

Occupancy of wild southern pig-tailed macaques in intact and degraded forests in Peninsular Malaysia

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Deforestation is a major threat to terrestrial tropical ecosystems, particularly in Southeast Asia where human activities have dramatic consequences for the survival of many species. However, responses of species to anthropogenic impact are highly variable. In order to establish effective conservation strategies, it is critical to determine a species' ability to persist in degraded habitats. Here, we used camera trapping to provide first insights into the temporal and spatial distribution of southern pig-tailed macaques (*Macaca nemestrina*, listed as 'Vulnerable' by the IUCN) across intact and degraded forest habitats in Peninsular Malaysia, with a particular focus on the effects of clear cutting and selective logging on macaque occupancy. Specifically, we found a 10% decline in macaque site occupancy in the highly degraded Pasoh Forest Reserve from 2013 to 2017. This may be strongly linked to the macaques' sensitivity to clear cutting which significantly increased the probability that *M. nemestrina* became locally extinct at a previously occupied site. In contrast, no clear relationship was found between site occupancy and selective logging. Accordingly, the macaques' age and sex structure did not differ between undisturbed and selectively logged habitats within the Belum-Temengor Forest Complex. This suggests that selectively logged forests still constitute valuable habitats for *M. nemestrina* that need to be protected against further degradation. Our results emphasize the significance of population monitoring through camera trapping for understanding the ability of threatened species to cope with anthropogenic disturbance. This can inform species management

plans and facilitate the development of effective conservation measures to protect biodiversity.

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Abstract

Deforestation is a major threat to terrestrial tropical ecosystems, particularly in Southeast Asia where human activities have dramatic consequences for the survival of many species. However, responses of species to anthropogenic impact are highly variable. In order to establish effective conservation strategies, it is critical to determine a species' ability to persist in degraded habitats. Here, we used camera trapping to provide first insights into the temporal and spatial distribution of southern pig-tailed macaques (*Macaca nemestrina*, listed as 'Vulnerable' by the IUCN) across intact and degraded forest habitats in Peninsular Malaysia, with a particular focus on the effects of clear cutting and selective logging on macaque occupancy. Specifically, we found a 10% decline in macaque site occupancy in the highly degraded Pasoh Forest Reserve from 2013 to 2017. This may be strongly linked to the macaques' sensitivity to clear cutting which significantly increased the probability that *M. nemestrina* became locally extinct at a previously occupied site. In contrast, no clear relationship was found between site occupancy and selective logging. Accordingly, the macaques' age and sex structure did not differ between undisturbed and selectively logged habitats within the Belum-Temengor Forest Complex. This suggests that selectively logged forests still constitute valuable habitats for *M. nemestrina* that need to be protected against further degradation. Our results emphasize the significance of population monitoring through camera trapping for understanding the ability of threatened species to cope with anthropogenic disturbance. This can inform species management plans and facilitate the development of effective conservation measures to protect biodiversity.

Introduction

Tropical rainforests are highly complex ecosystems that exhibit exceptional biodiversity (Gallery, 2014). Yet, continuing human population growth, expanding infrastructure and the intensive cultivation of crops lead to dramatically increasing deforestation rates, which are the major threat to these remarkable habitats (Rosa et al., 2016). Malaysia is a biodiversity hotspot with high primate diversity but is still losing large parts of its natural habitat to new oil palm plantations, mining operations and the timber industry (Vijay et al., 2016; Omran & Schwarz-Herion, 2020). During the past decade, the country has lost 11.3% of its primary forest and 16.8% of tree cover (Mongabay, 2021). As reported by the International Union for Conservation

of Nature (IUCN, 2020), more than one fourth of Malaysia's mammals are threatened with extinction. Among them are 23 non-human primates (hereafter 'primates'), one of which is the southern pig-tailed macaque (*Macaca nemestrina*), a little-studied, predominantly terrestrial species native to Southeast Asia (Bernstein, 1967).

