 2009 monitoring report, the Iwokrama International Centre noted an increase in caught fish in the Iwokrama reserve (About Us – Iwokrama International Centre, n.d.). As such, medium and large mammal populations do not seem to be experiencing further declines related to the allowance of wildmeat hunting in Iwokrama's RIL rainforest.

At the species-level, only the red-rumped agouti showed a statistically significant increase in occupancy further from the village (Table S5), whereas no species showed a statistically significant preference for logging-disturbed habitat. Additionally, the red-rumped agouti, lowland paca, collared peccary and lowland tapir all had statistically significant decreases in detection closer to open roads, where there is an increased probability of encountering hunters and loggers. This was similar to Roopsind et al (2017) in the same area, who found that mean monthly hunting effects on species-level occupancy was strongest for agoutis (2.38 individuals), lowland paca (2.24 individuals) and peccary species (1.33 individuals). Red-rumped agoutis are medium-sized, diurnal, terrestrial rodents (2–5 kg) with high population densities between 1 and 63 individuals per km$^2$ (Silvius & Fragoso, 2003; Wright et al., 1999) in neotropical moist and dry habitats. Agoutis interact via "scatter-hoarding" with a range of tropical tree families including Leguminaceae, Palmae and Meliaceae (Brewer & Rejmánek, 1999; Silvius & Fragoso, 2003) with notable commercial trees from these families including Greenheart (*Chlorocardium rodei*) and Crabwood (*Carapa guianensis*). Indeed, through these interactions, frugivores including seed predators, and some herbivores, they play a key role in primary and secondary dispersal of tree species which are important for recruitment in tropical rainforests (Forget et al., 2001; Gardner et al., 2019; Houngbégnon et al., 2023; Silvius & Fragoso, 2003). Hunting of agoutis highlight their rise in preference as a protein source in addition to traditionally hunted species such as peccaries and tapir (Iwamura et al., 2014; Sousa & Srbek-Araujo, 2017). This rise in preference was explored by Iwamura et al (2014) as an interaction result between distance between animal-kill locations and average body mass of killed animals which inferred that as subsistence hunting range decreased (due to increase in farming range), hunters may opt for more abundant, easily found, small-bodied prey. In their 2017 report, Iwokrama stated that residents of their Makushi village list the red-rumped Agouti as one of their preferred wild meat sources alongside brocket deer and lowland paca (About Us – Iwokrama International Centre, n.d.). Overall, red-rumped agouti occupancy still remained higher within the logged areas compared to control sites, further demonstrating the minimal impact of RIL.

## 5. Conclusion

Our findings highlight the conservation importance of properly managed road networks and the low impact of RIL in tropical forests. As such, the impact of Reduced-Impact logging on terrestrial mammal occupancy can be minimized, and this may be the result of limits on logging road activity and guarded access to forest interiors. We recommend continued monitoring of anthropogenic pressures, specifically from subsistence hunting of hoarding rodents such as the red-rumped agouti, which remains a principal seed disperser of hardwood species. Most of all, our research concurs with the mounting literature showing the relatively benign impact of RIL on biodiversity, further emphasizing the positive effect that the wide adoption of RIL could have if implemented across the 4 million km$^2$ of tropical production forests.

Funding.

This work was supported by the Jacksonville Zoo & Gardens though the zoo's annual contribution to the Guyana Conservation Initiative from which is funded by ticket sales.

## CRediT authorship contribution statement

**Arianne E. Harris:** Conceptualization. **Matthew Hallett:** Data curation, Supervision, Methodology. **Micah Davis:** Data curation, Methodology. **Martin Carter:** Data curation, Methodology. **Dwarka Singh:** Data curation, Methodology. **Anand Roopsind:** Supervision. **Gyanpriya Maharaj:** Supervision. **Jake E. Bicknell:** Supervision.

## Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

## Data availability

The data that support the findings of this study will be openly available in Github at https://github.com/Arianne96/mammal.RILLogging

## Acknowledgements

We would like to thank the staff of the Iwokrama International Centre for allowing us to conduct this research within the Iwokrama rainforest. Thanks, are also extended to Iwokrama staff: Rohanie Roopnarine and Ken Rodney for providing the GIS information required for this research. Additionally, we thank the Jacksonville Zoo & Gardens, from which this research was funded and the research team of Operation Wallacea: Guyana expedition, who helped manage accomodation and logistics.

## Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2023.121401.

## References

*About Us – Iwokrama International Centre*. (n.d.). Retrieved May 28, 2020, from https://iwokrama.org/about-us/.

Alveira, M., de Bustos, S., Tálamo, A., 2023. Certified forest management and conservation of medium and large-sized mammals: biodiversity, trampling, browsing and seed removal in the Argentine Austral Yungas. For. Ecol. Manage. 533, 120860 https://doi.org/10.1016/j.foreco.2023.120860.

Asner, G. P., Keller, M., Jr, R. P., Zweede, J. C., & Silva, J. N. M. (2004). Canopy Damage and Recovery After Selective Logging in Amazonia: Field and Sa$^{TEL}$lite Studies. *Ecological Applications*, *14*(sp4), 280–298. doi: 10.1890/01-6019.

Azevedo-Ramos, C., de Carvalho, O., & do Amaral, B. D. (2006). Short-term effects of reduced-impact logging on eastern Amazon fauna. *Forest Ecology and Management*, *232*(1–3), 26–35. doi: 10.1016/j.foreco.2006.05.025.

Barcelos, A.R., Bobrowiec, P.E.D., Sanaiotti, T.M., Gribel, R., 2013. Seed germination from lowland tapir (Tapirus terrestris) fecal samples collected during the dry season in the northern Brazilian Amazon. Integrative Zoology 8 (1), 63–73. https://doi.org/10.1111/1749-4877.12003.

Bennett, E. L., & Robinson, J. G. (2000). *Hunting of Wildlife in Tropical Forests: Implications for Biodiversity and Forest Peoples*. http://hdl.handle.net/10986/18297.

Bicknell, J. E., Struebig, M. J., Edwards, D. P., & Davies, Z. G. (2014). Improved timber harvest techniques maintain biodiversity in tropical forests. *Current Biology*, *24*(23), R1119–R1120. doi: 10.1016/j.cub.2014.10.067.

Bicknell, J.E., Gaveau, D.L., Davies, Z.G., Struebig, M.J., 2015. Saving logged tropical forests: closing roads will bring immediate benefits. Front. Ecol. Environ. 13 (2), 73–74. https://doi.org/10.1890/15.WB.001.

Bicknell, J., Peres, C.A., 2010. Vertebrate population responses to reduced-impact logging in a neotropical forest. For. Ecol. Manage. 259 (12), 2267–2275. https://doi.org/10.1016/j.foreco.2010.02.027.

Boltz, F., Holmes, T.P., Carter, D.R., 2003. Economic and environmental impacts of conventional and reduced-impact logging in Tropical South America: a comparative review. Forest Policy Econ. 5 (1), 69–81.

Brewer, S.W., Rejmánek, M., 1999. Small rodents as significant dispersers of tree seeds in a Neotropical forest. J. Veg. Sci. 10 (2), 165–174. https://doi.org/10.2307/3237138.

Brodie, J.F., Giordano, A.J., Zipkin, E.F., Bernard, H., Mohd-Azlan, J., Ambu, L., 2015. Correlation and persistence of hunting and logging impacts on tropical rainforest mammals: logging, hunting, and mammal diversity. Conserv. Biol. 29 (1), 110–121. https://doi.org/10.1111/cobi.12389.

Burton, A.C., Neilson, E., Moreira, D., Ladle, A., Steenweg, R., Fisher, J.T., Bayne, E., Boutin, S., Stephens, P., 2015. REVIEW: Wildlife camera trapping: a review and recommendations for linking surveys to ecological processes. J. Appl. Ecol. 52 (3), 675–685.

Camargo-Sanabria, A.A., Mendoza, E., Guevara, R., Martínez-Ramos, M., Dirzo, R., 2015. Experimental defaunation of terrestrial mammalian herbivores alters tropical rainforest understorey diversity. Proc. R. Soc. B Biol. Sci. 282 (1800), 20142580. https://doi.org/10.1098/rspb.2014.2580.

