Received: 26 May 2023 | Revised: 4 June 2024 | Accepted: 5 June 2024

DOI: 10.1002/jwmg.22633

THE JOURNAL OF WILDLIFE MANAGEMENT

THE WILDLIFE SOCIETY

RESEARCH ARTICLE

High freshwater turtle occupancy of streams within a sustainably managed tropical forest in Borneo

Wei Cheng Tan[1] | **Victor Vitalis**[2] | **Julsun Sikuim**[3] | **Dennis Rödder**[1] | **Mark-Oliver Rödel**[4] | **Sami Asad**[5]

[1]Herpetology Section, Museum Koenig - Leibniz Institute for the Analysis of Biodiversity Change (LIB), Adenauerallee 127, Bonn 53113, Germany

[2]Panthera Malaysia, Petaling Jaya, Selangor 46200, Malaysia

[3]Forest Research Centre, Sabah Forestry Department, Sandakan, Sabah 90009, Malaysia

[4]Museum für Naturkunde - Leibniz Institute for Evolution and Biodiversity Science, Invalidenstraße 43, Berlin 10115, Germany

[5]Tomorrow University of Applied Science, Platz der Einheit 2, Frankfurt am Main 60327, Germany

Correspondence

Wei Cheng Tan, Herpetology Section, Museum Koenig - Leibniz Institute for the Analysis of Biodiversity Change (LIB), Adenauerallee 127, Bonn 53113, Germany.
Email: n.tan@leibniz-lib.de

Funding information

Deutscher Akademischer Austauschdienst; Museum für Naturkunde; Leibniz-Institut für Zoo- und Wildtierforschung; German Society for Herpetology and Hereptoculture; The Auckland Zoo; Columbus Zoo and Aquarium

Abstract

Despite suffering dramatic declines due to habitat loss and overexploitation, tortoises and freshwater turtles in Southeast Asia remain understudied. Sustainable forest management offers a promising approach for advancing the conservation of threatened turtle populations. This study examines the effect of reduced impact logging (RIL), a sustainable forestry method, on 2 freshwater turtle species. We examined detectability patterns and habitat relationships for the threatened Malayan flat-shelled turtle (*Notochelys platynota*) and the non-threatened Malayan soft-shelled turtle (*Dogania subplana*) in 8 streams within a commercial forest reserve between March and July 2019, in Sabah, Malaysian Borneo. Using single-species occupancy models, we identified covariates associated with the detection and occupancy probabilities of these species across a post-harvest recovery gradient (1–21 years since logging). Covariates used in the models were obtained directly from the field or from open-source remote sensing data. Results for soft-shelled turtles were inconclusive. In contrast, we found a negative association between monthly rainfall and flat-shelled turtle detectability. The occupancy probability of flat-shelled turtles was positively associated with greater distance from logging roads and higher stream flow accumulation. Occupancy probability for flat-shelled turtles and soft-shelled turtles was relatively high throughout the reserve (0.79 ± 0.1 [SD] and

0.57 ± 0.22, respectively). These results, suggest that appropriately managed forests, could serve as invaluable conservation areas for imperiled freshwater turtle species in the region.

KEYWORDS

Chelonia, detectability, *Dogania subplana*, forest management, logging roads, *Notochelys platynota*, reduced impact logging

Freshwater turtles and tortoises are currently considered the most threatened vertebrate taxa, with more than half of all 356 species classified as threatened (Stanford et al. 2018). While Southeast Asia represents a freshwater turtle diversity hotspot with high levels of phylogenetic endemism (Roll et al. 2017, Gumbs et al. 2020), the region also faces widespread species declines (Böhm et al. 2013, Roll et al. 2017). Turtle populations within Southeast Asia are currently being extirpated because of urban development, commercial logging, agriculture, pollution, and climate change (Stanford et al. 2018, Cox et al. 2022). Additionally, the region serves as both a source and market for a thriving turtle trade, with the majority of species facing unsustainable levels of harvesting for regional and international pet, medicine, and food markets (Dijk et al. 2000, Cox et al. 2022, Mohd Salleh et al. 2022). The growing demand and increased market prices for freshwater turtles and tortoises drive an ever-expanding, highly lucrative trade in many Southeast Asian countries (Van et al. 2019, Shepherd et al. 2020, Nijman and Shepherd 2022). In Kalimantan, Indonesia alone, up to 45,000 Southeast Asian box turtles are traded annually (Nijman and Shepherd 2022). While trade in the region is well documented, quantitative data on freshwater turtle responses to anthropogenic disturbance are lacking. Many studies (mainly conducted in America and Australia) of native freshwater turtles have shown negative physiological and behavioral responses to anthropogenic disturbances such as agriculture (Čapkun-Huot et al. 2021, Fulton et al. 2022), urbanization (Selman et al. 2013), and roads (Cassel et al. 2019). Determining the effects of human-induced land use change in Southeast Asia is essential for quantifying these impacts, damage mitigation, and identifying conservation priority areas for the region's threatened freshwater turtles.

Commercial logging activities occur in more than half of the remaining tropical forests (Food and Agriculture Organization [FAO] and United Nations Environment Programme [UNEP] 2020) and represent one of the greatest potential threats to freshwater turtle habitats in Southeast Asia (Huth and Ditzer 2001, Gaveau et al. 2014). Unsustainable management of these timber concessions has led to widespread habitat degradation and declining biodiversity throughout the region (Gibson et al. 2011, Burivalova et al. 2014).

Whilst many logging reserves in the region have been subject to conventional selective logging since the 1970s (Gaveau et al. 2014), the implementation of sustainable forestry methods could present a promising, economically viable alternative (Pinard et al. 1995). Although various sustainable forestry methods are available, reduced impact logging (RIL) has been the most widely adopted and tested in the tropics (Dykstra 2007). This method implements strict timber harvesting guidelines including reduced harvest rates (< 30 m^3 timber per ha) compared to conventional logging, and a series of best practice techniques including directional felling, reduced skid trail construction, pre- and post-harvest planning, and 30-m riparian buffer zones along both sides of permanent water courses >5 m in width (Pinard et al. 1995, Putz et al. 2008, Sabah Forestry Department 2024). These methods result in 50% less damage to remnant forests, thus maintaining watersheds while reducing sedimentation and riparian habitat disturbance (Pinard et al. 1995, Sabah Forestry Department 2024). As such, RIL-managed forests maintain higher biodiversity compared to conventionally logged sites (Bicknell et al. 2014, Brozovic et al. 2018, Bohnett et al. 2022). While responses of various taxa to RIL practices are documented (amphibians, Asad et al. 2021*a*; mammals, Brozovic et al. 2018, Guharajan et al. 2021, Bohnett et al. 2022; birds, Edwards et al. 2012), the impact of RIL on Southeast Asia's freshwater turtles remains unstudied but should prove valuable for informing future conservation measures (Cox et al. 2022).

Quantifying abundance and occupancy are an effective approach for determining the effects of disturbances, such as logging, on turtles (Horn and Gervais 2018, Čapkun-Huot et al. 2021). However, the detection of turtles is typically imperfect because of observer error (Nichols et al. 2000), low population density, cryptic behaviors of individuals, or environmental conditions that influence the likelihood of detection (Gu and Swihart 2004). As such, failure to correct for imperfect detection can result in biased estimation of habitat associations and thus erroneous conclusions (Gu and Swihart 2004, Kellner and Swihart 2014). Temporal or climatological variables have been previously identified as factors associated with detection probability in diurnal (e.g., weather conditions, air and water temperature; Brown 2001, Armstrong 2016, Ocock et al. 2018, Buchanan et al. 2019), and nocturnal freshwater turtles (e.g., lunar phases and cloud coverage; Jensen and Das 2008). These climatological factors may influence the availability of food resources, shelters, nesting sites, and predator activity (Parlin et al. 2018, Escalona et al. 2019, Geller et al. 2022). Thus, it is essential to incorporate detection probability when studying the responses of freshwater turtles to disturbance, and their compatibility with sustainable forest management (Buchanan et al. 2019).