Carvalho Jr, E.A.R., Nienow, S.S., Bonavigo, P.H., Haugaasen, T., 2021. Mammal responses to reduced-impact logging in Amazonian forest concessions. For. Ecol. Manage. 496, 119401 https://doi.org/10.1016/j.foreco.2021.119401.

Corlett, R.T., 2007. The impact of hunting on the mammalian fauna of tropical asian forests. Biotropica 39 (3), 292–303. https://doi.org/10.1111/j.1744-7429.2007.00271.x.

Costa, F.R.C., Magnusson, W.E., 2003. Effects of selective logging on the diversity and abundance of flowering and fruiting understory plants in a central amazonian forest. Biotropica 35 (1), 103–114. https://doi.org/10.1111/j.1744-7429.2003.tb00267.x.

Dorazio, R.M., 2016. Bayesian data analysis in population ecology: Motivations, methods, and benefits. Popul. Ecol. 58 (1), 31–44.

Dorazio, R.M., Royle, J.A., Söderström, B., Glimskär, A., 2006. Estimating species richness and accumulation by modeling species occurrence and detectability. Ecology 87 (4), 842–854. https://doi.org/10.1890/0012-9658(2006)87[842:ESRAAB]2.0.CO;2.

Forget, P.-M., Merona, J.-M.-R.-D., Juillot, C., 2001. The effects of forest type, harvesting and stand refinement on early seedling recruitment in a tropical rain forest. J. Trop. Ecol. 17 (4), 593–609. https://doi.org/10.1017/S0266467401001444.

Fragoso, J.M.V., Levi, T., Oliveira, L.F.B., Luzar, J.B., Overman, H., Read, J.M., Silvius, K.M., Crowther, M.S., 2016. Line transect surveys underdetect terrestrial mammals: implications for the sustainability of subsistence hunting. PLoS One 11 (4), e0152659.

Gardner, C.J., Bicknell, J.E., Baldwin-Cantello, W., Struebig, M.J., Davies, Z.G., 2019. Quantifying the impacts of defaunation on natural forest regeneration in a global meta-analysis. Nat. Commun. 10(1), Article 1 https://doi.org/10.1038/s41467-019-12539-1.

Gibson, L., Lee, T.M., Koh, L.P., Brook, B.W., Gardner, T.A., Barlow, J., Peres, C.A., Bradshaw, C.J.A., Laurance, W.F., Lovejoy, T.E., Sodhi, N.S., 2011. Primary forests are irreplaceable for sustaining tropical biodiversity. Nature 478 (7369), 378–381. https://doi.org/10.1038/nature10425.

Gordon, C. H., & Stewart, A.-M. E. (n.d.). *The Use of Logging Roads by Clouded Leopards*.

Griscom, B. W., Ellis, P. W., Burivalova, Z., Halperin, J., Marthinus, D., Runting, R. K., Ruslandi, Shoch, D., & Putz, F. E. (2019). Reduced-impact logging in Borneo to minimize carbon emissions and impacts on sensitive habitats while maintaining timber yields. *Forest Ecology and Management*, *438*, 176–185. doi: 10.1016/j.foreco.2019.02.025.

Hallett, M.T., Kinahan, A.A., McGregor, R., Baggallay, T., Babb, T., Barnabus, H., Wilson, A., Li, F.M., Boone, W.W., Bankovich, B.A., 2019. Impact of low-intensity hunting on game species in and around the kanuku mountains protected area. Guyana. *Frontiers in Ecology and Evolution* 7. https://doi.org/10.3389/fevo.2019.00412.

Harmsen, B.J., Foster, R.J., Silver, S., Ostro, L., Doncaster, C.P., 2010. Differential use of trails by forest mammals and the implications for camera-trap studies: a case study from belize: trail use by neotropical forest mammals. Biotropica 42 (1), 126–133. https://doi.org/10.1111/j.1744-7429.2009.00544.x.

Harris, A.-E., Maharaj, G., Hallett, M. T., Pierre, M. A., Chesney, C., & Melville, A. (n.d.). Influence of diet overlap and nest-site aggression on human– black caiman conflict in Guyana. *HUMAN DIMENSIONS OF WILDLIFE*, 10.