In Malaysian Borneo, Deramakot is a sustainably managed forest reserve using RIL techniques and is occupied by several freshwater turtle species. The Malayan soft-shelled turtle (*Dogania subplana*) is a non-threatened (least concern; Cota et al. 2021), soft-shelled Trionychidae and the Malayan flat-shelled turtle (*Notochelys platynota*) is a threatened (vulnerable; Kusrini et al. 2021) hard-shelled Geoemydidae. Both are harvested throughout the region for local food markets (Walter 2000, Jensen 2006, Jensen and Das 2008), while flat-shelled turtles are also traded internationally (Cheung and Dudgeon 2006, Gong et al. 2009). Several other freshwater turtle species (spiny turtle [*Heosemys spinosa*], Southeast Asian box turtle [*Cuora amboinensis*], and Asian leaf turtle [*Cyclemys dentata*]) occur in the reserve but are detected less frequently. The Malayan soft-shelled turtle is a medium-sized (maximum carapace length = 310 mm) predominately aquatic, omnivorous species (Lim and Das 1999, Pritchard 2001). Although limited ecological information is available, the species is primarily nocturnal and commonly found in small, silted forest streams and fast-flowing rivers (Premono et al. 2015, Mohd Ibrahim et al. 2019, Asad et al. 2021*b*). The Malayan flat-shelled turtle is a medium-sized (maximum carapace length = 360 mm) primarily herbivorous species, although it is reported to occasionally prey or scavenge on animals (Manthey and Grossmann 1997, Lim and Das 1999). This species is diurnal and nocturnal, preferring shallow, clear, sandy-bottomed streams in forested areas and is less aquatic than soft-shelled turtles (Lim and Das 1999, Asad et al. 2021*b*). Previous research indicates that potential fine-scale spatial separation of the 2 species may occur along sedimentation gradients within the same stream (Asad et al. 2021*b*).

In the face of rapid economic development and accompanying road expansion in Borneo (Sloan et al. 2019) and throughout the region (Bradshaw et al. 2009), we attempted to determine detectability and occupancy associations of these 2 freshwater turtle species within Deramakot. Our first objective was to examine the effect of climatological covariates on the detectability of these 2 species. We predicted that temperature and rainfall would be important covariates, as found in previous studies (of other species in other geographic regions; North America, Rowe 2003, Rowe et al. 2009, Anthonysamy et al. 2013; Oceania, Roe and Georges 2008). We also expected lunar phases to play a significant role in the detectability of these nocturnally active turtles (Jensen and Das 2008). Our second objective was to examine the effects of habitat and RIL-associated covariates on the occurrence of these 2 species. We expected that occupancy would be negatively influenced by covariates associated with logging (proximity to logging roads and time since logging). Our final objective was to determine the occupancy probability of the 2 species at sites within an active sustainable logging reserve. Because RIL affects forest structures less than other practices, and thus freshwater turtle habitat quality, we estimated moderate occupancy probabilities (<50%) in the reserve for both species.

STUDY AREA

We conducted this study between March and July 2019 in the Deramakot Forest Reserve (5°14-28′N, 117°19-36′E), in the Malaysian state of Sabah, on the island of Borneo (Figure 1). The climate is humid equatorial (average annual temperature = 26°C) and heavily influenced by both northeast (Nov–Feb) and southeast (May–Aug)

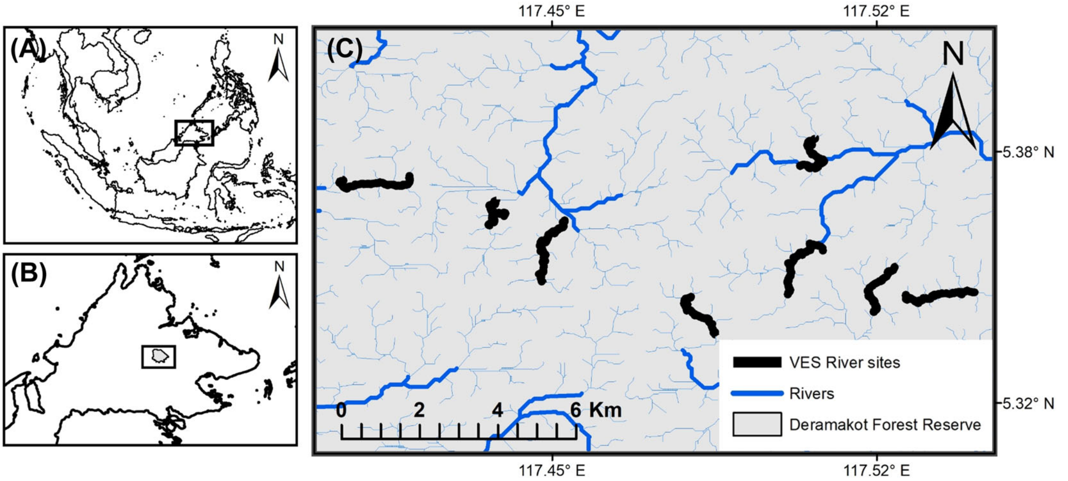

FIGURE 1 Location of A) Sabah, Malaysian Borneo, B) the Deramakot Forest Reserve in central Sabah, and C) the visual encounter survey (VES) stream sites within the center of the reserve used in single-species occupancy modeling of flat-shelled turtles and soft-shelled turtles in 2019.

monsoons with annual precipitation ranging between 1,700 mm and 5,100 mm (Kleine and Heuveldop 1993, Huth and Ditzer 2001). Geologically, Deramakot is characterized by tertiary sediments, mostly mud and sandstone (Huth and Ditzer 2000). The predominant Acrisols are poor in nutrients and easily eroded, especially when plant cover is removed (Sabah Forestry Department 2024). The reserve encompasses a 550-km² area of predominantly hilly, lowland (50–350 m above sea level) dipterocarp forest, dominated by *Dipterocarpus*, *Shorea*, and *Parashorea* species (Sabah Forestry Department 2024). Sustainable forest management techniques (predominately RIL) have been implemented in the reserve since September 1989 (Huth and Ditzer 2000). In 1997, Deramakot became the first tropical production forest to receive Forest Stewardship Council (FSC) certification and has been recognized for its sustainable forest management (Lagan et al. 2007). Since 1997, RIL techniques have been used throughout the reserve in accordance with the certified FSC guidelines (Pinard et al. 1995). The reserve now contains a mosaic of dipterocarp forests at varying levels of regeneration following logging (0–25 years). Previous research indicates that Deramakot contains a high diversity of mammals and amphibians despite logging (Sollmann et al. 2017, Asad et al. 2022).

METHODS

Freshwater turtle sampling and covariate collection

Within Deramakot, we established 8 standardized visual encounter survey (VES) sites (800–3,000 m in length) along separate river reaches (Figure 1). We selected these 8 sites within forestry compartments at varying levels of forest regeneration following RIL (1, 2, 6, 10, 11, 19, and 22 years since logging; Table A1). To ensure standardization of survey effort across reaches varying in length, we divided all VES sites into contiguous subplots 200 m in length (with varying widths depending on the river). We surveyed each VES and nested subplots on 3 occasions between March and July 2019, with 30–55 days between surveys. Two surveyors conducted surveys between 1830 and 2200 hours by walking the length of each subplot (0.33–0.66 m/sec), along opposite banks of the river. We recorded all flat-shelled turtles and soft-shelled turtles detected within or directly adjacent to the water body (<1 m removed). For detected turtles, we collected global positioning system location and time of observation. We hand-captured all flat-shelled turtles and determined adult or juvenile status, curved carapace or straight plastron length, and parasite (e.g., freshwater leeches and nematodes) burden at the point of capture (pausing the survey during processing). We took photographs of the carapace and plastron of flat-shelled turtles for individual identification. Only 8 flat-shelled turtles were not captured (because of escape) during the study (roughly 5%). We did not capture soft-shelled turtles because of the difficulty in handling this species. Following processing, we released turtles behind the observers to reduce the possibility of counting individuals repeatedly. Because of the speed of these species and our personal observations in the field, we find it highly unlikely that our study species swam past the observers and were thus double counted. For both species, we also recorded the stream width, depth, and siltation cover at each turtle detection locality. As these data were not collected systematically throughout each subplot, we could not include them in the modeling process, but we conducted non-parametric testing to determine variation between stream width, depth, and siltation at flat-shelled turtle and soft-shelled turtle detection localities. This data, along with other observations of the species' natural history can be found in Asad et al. (2021*b*).

We collected covariates associated with the detectability or activity of other freshwater turtle species in Borneo (Jensen and Das 2008), and other geographic regions (Rowe 2003, Roe and Georges 2008, Rowe et al. 2009, Anthonysamy et al. 2013): daily average temperature (°C) and humidity (%), maximum daily rainfall (MDR; mm), 30-day rainfall (mm), and lunar phase (%). We collected temperature and humidity daily averages and maximum daily rainfall from the Sabah Forestry Department (SFD) weather station located 0.4–13.5 km from survey sites. As 3 of the sampling months coincided with conditions caused by a dry El Niño event, we summed rainfall to represent total rainfall over a 30-day period before each survey to determine the impact of longer-term rainfall patterns on species detection probability. At the start of each transect visit, we recorded the moon phase (0–100% of lunar disc visible).

To determine habitat associations and responses to RIL in flat-shelled turtles and soft-shelled turtles, we collected environmental covariates previously linked to freshwater turtle occurrence, and covariates that have direct or indirect associations with RIL. These latter covariates were time since RIL (in years), which was recorded for each VES stream survey, and distance to logging road (m), forest height (m), and stream flow accumulation value, which we recorded at each 200-m-long subplot. We obtained time since RIL (1–21 years) from SFD logging records. As logging roads have a direct (Laurance et al. 2009, Yamada et al. 2014) and indirect (Kreutzweiser et al. 2005, Mollinari et al. 2019) impact on biodiversity, we obtained a logging road map (shapefile) from the SFD Deramakot management team. We then determined distance to nearest logging road from each VES subplot as a function of Euclidean distance (m) calculated in ArcGIS 10.3.1 (Esri, Redlands, CA, USA). For quantification of forest height (m), we used a recent model of forest canopy height estimation for the year 2019 provided by Potapov et al. (2021). This new 30-m resolution global forest canopy height dataset was derived from the integration of the Global Ecosystem Dynamics Investigation (GEDI) lidar forest structure measurements and Landsat analysis-ready data time-series (Potapov et al. 2021). It provides a measure of forest disturbance and vegetation structural complexity (Potapov et al. 2021). We computed an average forest height (m) within each VES subplot. Flow accumulation reflects the total flow into a downslope stream (Jenson and Domingue 1988, Manchado et al. 2021) and may be used to identify stream channels and quantify their size (i.e., width and depth); streams with high flow accumulation are areas of concentrated flow. As such, we used flow accumulation as a rough proxy for river size. We calculated flow accumulation values from a 30-m Shuttle Radar Topography Mission (SRTM) digital elevation model using the hydrology tool kit within ArcGIS 10.3.1. The result is a raster of accumulated flow value to each grid cell, as determined by accumulated weight for all cells that flow into each downslope cell. Subsequently, we extracted the highest flow accumulation value within each VES subplot for our analysis. Unfortunately, we were unable to collect measurements such as stream width, depth, siltation, speed, and substrate at consistent intervals along the length of VES river reaches and their subplots. However, based on stream width and depth measurements collected at each turtle capture location, all rivers within the study exhibit similar structural dynamics (Table A1).

Data analysis

To determine the association of flat-shelled and soft-shelled turtle detection and occupancy probability associations with environmental metrics, we used single-species occupancy models within a Bayesian framework. This method allows the estimation of occupancy where species may be detected imperfectly whilst allowing occupancy and detection probability to be modeled as a function of covariates (MacKenzie et al. 2018).

We scaled all climatological, environmental, and logging-associated covariates to have a mean of 0 and a standard deviation of 1 prior to modeling. We tested collinearity between covariates using Spearman's rank correlation in the package Hmsic version 4.2-0 (Harrell 2019) and removed all correlated covariates ($|r| > 0.7$) from subsequent analysis. Additionally, as our data set consisted of 82 subplots (sampling units), with unique covariate values nested within 8 VES river reach sites, we included a random effect in all models to account for the nested spatial effect among subplots within the same VES river reach. Additionally, we treated the 3 survey periods as separate survey occasions in subsequent analysis.

We conducted all single-species occupancy models in the R package ubms version 1.1.0 (Kellner et al. 2022) and used default vague priors for all models: normal distribution with mean = 0, and standard deviation = 10. We ran 3 parallel Markov chains with 10,000 iterations each discarding the first 5,000 as burn-in. We assessed model convergence via the Rhat statistics, whereby values between 1.05 and 1 indicate convergence. As occupancy models assume a linear relationship between coefficients and covariates, we visually confirmed the direction of effects prior to model selection. If species detections exhibited a non-linear association with a covariate, we used a squared version of the scaled covariate in place of the original.

For each species, we conducted model selection via a 2-step process. First, we created single covariate models for each detectability covariate (including a null model with no covariate effects on detection) to determine the optimum detectability model for each species. Following this, we created single-covariate models for each occupancy covariate (including a null model with no effects on occupancy) in combination with the previously selected optimum detection covariate to determine the optimum single-covariate occupancy model for each species. We used single covariates during model selection to determine individual associations between covariates and species occupancy and detectability to avoid the masking of covariate associations, which can occur with additive and interactive models.

For each model's covariate selection stage, we ranked candidate models in ubms using expected log pointwise predictive density (elpd) as a measure of each model's predictive power. To calculate elpd, we used leave-one-out cross validation for pairwise model comparisons (Vehtari et al. 2017). To assess model support in relation to the top model, we calculated pairwise differences in elpd (Δelpd) between each model and the top model along with each model's standard error (SE Δelpd). We considered models with an elpd difference greater than their standard error to be less supported than the top model, and hence we considered the predictive inference of the associated covariate to be limited.

To determine the significance of covariate effects on detection and occupancy probabilities for optimum models, we generated 95% credible intervals of the posterior distributions. We considered 95% Bayesian credible intervals that did not overlap zero to indicate strong, significant support for covariate effects.

RESULTS

We detected 127 hard-shelled turtles and 30 soft-shelled turtles (all for turtles within water) during the study period (Table A1). Although determining recaptures for soft-shelled turtles proved unsuccessful, we recaptured 4 flat-shelled turtles (within 2 sites on different surveys) during the study (details of recaptures and movements can be found in Asad et al. 2021*b*). Hard-shelled turtle and soft-shelled turtle detections occurred at least once in

64.6% and 28.1% of the 82 subplots, respectively, and in 100% of all sampled VES river reaches. Based on Spearman rank correlations, no covariates were strongly correlated; thus, we included all covariates in the model-selection process.

Prior to the development of single-species occupancy models, we determined that soft-shelled turtle detections exhibited a non-linear relationship with time since RIL, with the majority of detections occurring in areas subject to RIL 10–11 years ago (Figure B1). As occupancy models assume linear relationships between species occurrence and covariates, we squared time since RIL to account for this non-linear relationship, and included this covariate in the subsequent model-selection process.

Malayan flat-shelled turtle

Within detection model selection, 30-day rainfall had higher predictive power compared to other detectability covariates (Table C1). Pairwise Δelpd values for the remaining single-covariate (and null) models were greater than their respective SE(Δelpd) values. Therefore, the detectability model based on 30-day rainfall was the best supported for this species; 30-day rainfall exhibited a negative association with flat-shelled turtle detection probability (Figure 2A), with detectability reduced by approximately 15-20% per 100-mm increase in monthly rainfall.

Within occupancy model selection, distance to logging roads had the highest predictive power (Table C1). Pairwise Δelpd of the second ranked model (flow accumulation), was lower than its respective SE(Δelpd); thus, flow accumulation and distance to logging roads were equally effective at predicting flat-shelled turtle occupancy. In the first ranked model, occupancy probability exhibited a positive relationship with distance to logging roads. Sites adjacent to roads (<50 m) exhibited an almost 50% lower probability of occupancy than those >1 km from roads (Figure 3A). In the second ranked model, flow accumulation was positively associated with occupancy probability (Figure 3B), indicating that flat-shelled turtles occurred more frequently in wider or deeper river stretches (with higher flow volume).

Despite negative associations with logging roads, the average occupancy probability (ψ) of flat-shelled turtles predicted by the distance to logging road model was relatively high (ψ = 0.79 ± 0.1 [SD]) at surveyed sites within the reserve (Figure 4A).