Houngbégnon, F.G.A., Gillet, J.-F., Michaux, J., Brostaux, Y., Zébazé, D., Lhoest, S., Vermeulen, C., Sonké, B., Doucet, J.-L., 2023. Seed dispersal by duikers in selectively logged rainforests: overlooked dispersal of an important animal community. For. Ecol. Manage. 529, 120650 https://doi.org/10.1016/j.foreco.2022.120650.

Iwamura, T., Lambin, E.F., Silvius, K.M., Luzar, J.B., Fragoso, J.M.V., 2014. Agent-based modeling of hunting and subsistence agriculture on indigenous lands: understanding interactions between social and ecological systems. Environ. Model. Softw. 58, 109–127. https://doi.org/10.1016/j.envsoft.2014.03.008.

Johns, A.D., 1985. Selective logging and wildlife conservation in tropical rain-forest: problems and recommendations. Biol. Conserv. 31 (4), 355–375. https://doi.org/10.1016/0006-3207(85)90091-6.

Chaves Baía Júnior, P., Guimarães, D. A., & Le Pendu, Y. (2010). Non-legalized commerce in game meat in the Brazilian Amazon: A case study. *Revista de Biología Tropical*, *58*(3), 1079–1088.

Keller, G.R., Berry, J., 2007. Reduced Impact Logging Road Issues in Tropical Forests. Transp. Res. Rec.: J. Transp. Res. Board 1989–1 (1), 98–106. https://doi.org/10.3141/1989-11.

Kleinschroth, F., Healey, J.R., 2017. Impacts of logging roads on tropical forests. Biotropica 49 (5), 620–635. https://doi.org/10.1111/btp.12462.

Kleinschroth, F., Gourlet-Fleury, S., Gond, V., Sist, P., Healey, J.R., 2017. Logging roads in tropical forests: synthesis of literature written in french and english highlights environmental impact reduction through improved engineering. Bois & Forets Des Tropiques 328 (328), 13. https://doi.org/10.19182/bft2016.328.a31299.

Laufer, J., Michalski, F., Peres, C.A., 2015. Effects of reduced-impact logging on medium and large-bodied forest vertebrates in eastern Amazonia. Biota Neotropica 15. https://doi.org/10.1590/1676-06032015013114.

Laurance, W.F., Croes, B.M., Guissouegou, N., Buij, R., Dethier, M., Alonso, A., 2008. Impacts of roads, hunting, and habitat alteration on nocturnal mammals in african rainforests. Conserv. Biol. 22 (3), 721–732. https://doi.org/10.1111/j.1523-1739.2008.00917.x.

Laurance, W.F., Goosem, M., Laurance, S.G.W., 2009. Impacts of roads and linear clearings on tropical forests. Trends Ecol. Evol. 24 (12), 659–669. https://doi.org/10.1016/j.tree.2009.06.009.

Leighton, M., Leighton, D.R., 1982. The relationship of size of feeding aggregate to size of food patch: howler monkeys (alouatta palliata) feeding in trichilia cipo fruit trees on barro colorado island. Biotropica 14 (2), 81–90. https://doi.org/10.2307/2387735.

Lindenmayer, D.B., Franklin, J.F., Fischer, J., 2006. General management principles and a checklist of strategies to guide forest biodiversity conservation. Biol. Conserv. 131 (3), 433–445. https://doi.org/10.1016/j.biocon.2006.02.019.

MacKenzie, D. I., Nichols, J. D., Royle, A., Pollock, K. H., Bailey, L. L., & Hines, J. E. (2018). *Occupancy in community-level studies*. 557–583. doi: 10.1016/B978-0-12-407197-1.00020-X.

MacKenzie, D.I., Nichols, J.D., Lachman, G.B., Droege, S., Andrew Royle, J., Langtimm, C.A., 2002. Estimating site occupancy rates when detection probabilities are less than one. Ecology 83 (8), 2248–2255. https://doi.org/10.1890/0012-9658(2002)083[2248:ESORWD]2.0.CO;2.

Malhi, Y., Gardner, T.A., Goldsmith, G.R., Silman, M.R., Zelazowski, P., 2014. Tropical forests in the anthropocene. Annu. Rev. Env. Resour. 39 (1), 125–159. https://doi.org/10.1146/annurev-environ-030713-155141.