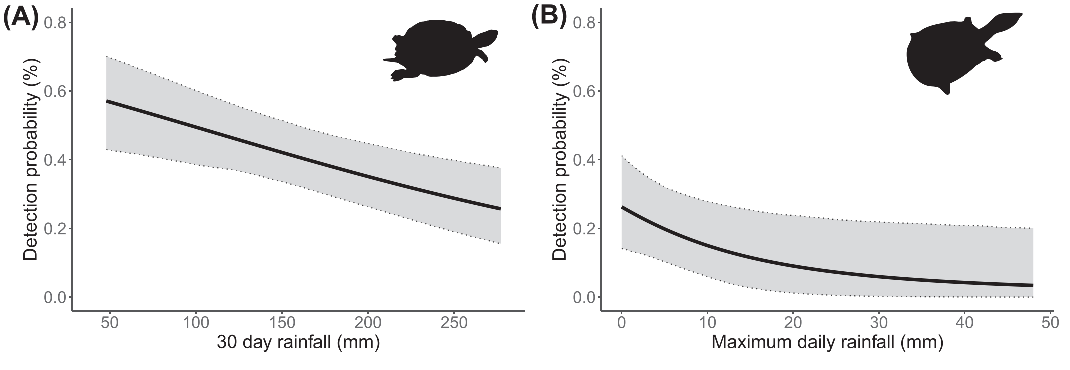

FIGURE 2 Marginal effect plots (posterior means and 95% credible intervals) displaying optimum detection model associations for each of the turtle species in Deramakot Forest Reserve, Sabah, Malaysian Borneo, 2019: A) effects of 30-day rainfall on flat-shelled turtle detection probability and B) effects of maximum daily rainfall on soft-shelled turtle detection probability.

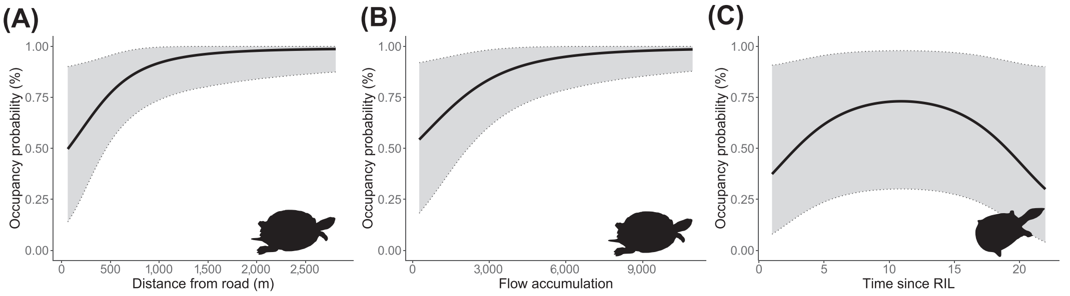

FIGURE 3 Marginal effect plots (posterior means and 95% credible intervals) displaying optimum occupancy model associations for each of the turtle species using data collected on 3 occasions in 8 sites using visual encounter surveys between March to July 2019, in Deramakot Forest Reserve, Sabah, Malaysian Borneo: A) effect of distance to nearest logging road on flat-shelled turtle occupancy probability, B) effect of stream flow accumulation on flat-shelled turtle occupancy probability, and C) effect of time since reduced impact logging (RIL; in years) on soft-shelled turtle occupancy probability.

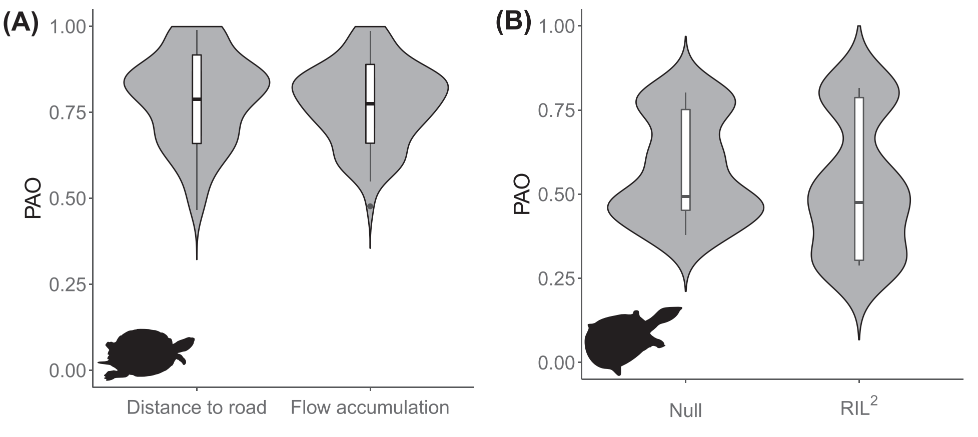

FIGURE 4 Probability of average occupancy (PAO) violin plots generated from the 2 best supported occupancy models for each species using data collected on 3 occasions in 8 sites using visual encounter surveys between March to July 2019, in Deramakot Forest Reserve, Sabah, Malaysian Borneo: A) flat-shelled turtle occupancy based on models including distance to logging road or flow accumulation, and B) soft-shelled turtle occupancy based on the null model and a model including the quadratic effect of time in years since reduced impact logging (RIL^2). White bar represents the interquartile range with the black bar in the middle representing the median and the thin black line representing the rest of the distributions. Grey shades on each side of the bar constitutes a kernel density estimation indicating the distribution of the data with wider sections reflecting higher concentrations or probabilities for occurrence of individuals.

Malayan soft-shelled turtles

Within detection model selection, maximum daily rainfall (MDR) displayed higher predictive power than the other covariates (Table C2). This covariate exhibited a negative association with soft-shelled turtle detection probability, but 95% credible intervals overlapped zero indicating there was little to no evidence of an effect (Figure 2B). All other detection covariate models (including the null model) produced Δelpd values that were lower than their respective SE(Δelpd) values. Overall, the power of MDR (and other covariates) describing soft-shelled turtle detectability was low. Despite its weak performance, we used MDR as the detectability covariate in subsequent models to improve model fit.

Within occupancy model selection, the quadratic form of time since RIL (RIL^2) had the greatest predictive power (Table C2). This covariate displayed a weak negative relationship with occupancy but indicated a slightly higher probability of soft-shelled turtle occurrence 8–12 years after RIL (Figure 3C). However, as with the detection covariates, the Δelpd of the null model (no effects of covariate on occupancy) was lower than its SE(Δelpd). The Δelpd of all other occupancy covariates were only slightly higher than their respective SE(Δelpd). Therefore, although the model containing time since RIL had similar predictive power as the null model, its performance was considerably higher than all other covariates.

Although Rhat values for soft-shelled turtles were within the parameters of model fit (1-1.05), support for optimum detection and occupancy models was considerably poorer than flat-shelled turtle models. Our models did suggest that soft-shelled turtles occupied roughly half ($\psi = 0.57 \pm 0.22$ [SD]) of all surveyed sites within the reserve (Figure 4B).

DISCUSSION

Our study is the first to examine the impacts of RIL practices on freshwater turtles and could provide an essential foundation for future studies and management decisions. While we could not determine detectability or occupancy patterns for the soft-shelled turtles, we successfully identified detection and occupancy relationships for the globally threatened flat-shelled turtle. This turtle exhibited a negative association between its detectability and monthly rainfall. Occupancy was positively associated with higher stream flow accumulation and greater distance from logging roads and was more common in wider or deeper stream stretches, suggesting that flat-shelled turtles may be negatively affected by roads. Regardless, our models predicted high levels of occupancy (> 50%) for both species throughout the reserve.

Influence of rainfall on detectability

Long-term (30-day) rainfall patterns appeared to be the best predictor of detectability for flat-shelled turtles in this study. Higher rainfall is generally expected to decrease the risk of desiccation while increasing the availability of aquatic and fossorial prey, thus favoring increased turtle activity (Rowe 2003, Roe and Georges 2008). Flat-shelled turtles were also encountered during periods of low rainfall in our surveys. This observation could be attributed to the exposure of riverine sandbanks suitable for nesting during low water volume periods caused by low precipitation. This, in turn, could increase rates of nest establishment and related behavior (Eisemberg et al. 2015). A recent review showed that nests of some species of freshwater turtles experience enhanced survivorship if constructed before rainfall (Geller et al. 2022), possibly owing to the removal of olfactory and physical signs of nest deposition. Although the authors also observed potential lekking behavior in flat-shelled turtles (Asad et al. 2021*b*), we cannot determine if rain-associated shifts in breeding caused increased detection during periods of low rainfall.

Although the relationship was weak, maximum daily rainfall was the covariate that best described soft-shelled turtle detectability. Water turbidity and increased silt deposition may have reduced visibility of this species immediately after rainfall. However, more data and further analysis would be required to confirm this linkage. Based on the literature (see Introduction), we assumed both species to be nocturnal. More nocturnal ($n = 151$) compared to diurnal ($n = 7$) encounters with flat-shelled turtles during 3 years of co-occurring amphibian and habitat sampling (S. Asad, Tomorrow University of Applied Science, personal observation) support this assumption. Although primarily nocturnal (Lim and Das 1999), we encountered soft-shelled turtles much less frequently during our surveys (only 30 sightings vs. 127 for flat-shelled turtles). Lower detection rates could accurately reflect lower occurrence of soft-shelled turtles in the reserve consistent with our models. However, such rates could also reflect the difficulty in detecting this species with visual surveys because it can bury itself in sand to hide or ambush prey (Lim and Das 1999, Asad et al. 2021*b*). During surveys, we observed disturbed individuals rapidly burying themselves within sandy substrates. As such, future surveys should combine visual survey methods with traditional trapping to quantify the utility of visual sampling methods for detecting this species.

Habitat and disturbance associations with occupancy

Although habitat associations of flat-shelled turtles are poorly documented, previous research by the authors identified this species in moderately sized, relatively shallow rivers, with an average width of 459 cm (104–964) and depth of 37 cm (11–100; Asad et al. 2021*b*). Shallow, fast-flowing streams with sandy bottoms and an abundance of water plants have been associated with previous records of this species (Lim and Das 1999, Mohd Ibrahim et al. 2019). Data presented herein suggest an association with relatively larger streams as flat-shelled turtle occupancy was positively associated with higher flow accumulation. However, the broadest stream section surveyed was <12 m in width; thus, flat-shelled turtle associations with even wider, higher order streams is untested. The morphological adaptations and ecology of the species are poorly suited to large rivers. Our results likely pertain to streams within hilly forest areas rather than large rivers in lowland or swamp forest areas (>20 m in width). Regardless, larger streams in similar land cover types (hilly, lowland dipterocarp forest) may serve as an important habitat for this species, and as such should be protected for its conservation. We recommend habitat measurements (e.g., stream depth, width, siltation) at finer spatial scales to clarify its habitat associations.

Most records of flat-shelled turtles are restricted to clear streams of undisturbed forests (Sharma and Tisen 2000, Mohd Ibrahim et al. 2019). Our findings somewhat support this, we recorded lower flat-shelled turtle occupancy closer to logging roads, suggesting that roads negatively affected the species. Roads result in mortalities during overland movements, create dispersal barriers, and elevate predation risk (Laurance et al. 2009, Rytwinski and Fahrig 2012, Steen et al. 2012). Although logging roads support less traffic than wider or paved roads, they can cause major changes to the soil, hydrology and water quality of surrounding habitats (Kleinschroth and Healey 2017, Laurance, Goosen and Laurance 2009). Furthermore, logging roads often provide easier accessibility for poachers (Laurance et al. 2006, Kleinschroth and Healey 2017).

Although our results for soft-shelled turtles were less conclusive, we detected the greatest number of soft-shelled turtles in sites subject to RIL 10–11 years earlier, consistent with predicted increased occupancy of these sites (although support for this pattern was weak). Previous research identified a preference by this species for sites experiencing heavy siltation (Asad et al. 2021*b*), which could align with an intermediate level of disturbance. More data and analysis are required to confirm these relationships. Exploring other potential habitat covariates (such as siltation cover and substrate type) that may better describe the occupancy patterns of this species could be useful in future studies.

Freshwater turtle responses to RIL

Although our lack of data from undisturbed primary forests undermines our ability to determine baseline occupancy patterns of these 2 species, they exhibited high occupancy of streams throughout Deramakot Forest Reserve. Previous research indicates that RIL has less impact on forest structure compared to conventional logging methods (Zarin et al. 2007, Putz et al. 2008), and subsequently maintains higher biodiversity (Bicknell et al. 2014, Bohnett et al. 2022). Additionally, the preservation of 30-m riparian buffers throughout the reserve potentially reduces the negative impacts of logging on sensitive aquatic habitats (Asad et al. 2021*a* 2022). Our findings support these conclusions and suggest that sustainably managed forests using RIL methods maintain habitat for some turtle species at the landscape scale. Although logging impacts may penetrate into adjacent buffer zones and streams (Gomi et al. 2006), the terrestrial habitat features assessed in this study (forest height, time since RIL, proximity to logging roads) did not appear to affect adjacent riparian areas, and therefore may not affect the ecology or behavior of primarily aquatic freshwater turtles (particularly for soft-shelled turtles).

Besides forestry practices, another explanation for the high occupancy probabilities of the 2 turtle species in Deramakot Forest Reserve is reduced poaching activities. Thanks to passive (secured gates on reserve borders and forest department presence within the reserve) and active (frequent river and ground patrols and aerial surveillance) site security within the reserve (Lagan et al. 2007), trade-driven poaching of freshwater turtles appears to be minimal.

CONSERVATION IMPLICATIONS

Our study suggests that soft-shelled turtles and particularly flat-shelled turtles can thrive within sustainably managed forests using RIL methods in Southeast Asia. This could be due to the creation of riparian buffers, maintenance of forest structure, and reduced poaching pressure. We recommend that logging roads should be carefully managed in reserves, for example, placing them at a greater distance from larger stream networks, to reduce their negative impact on flat-shelled turtle occupancy. Our detectability results suggest that weather conditions (namely long-term rainfall) should be incorporated into further monitoring of turtle populations (particularly flat-shelled turtles) to ensure reliable population and occurrence estimates. Finally, we strongly recommend that future comparative studies examine occupancy between RIL, conventionally logged, and primary forest sites to resolve the impacts of logging and the role of key habitat features on the distribution of turtles on forest streams in Malaysia.

ACKNOWLEDGMENTS

We thank R. Guharajan, S. T. Wong, A. Wilting, and J. Jeschke who provided invaluable assistance for the entirety of this project, and without whom this research would not have been possible. In addition, the Sabah Forestry Department, in particular P. Lagan and J. Kissing, facilitated access to the study site, assisted with field accommodations, and provided a wealth of weather, logging, and management data. The authors also thank C. Paszkowski and 4 anonymous reviewers for critiques on this manuscript. Funding for this research was provided by The Auckland Zoo, Columbus Zoo, the German Academic Exchange Service (DAAD), the German Society for Herpetology and Hereptoculture, the Museum für Naturkunde, Berlin, and the Leibniz Institute for Zoo and Wildlife Research, Berlin. Open Access funding enabled and organized by Projekt DEAL.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

ETHICS STATEMENT

All animal handling and welfare during this study was compliant with a license granted by Sabah Biodiversity Council (SaBC; permit number: JKM/MBS.1000-2/2 JLD.7 (63)).

DATA AVAILABILITY STATEMENT

Data available on request from the authors.

ORCID

Wei Cheng Tan http://orcid.org/0000-0002-6067-3528

REFERENCES

Anthonysamy, W. J. B., M. J. Dreslik, and C. A. Phillips. 2013. Disruptive influences of drought on the activity of a freshwater turtle. American Midland Naturalist 169:322–335.

Armstrong, D. P. 2016. Using reference sites to account for detection probability in occupancy surveys for freshwater turtles. Herpetological Conservation Biology 11:505–518.

Asad, S., J. F. Abrams, R. Guharajan, P. Lagan, J. Kissing, J. Sikui, A. Wilting, and M.-O. Rödel. 2021*a*. Amphibian responses to conventional and reduced impact logging. Forest Ecology and Management 484:118949.

Asad, S., J. Sikui, B. Binjamin, and M.-O. Rödel. 2021*b*. Natural history of three freshwater turtle species within two logging reserves in Sabah, Malaysian Borneo. Salamandra 57:251–262.

Asad, S., V. Vitalis, R. Guharajan, J. F. Abrams, P. Lagan, J. Kissing, J. Sikui, A. Wilting, and M.-O. Rödel. 2022. Variable species but similar amphibian community responses across habitats following reduced impact logging. Global Ecology and Conservation 35:e02061.

Bicknell, J. E., M. J. Struebig, D. P. Edwards, and Z. G. Davies. 2014. Improved timber harvest techniques maintain biodiversity in tropical forests. Current Biology 24:R1119–R1120.

Böhm, M., B. Collen, J. E. M. Baillie, P. Bowles, J. Chanson, N. Cox, G. Hammerson, M. Hoffmann, S. R. Livingstone, M. Ram, et al. 2013. The conservation status of the world's reptiles. Biological Conservation 157:372–385.

Bohnett, E., B. Goossens, M. S. A. Bakar, T. R. Abidin, H.-Y. Lim, D. Hulse, B. Ahmad, T. Hoctor, and P. Gardner. 2022. Examining diversity of terrestrial mammal communities across forest reserves in Sabah, Borneo. Biodiversity and Conservation 31:1709–1734.