Mason, D.J., Putz, F.E., 2001. Reducing the Impacts of Tropical Forestry on Wildlife. In *21. Reducing the Impacts of Tropical Forestry on Wildlife* 21, 473–510.

Medjibe, V.P., Putz, F.E., 2012. Cost comparisons of reduced-impact and conventional logging in the tropics. J. For. Econ. 18 (3), 242–256. https://doi.org/10.1016/j.jfe.2012.05.001.

Meijaard, E., Sheil, D., 2007. The persistence and conservation of Borneo's mammals in lowland rain forests managed for timber: observations, overviews and opportunities. Ecol. Res. 23 (1), 21. https://doi.org/10.1007/s11284-007-0342-7.

Niedballa, J., Sollmann, R., Courtiol, A., Wilting, A., Jansen, P., 2016. camtrapR: an R package for efficient camera trap data management. Methods Ecol. Evol. 7 (12), 1457–1462.

Pangau-Adam, M., Noske, R., Muehlenberg, M., 2012. Wildmeat or bushmeat? subsistence hunting and commercial harvesting in papua (west new guinea). Indonesia*Human Ecology* 40 (4), 611–621. https://doi.org/10.1007/s10745-012-9492-5.

Pinard, M., Putz, F.E., Tay, J., Sullivan, T.E., 1995. Creating timber harvest guidelines for a Reduced-Impact Logging Project in Malaysia. J. For. 93, 41–45.

Poulsen, J.R., Clark, C.J., Bolker, B.M., 2011. Decoupling the effects of logging and hunting on an Afrotropical animal community. Ecol. Appl. 21 (5), 1819–1836. https://doi.org/10.1890/10-1083.1.

Prado, H.M., 2013. Feeding ecology of five neotropical ungulates: a critical review. Oecologia Australis 17 (4), 459–473. https://doi.org/10.4257/oeco.2013.1704.02.

Putz, F.E., Dykstra, D.P., Heinrich, R., 2000. Why poor logging practices persist in the tropics. Conserv. Biol. 14 (4), 951–956. https://doi.org/10.1046/j.1523-1739.2000.99137.x.

Rist, L., Shanley, P., Sunderland, T., Sheil, D., Ndoye, O., Liswanti, N., Tieguhong, J., 2012. The impacts of selective logging on non-timber forest products of livelihood importance. For. Ecol. Manage. 268, 57–69. https://doi.org/10.1016/j.foreco.2011.04.037.

Robinson, J.G., Bennett, E.L., 2004. Having your wildlife and eating it too: an analysis of hunting sustainability across tropical ecosystems. Anim. Conserv. 7 (4), 397–408. https://doi.org/10.1017/S1367943004001532.

Robinson, J.G., Redford, K.H., Bennett, E.L., 1999. Wildlife harvest in logged tropical forests. Science 284 (5414), 595–596. https://doi.org/10.1126/science.284.5414.595.

Roopsind, A., Caughlin, T.T., Sambhu, H., Fragoso, J.M.V., Putz, F.E., 2017. Logging and indigenous hunting impacts on persistence of large Neotropical animals. Biotropica 49 (4), 565–575. https://doi.org/10.1111/btp.12446.

Rosin, C., 2014. Does hunting threaten timber regeneration in selectively logged tropical forests? For. Ecol. Manage. 331, 153–164. https://doi.org/10.1016/j.foreco.2014.08.001.

Royle, J.A., Nichols, J.D., Karanth, K.U., Gopalaswamy, A.M., 2009. A hierarchical model for estimating density in camera-trap studies. J. Appl. Ecol. 46 (1), 118–127. https://doi.org/10.1111/j.1365-2664.2008.01578.x.

Scalbert, M., Stiernon, Q., Franceschini, S., Vermeulen, C., Brostaux, Y., Ngwet, R., Doucet, J.-L., 2023. Not all roads are barriers: Large mammals use logging roads in a timber concession of south-eastern Cameroon. For. Ecol. Manage. 541, 120910 https://doi.org/10.1016/j.foreco.2023.120910.

Sheil, D., Van Heist, M., 2000. Ecology for tropical forest management. Int. Forestry Rev. 2 (4), 261–270.