Bradshaw, C. J., N. S. Sodhi, and B. W. Brook. 2009. Tropical turmoil: a biodiversity tragedy in progress. Frontiers in Ecology and the Environment 7:79–87.

Brown, G. W. 2001. The influence of habitat disturbance on reptiles in a Box-Ironbark eucalypt forest of south-eastern Australia. Biodiversity and Conservation 10:161–176.

Brozovic, R., J. F. Abrams, A. Mohamed, S. T. Wong, J. Niedballa, T. Bhagwat, R. Sollmann, S. Mannan, J. Kissing, and A. Wilting. 2018. Effects of forest degradation on the moonrat *Echinosorex gymnura* in Sabah, Malaysian Borneo. Mammalian Biology 93:135–143.

Buchanan, S. W., B. Buffum, G. Puggioni, and N. E. Karraker. 2019. Occupancy of freshwater turtles across a gradient of altered landscapes. Journal of Wildlife Management 83:435–445.

Burivalova, Z., Ç. H. Şekercioğlu, and L. P. Koh. 2014. Thresholds of logging intensity to maintain tropical forest biodiversity. Current Biology 24:1893–1898.

Čapkun-Huot, C., V. K. Fyson, and G. Blouin-Demers. 2021. Landscape composition predicts the local abundance of painted turtles (*Chrysemys picta*). Herpetology Notes 14:215–223.

Cassel, K., J. Vanek, G. Glowacki, T. Preuss, and C. Nielsen. 2019. Multiscale habitat factors influence the occupancy and turnover of the suburban herpetofauna of Chicago, USA. Herpetological Conservation and Biology 14:438–454.

Cheung, S. M., and D. Dudgeon. 2006. Quantifying the Asian turtle crisis: market surveys in southern China, 2000–2003. Aquatic Conservation: Marine and Freshwater Ecosystems 16:751–770.

Cota, M., A. Hamidy, K. Platt, M. D. Kusrini, J. Guntoro, C. R. Shepherd, and S. Schoppe. 2021. IUCN Red List of Threatened Species: *Dogania subplana*. IUCN Red List of Threatened Species. <https://www.iucnredlist.org/species/46578/3008869>. Accessed 17 Apr 2023.

Cox, N., B. E. Young, P. Bowles, M. Fernandez, J. Marin, G. Rapacciuolo, M. Böhm, T. M. Brooks, S. B. Hedges, C. Hilton-Taylor, et al. 2022. A global reptile assessment highlights shared conservation needs of tetrapods. Nature 605:285–290.

Dijk, P. P., B. L. Stuart, and A. Rhodin. 2000. Asian turtle trade: Proceedings of a workshop on conservation and trade of freshwater turtles and tortoises in Asia. Executive summary. Chelonian Research Monograph 2:13–14.

Dykstra, D. P. 2007. Promoting Reduced-Impact Logging in tropical developing countries: a success story of technology transfer. Page 139 *in* C. Miner, R. Jacobs, D. Dykstra, and B. Bittner, editors. Proceedings: International Conference on Transfer of Forest Science Knowledge and Technology. General Technical Report PNW-GTR-726. U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, Oregon, USA.

Eisemberg, C. C., M. Rose, B. Yaru, Y. Amepou, and A. Georges. 2015. Salinity of the coastal nesting environment and its association with body size in the estuarine pig-nosed turtle. Journal of Zoology 295:65–74.

Escalona, T., N. Valenzuela, and D. C. Adams. 2019. Do local environmental factors and lunar cycle influence timing and synchrony of oviposition of a turtle with strict nocturnal nesting? Diversity 11:78.

Food and Agriculture Organization [FAO] and United Nations Environment Programme [UNEP]. 2020. The state of the world's forests 2020: forests, biodiversity and people. FAO and UNEP, Rome, Italy. https://doi.org/10.4060/ca8642en

Fulton, A. M., J. P. Rose, and B. J. Halstead. 2022. Rural turtles: estimating the occupancy of northwestern pond turtles and non-native red-eared sliders in agricultural habitats in California's Sacramento Valley and Sacramento-San Joaquin River Delta. Northwestern Naturalist 103:97–109.

Gaveau, D. L. A., S. Sloan, E. Molidena, H. Yaen, D. Sheil, N. K. Abram, M. Ancrenaz, R. Nasi, M. Quinones, N. Wielaard, and E. Meijaard. 2014. Four decades of forest persistence, clearance and logging on Borneo. PloS ONE 9:e101654.

Geller, G. A., J. S. Doody, S. Clulow, and R. P. Duncan. 2022. Do freshwater turtles use rainfall to increase nest success? Frontiers in Ecology and Evolution 10:852175.

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

Gomi, T., R. C. Sidle, S. Noguchi, J. N. Negishi, A. R. Nik, and S. Sasaki. 2006. Sediment and wood accumulations in humid tropical headwater streams: effects of logging and riparian buffers. Forest Ecology and Management 224:166–175.

Gong, S.-P., A. T. Chow, J. J. Fong, and H.-T. Shi. 2009. The chelonian trade in the largest pet market in China: scale, scope and impact on turtle conservation. Oryx 43:213–216.

Gu, W., and R. K. Swihart. 2004. Absent or undetected? Effects of non-detection of species occurrence on wildlife–habitat models. Biological Conservation 116:195–203.

Guharajan, R., A. Mohamed, S. T. Wong, J. Niedballa, A. Petrus, J. Jubili, R. Lietz, G. R. Clements, W.-M. Wong, J. Kissing, P. Lagan, and A. Wilting. 2021. Sustainable forest management is vital for the persistence of sun bear *Helarctos malayanus* populations in Sabah, Malaysian Borneo. Forest Ecology and Management 493:119270.

Gumbs, R., C. L. Gray, M. Böhm, M. Hoffmann, R. Grenyer, W. Jetz, S. Meiri, U. Roll, N. R. Owen, and J. Rosindell. 2020. Global priorities for conservation of reptilian phylogenetic diversity in the face of human impacts. Nature Communications 11:2616.

Harrell, Jr. F. E. 2019. Hmisc: Harrell miscellaneous. R package version 4.2-0. https://cran.r-project.org/package=Hmisc

Horn, R. B., and J. A. Gervais. 2018. Landscape influence on the local distribution of western pond turtles. Ecosphere 9:e02346.

Huth, A., and T. Ditzer. 2000. Simulation of the growth of a lowland Dipterocarp rain forest with FORMIX3. Ecological Modelling 134:1–25.

Huth, A., and T. Ditzer. 2001. Long-term impacts of logging in a tropical rain forest—a simulation study. Forest Ecology and Management 142:33–51.

Jensen, K. A. 2006. Ecology and use of Asian soft-shell turtle (*Amyda cartilaginea*) with notes on other species. Thesis, Universiti Malaysia Sarawak (UNIMAS), Kota Samarahan, Sarawak, Malaysia.

Jensen, K. A., and I. Das. 2008. Observations on the influence of seasonality, lunar cycles, and weather condition on freshwater turtle activity in Sarawak, East Malaysia (Borneo). Asiatic Herpetological Research 11:39–44.

Jenson, S. K., and J. O. Domingue. 1988. Extracting topographic structure from digital elevation data for geographic information-system analysis. Photogrammetric Engineering and Remote Sensing 54:1593–1600.

Kellner, K. F., N. L. Fowler, T. R. Petroelje, T. M. Kautz, D. E. Beyer Jr., and J. L. Belant. 2022. ubms: an R package for fitting hierarchical occupancy and N-mixture abundance models in a Bayesian framework. Methods in Ecology and Evolution 13:577–584.

Kellner, K. F., and R. K. Swihart. 2014. Accounting for imperfect detection in ecology: a quantitative review. PloS ONE 9:e111436.

Kleine, M., and J. Heuveldop. 1993. A management planning concept for sustained yield of tropical forests in Sabah, Malaysia. Forest Ecology and Management 61:277–297.

Kleinschroth, F., and J. R. Healey. 2017. Impacts of logging roads on tropical forests. Biotropica 49:620–635.

Kreutzweiser, D. P., S. S. Capell, and K. P. Good. 2005. Effects of fine sediment inputs from a logging road on stream insect communities: a large-scale experimental approach in a Canadian headwater stream. Aquatic Ecology 39:55–66.

Kusrini, M. D., A. Hamidy, J. Guntoro, M. Cota, and S. Schoppe. 2021. IUCN Red List of Threatened Species: *Notochelys platynota*. IUCN Red List of Threatened Species. <https://www.iucnredlist.org/en>. Accessed 24 Feb 2023.

Lagan, P., S. Mannan, and H. Matsubayashi. 2007. Sustainable use of tropical forests by reduced-impact logging in Deramakot Forest Reserve, Sabah, Malaysia. Pages 414–421 *in* T. Nakashizuka, editor. Sustainability and diversity of forest ecosystems: an interdisciplinary approach. Springer Japan, Tokyo, Japan.

Laurance, W. F., B. M. Croes, L. Tchignoumba, S. A. Lahm, A. Alonso, M. E. Lee, P. Campbell, and C. Ondzeano. 2006. Impacts of roads and hunting on central African rainforest mammals. Conservation Biology 20:1251–1261.

Laurance, W. F., M. Goosem, and S. G. W. Laurance. 2009. Impacts of roads and linear clearings on tropical forests. Trends in Ecology and Evolution 24:659–669.

Lim, B. L., and I. Das. 1999. Turtles of Borneo and Peninsular Malaysia. Natural History Publications (Borneo), Kota Kinabalu, Malaysia.

MacKenzie, D. I., J. D. Nichols, J. A. Royle, K. H. Pollock, L. L. Bailey, and J. E. Hines. 2018. Chapter 4—Basic presence/absence situation. Pages 115–215 *in* D. I. MacKenzie, J. D. Nichols, J. A. Royle, K. H. Pollock, L. L. Bailey, and J. E. Hines, editors. Occupancy estimation and modeling (second edition). Academic Press, Boston, Massachusetts, USA.

Manchado, C., A. Roldán-Valcarce, D. Jato-Espino, and I. Andrés-Doménech. 2021. ArcDrain: a GIS add-in for automated determination of surface runoff in urban catchments. International Journal of Environmental Research and Public Health 18:8802.

Manthey, U., and W. Grossmann. 1997. Amphibien und Reptilien Südostasiens. Natur und Tier Verlag, Münster, Germany.

Mohd Ibrahim, N. S., B. H. Badli Sham, N. Shafie, and A. Ahmad. 2019. Species diversity of freshwater turtles and tortoises in Terengganu, Malaysia. Journal of Sustainability Science and Management 2018:1–27.

Mohd Salleh, M. H., Y. Esa, S. M. Salleh, and S. A. Mohd Sah. 2022. Turtles in Malaysia: a review of conservation status and a call for research. Animals 12:2184.

Mollinari, M. M., C. A. Peres, and D. P. Edwards. 2019. Rapid recovery of thermal environment after selective logging in the Amazon. Agricultural and Forest Meteorology 278:107637.

Nichols, J. D., J. E. Hines, J. R. Sauer, F. W. Fallon, J. E. Fallon, and P. J. Heglund. 2000. A double-observer approach for estimating detection probability and abundance from counts. Auk 117:393–408.

Nijman, V., and C. R. Shepherd. 2022. Trade in southeast Asian box turtles from Indonesia: legality, livelihoods, sustainability and overexploitation. Diversity 14:970.

Ocock, J. F., G. Bino, S. Wassens, J. Spencer, R. F. Thomas, and R. T. Kingsford. 2018. Identifying critical habitat for Australian freshwater turtles in a large regulated floodplain: implications for environmental water management. Environmental Management 61:375–389.

Parlin, A. F., J. A. Nardone, J. K. Dougherty, M. Rebein, K. Safi, and P. J. Schaeffer. 2018. Activity and movement of free-living box turtles are largely independent of ambient and thermal conditions. Movement Ecology 6:12.

Pinard, M. A., F. E. Putz, J. Tay, and T. E. Sullivan. 1995. Creating timber harvest guidelines for a reduced-impact logging project in Malaysia. Journal of Forestry 93:41–45.

Potapov, P., X. Li, A. Hernandez-Serna, A. Tyukavina, M. C. Hansen, A. Kommareddy, A. Pickens, S. Turubanova, H. Tang, C. E. Silva, et al. 2021. Mapping global forest canopy height through integration of GEDI and Landsat data. Remote Sensing of Environment 253:112165.

Premono, B., R. Rizaldi, and I. Izmiarti. 2015. Kelimpahan populasi dan kondisi habitat labi-labi (*Dogania subplana*: Reptilia: Trionychidae) di kawasan kampus Universitas Andalas Padang. Jurnal Biologi UNAND 4:26–30.

Pritchard, P. C. 2001. Observations on body size, sympatry, and niche divergence in softshell turtles (Trionychidae). Chelonian Conservation and Biology 4:5–27.

Putz, F. E., P. Sist, T. Fredericksen, and D. Dykstra. 2008. Reduced-impact logging: challenges and opportunities. Forest Ecology and Management 256:1427–1433.

Roe, J. H., and A. Georges. 2008. Terrestrial activity, movements and spatial ecology of an Australian freshwater turtle, *Chelodina longicollis*, in a temporally dynamic wetland system. Austral Ecology 33:1045–1056.

Roll, U., A. Feldman, M. Novosolov, A. Allison, A. M. Bauer, R. Bernard, M. Böhm, F. Castro-Herrera, L. Chirio, B. Collen, et al. 2017. Publisher correction: the global distribution of tetrapods reveals a need for targeted reptile conservation. Nature Ecology and Evolution 1:1785.

Rowe, J. W. 2003. Activity and movements of midland painted turtles (*Chrysemys picta marginata*) living in a small marsh system on Beaver Island, Michigan. Journal of Herpetology 37:342–353.

Rowe, J. W., G. C. Lehr, P. M. McCarthy, and P. M. Converse. 2009. Activity, movements and activity area size in stinkpot turtles (*Sternotherus odoratus*) in a southwestern Michigan lake. American Midland Naturalist 162:266–275.

Rytwinski, T., and L. Fahrig. 2012. Do species life history traits explain population responses to roads? A meta-analysis. Biological Conservation 147:87–98.

Sabah Forestry Department. 2024. 3rd Forest Management Plan (1st January, 2015–31st December, 2024: Deramakot Forest Reserve Forest Management Unit No. 19A. Sabah Forestry Department, Sandakan, Sabah, Malaysia. <https://deramakot.sabah.gov.my/images/pdf/pub/3rd_FMP_Deramakot.pdf>

Selman, W., C. Qualls, and J. C. Owen. 2013. Effects of human disturbance on the behavior and physiology of an imperiled freshwater turtle. Journal of Wildlife Management 77:877–885.

Sharma, D. S. K., and O. B. Tisen. 2000. Freshwater turtle and tortoise utilization and conservation status in Malaysia. Chelonian Research Monographs 2:120–128.

Shepherd, C. R., L. Gomez, and V. Nijman. 2020. Illegal wildlife trade, seizures and prosecutions: a 7.5-year analysis of trade in pig-nosed turtles *Carettochelys insculpta* in and from Indonesia. Global Ecology and Conservation 24:e01249.

Sloan, S., M. J. Campbell, M. Alamgir, A. M. Lechner, J. Engert, and W. F. Laurance. 2019. Trans-national conservation and infrastructure development in the heart of Borneo. PloS ONE 14:e0221947.

Sollmann, R., A. Mohamed, J. Niedballa, J. Bender, L. Ambu, P. Lagan, S. Mannan, R. C. Ong, A. Langner, B. Gardner, and A. Wilting. 2017. Quantifying mammal biodiversity co-benefits in certified tropical forests. Diversity and Distributions 23:317–328.

Stanford, C., A. Rhodin, P. P. Dijk, B. Horne, T. Blanck, E. Goode, R. Hudson, R. Mittermeier, A. Currylow, C. Eisemberg, et al. 2018. Turtles in trouble: the world's 25+ most endangered tortoises and freshwater turtles – 2018. Turtle Conservation Coalition, Ojai, California, USA.