Sidle, R.C., Sasaki, S., Otsuki, M., Noguchi, S., Rahim Nik, A., 2004. Sediment pathways in a tropical forest: effects of logging roads and skid trails. Hydrol. Process. 18 (4), 703–720. https://doi.org/10.1002/hyp.1364.

Silvius, K.M., Bodmer, R.E., Fragoso, J.M.V., 2004. People in Nature. Wildlife Conservation in South and Central America. Columbia University Press.

Silvius, K.M., Fragoso, J.M.V., 2003. Red-rumped agouti (dasyprocta leporina) home range use in an amazonian forest: implications for the aggregated distribution of forest trees. Biotropica 35 (1), 74–83. https://doi.org/10.1111/j.1744-7429.2003.tb00264.x.

Sollmann, R., Mohamed, A., Niedballa, J., Bender, J., Ambu, L., Lagan, P., Mannan, S., Ong, R.C., Langner, A., Gardner, B., Wilting, A., Regan, H., 2017. Quantifying mammal biodiversity co-benefits in certified tropical forests. Divers. Distrib. 23 (3), 317–328.

Sousa, J.A.C., Srbek-Araujo, A.C., 2017. Are we headed towards the defaunation of the last large Atlantic Forest remnants? Poaching activities in one of the largest remnants of the Tabuleiro forests in southeastern Brazil. Environ. Monit. Assess. 189 (3), 129. https://doi.org/10.1007/s10661-017-5854-1.

Stoner, K.E., Riba-Hernández, P., Vulinec, K., Lambert, J.E., 2007. The role of mammals in creating and modifying seedshadows in tropical forests and some possible consequences of their elimination. Biotropica 39 (3), 316–327. https://doi.org/10.1111/j.1744-7429.2007.00292.x.

Struebig, M.J., Turner, A., Giles, E., Lasmana, F., Tollington, S., Bernard, H., Bell, D., 2013. Chapter Three - Quantifying the Biodiversity Value of Repeatedly Logged Rainforests: Gradient and Comparative Approaches from Borneo. In: Woodward, G., O'Gorman, E.J. (Eds.), Advances in Ecological Research, Vol. 48. Academic Press, pp. 183–224. https://doi.org/10.1016/B978-0-12-417199-2.00003-3.

Tobler, M.W., Garcia Anleu, R., Carrillo-Percastegui, S.E., Ponce Santizo, G., Polisar, J., Zuñiga Hartley, A., Goldstein, I., 2018. Do responsibly managed logging concessions adequately protect jaguars and other large and medium-sized mammals? two case studies from Guatemala and Peru. Biol. Conserv. 220, 245–253. https://doi.org/10.1016/j.biocon.2018.02.015.

Van Vliet, N., Antunes, A.P., Constantino, P.D.A.L., Gómez, J., Santos-Fita, D., Sartoretto, E., 2019. Frameworks regulating hunting for meat in tropical countries leave the sector in the limbo. Front. Ecol. Evol. 7, 280. https://doi.org/10.3389/fevo.2019.00280.

Watkins, G., Saul, W., Holm, E., Watson, L., Bicknell, J., 2004. The fish fauna of the Iwokrama Forest. Proc. Acad. Natl. Sci. Phila. 154, 39–53. https://doi.org/10.1635/0097-3157(2004)154[0039:TFFOTI]2.0.CO;2.

Wright, S.J., 2010. The future of tropical forests. Ann. N. Y. Acad. Sci. 1195 (1), 1–27. https://doi.org/10.1111/j.1749-6632.2010.05455.x.

Wright, S.J., Carrasco, C., Calderón, O., Paton, S., 1999. The El Niño Southern oscillation, variable fruit production, and famine in a tropical forest. Ecology 80 (5), 1632–1647. https://doi.org/10.1890/0012-9658(1999)080[1632:TENOSO]2.0.CO;2.

Yamada, T., Niino, M., Yoshida, S., Hosaka, T., Okuda, T., 2014. Impacts of logging road networks on dung beetles and small mammals in a malaysian production forest: implications for biodiversity safeguards. Land 3 (3), Article 3. https://doi.org/10.3390/land3030639.