Steen, D. A., J. P. Gibbs, K. A. Buhlmann, J. L. Carr, B. W. Compton, J. D. Congdon, J. S. Doody, J. C. Godwin, K. L. Holcomb, D. R. Jackson, et al. 2012. Terrestrial habitat requirements of nesting freshwater turtles. Biological Conservation 150: 121–128.
Van, T. P., V. Q. Luu, T. V. Tien, B. Leprince, L. T. T. Khanh, and L. Luiselli. 2019. Longitudinal monitoring of turtle trade through Facebook in Vietnam. Herpetological Journal 29:48–56.
Vehtari, A., A. Gelman, and J. Gabry. 2017. Practical Bayesian model evaluation using leave-one-out cross-validation and WAIC. Statistics and Computing 27:1413–1432.
Walter, O. 2000. A study of hunting and trade of freshwater turtles and tortoises (order Chelonia) at Danau Sentarum. Borneo Research Bulletin 31:323–336.
Yamada, T., M. Niino, S. Yoshida, T. Hosaka, and T. Okuda. 2014. Impacts of logging road networks on dung beetles and small mammals in a Malaysian production forest: implications for biodiversity safeguards. Land 3:639–657.
Zarin, D. J., M. D. Schulze, E. Vidal, and M. Lentini. 2007. Beyond reaping the first harvest: management objectives for timber production in the Brazilian Amazon. Conservation Biology 21:916–925.

Associate Editor: Cynthia Paszkowski.

How to cite this article: Tan, W. C., V. Vitalis, J. Sikuim, D. Rödder, M.-O. Rödel, and S. Asad. 2024. High freshwater turtle occupancy of streams within a sustainably managed tropical forest in Borneo. Journal of Wildlife Management e22633. https://doi.org/10.1002/jwmg.22633

APPENDIX A: SITE AND SURVEY SUMMARY

TABLE A1 Summary of the 8 visual encounter survey (VES) river reaches surveyed on 3 occasions between March and July 2019 in Deramakot Forest Reserve, Sabah, Malaysian Borneo, including their time since reduced impact logging (RIL), averaged covariates values (± SD) from each VES, averaged stream width and depth (recorded at turtle detection locations), and number of soft-shelled turtle and flat-shelled turtle detections (with detections during each occasion presented in parentheses).

VES river ID	Length (m)	Number of subplots	Time since RIL (years)	Stream flow accumulation	Forest height (m)	Distance to logging road (m)	Stream width (m)	Stream depth (m)	Soft-shelled turtle detections	Flat-shelled turtle detections
DF18-28_C64	2,400	12	1	3,642.54 ± 1,766.19	31.54 ± 1.39	463.01 ± 144.86	517.25 ± 156.65	37.72 ± 12.6	1 (0) (0) (1)	11 (5) (4) (2)
DF30_C72	2,000	10	2	1,295.45 ± 631.56	27.55 ± 2.65	394.54 ± 153.88	385.05 ± 123.67	36.1 ± 19.65	4 (1) (3) (0)	16 (3) (8) (5)
SDC43_C63	1,800	9	6	1,705.33 ± 510.17	30.94 ± 2.88	649.08 ± 92.9	395.33 ± 158.02	41.42 ± 27.82	2 (2) (0) (0)	19 (6) (11) (2)
DF40_C71	2,200	11	10	1,290.23 ± 725.71	26.95 ± 2.86	314.62 ± 50.88	354.29 ± 126.1	31.93 ± 16.79	6 (2) (1) (3)	11 (5) (4) (2)
SDC42_C61	2,400	12	11	1,991.67 ± 782.6	31.71 ± 0.72	682.34 ± 161.38	465.48 ± 156.44	42.63 ± 17.95	10 (4) (3) (3)	13 (9) (1) (3)
DF41_C43	2,000	10	19	6,735.45 ± 3,668.57	31.2 ± 1.38	1,004.02 ± 178.38	557.26 ± 192.04	33.68 ± 12.27	2 (0) (2) (0)	36 (7) (26) (3)
SDC31_C53	1,200	6	19	3,010 ± 305.12	32.33 ± 1.08	488.82 ± 197.26	396.43 ± 147.32	34.09 ± 20.84	3 (2) (1) (0)	4 (3) (1) (0)
SDC29_C55	2,400	12	22	2,589.08 ± 1,246.19	29.12 ± 2.65	590.36 ± 390.89	416.74 ± 154.94	33.02 ± 11.9	2 (1) (1) (0)	17 (5) (6) (6)

APPENDIX B: DETECTION AT SITES VARYING IN YEARS SINCE RIL

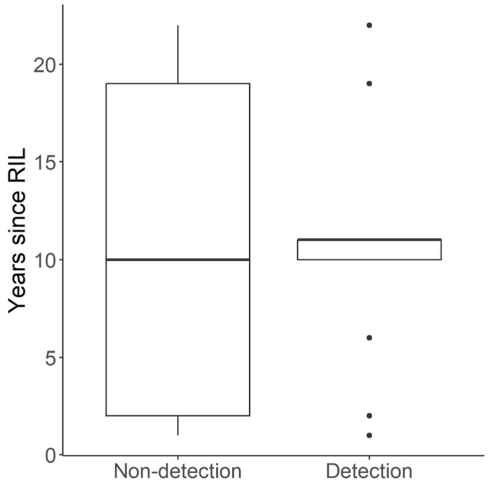

FIGURE B1 Soft-shelled turtle detections and non-detections throughout all 82 surveyed subplots within the 8 visual encounter survey transects at varying levels of regeneration following reduced impact logging (RIL; 1–22 years since logging). Survey data were collected on 3 occasions between March and July 2019 in Deramakot Forest Reserve, Sabah, Malaysian Borneo.

APPENDIX C: MODEL RESULTS

TABLE C1 Model covariate selection by ranking single-species occupancy models using expected log pointwise predictive density (elpd), number of parameters (nparam), and pairwise differences in elpd (Δelpd) between each model and the top model along with their standard errors (SE Δelpd) for flat-shelled turtle in Deramakot Forest Reserve, Sabah, Malaysian Borneo, 2019. We obtained the estimated effect sizes (estimate) of each covariate on the detection and occupancy probability from the models, with an asterisk (*) indicating significant evidence of an association (95% credible intervals not overlapping zero). Covariate abbreviations are as follows: MDR = maximum daily rainfall and RIL = years since reduced impact logging.

Covariate	elpd	nparam	Δelpd	SE Δelpd	Weight	Estimate
Detection						
30-day rainfall	152.887	3.927	0.000	0.000	0.999	−0.493 *
Temperature	156.455	4.211	−3.568	2.494	0.000	0.301
Humidity	−156.65	4.399	−3.763	2.152	0.000	−0.299
Null	157.179	3.011	−4.292	2.804	0.000	
MDR	157.642	4.211	−4.754	2.742	0.000	−0.193
Lunar phase	158.235	4.118	−5.348	2.799	0.000	−0.008
Occupancy						
Distance to logging road	150.064	4.325	0.000	0.000	0.609	2.058 *
Flow accumulation	150.347	4.513	−0.282	1.665	0.391	1.373 *
30-day rainfall	152.887	3.927	−2.823	1.879	0.000	
RIL	153.681	4.696	−3.617	1.987	0.000	0.0417
Forest height	153.736	4.961	−3.672	2.045	0.000	−0.225
Null	157.179	3.011	−7.115	3.277	0.000	

TABLE C2 Model covariate selection by ranking single-species occupancy models using expected log pointwise predictive density (elpd), number of parameters (nparam), and pairwise differences in elpd (Δelpd) between each model and the top model along with their standard errors (SE Δelpd) for soft-shelled turtle in Deramakot Forest Reserve, Sabah, Malaysian Borneo, 2019. We obtained the estimated effect sizes (estimate) of each covariate on the detection and occupancy probability from the models. Covariate abbreviations are as follows: MDR = maximum daily rainfall and RIL = years since reduced impact logging.

Covariate	elpd	nparam	Δelpd	SE Δelpd	Weight	Estimate
Detection						
MDR	−85.084	6.395	0.000	0.000	0.731	−0.749
Null	−85.594	5.006	−0.510	2.084	0.269	
Humidity	−86.038	5.964	−0.954	2.211	0.000	−0.246
30-day rainfall	−86.219	6.159	−1.135	2.321	0.000	−0.230
Lunar phase	−86.311	6.167	−1.227	2.276	0.000	−0.178
Temperature	−86.56	6.302	−1.476	2.198	0.000	0.104
Occupancy						
RIL^2	−83.739	5.523	0.000	0.000	0.836	−1.076
MDR	−85.084	6.395	−1.345	1.203	0.000	
Null	−85.594	5.006	−1.855	2.420	0.164	
Forest height	−85.699	6.774	−1.961	1.548	0.000	−0.524
Distance to logging road	−85.751	6.800	−2.013	1.393	0.000	−0.033
Flow accumulation	−86.710	7.940	−2.971	2.657	0.000	−0.373