Macaca nemestrina inhabits tropical rainforests of Malaysia, Indonesia and southern Thailand (Ang et al., 2020). The dramatic decline of primary forest habitat in the primates' range, human hunting of macaques for food and pet trade, and their widespread perception as crop pests have contributed to rapidly decreasing populations during the past few decades (Linkie et al., 2007; Ang et al., 2020). Only recently, Ang et al. (2020) confirmed the macaques' negative population trend and its current status as 'Vulnerable' (IUCN, 2020). Meijaard et al. (2007) reported a generally high sensitivity of this species to logging, yet the macaques' response to human disturbance remains poorly understood (Ang et al., 2020). To date, we lack detailed knowledge on *M. nemestrina*'s distribution, their abundance as well as their ability to cope in anthropogenically impacted habitats. However, this is crucial to understand in order to establish effective protection measures ensuring the long-term survival of this and other threatened wildlife species affected by human activities.

It is well known that human land use drastically reduces biodiversity and important ecosystem functions of primary forests (Marques et al., 2019; Alroy, 2017; Barnes et al., 2014). Degraded habitats, such as forest fragments, monocultures or urban environments were shown to include on average 41% fewer species than undisturbed forests (Alroy, 2017). Numerous studies have highlighted the negative impact of clear-felling on biodiversity, with the conversion of tropical forests into oil palm plantations being the main driver of deforestation in many Southeast Asian countries (Koh & Wilcove, 2007; Fitzherbert et al., 2008). The establishment of oil palm monocultures does not only imply severe losses in species richness, but also substantially contributes to habitat fragmentation and environmental pollution through chemical fertilizers or pesticide runoffs (reviewed in Fitzherbert et al., 2008). Particularly, larger mammals and specialized bird species may have difficulties in permanently adapting to and surviving in these monocultural landscapes (Danielsen & Heegaard, 1995; Fitzherbert et al., 2008). The negative effects of habitat degradation on animal populations may further be reinforced by the increase of so-called 'edge effects', describing ecological alterations that result from the development of abrupt, artificial edges of forest fragments (Didham et al., 1998). Forest edges open up the

canopy and dry out the wood, which increases the susceptibility of forests to fire (Cochrane, 2003).

Selective logging is one of the most widespread, yet a less intensive form of habitat degradation (Asner et al., 2005). It refers to the removal of a limited number of economically valuable tree species of a given age in a particular area and/or during a distinct logging cycle (Johns, 1985). However, it also implies secondary threats, such as an increased hunting pressure from local communities, as logging roads facilitate human access to forests (Robinson, Redford & Bennett, 1999; Milner-Gulland & Bennett, 2003). Previous research suggested that selective timber extraction may have less severe effects on species diversity and abundance than more intense forms of land use change, e.g. through clear cutting (Ibarra et al., 2017; Gibson et al., 2011). However, Tobias (2015) highlighted the high variability in the reaction of different species to habitat degradation, with both logging practices as well as species traits, such as diet and body mass, being important factors in determining the effects of selective timber harvesting on wildlife abundance. This is in line with other studies suggesting that generalist feeding tendencies in particular are indicative for the ability of a species to persist in selectively logged habitats (Vetter et al., 2011; Burivalova et al., 2015). Carnivores, as well as frugivorous and insectivorous forest specialists, on the other hand, were reported to be rather confined to undisturbed primary forests (Brodie, Giordano & Ambu, 2015; Tobias, 2015). In this context, caution is needed when inferring the adaptive capacity of one species from the response of another.

Macaca nemestrina is best adapted to lowland and hill dipterocarp forests (Ang et al., 2020). The macaques' diet primarily consists of fruits (Caldecott, 1986), indicating their value as seed dispersers and, consequently, their key role in forest regeneration (Albert et al., 2014, Ruppert et al., 2014), but also suggesting that they are frugivorous forest specialists with limited ecological flexibility. Although this species readily enters oil palm plantations in search of food (Ruppert et al., 2018; Holzner et al., 2019), previous studies highlighted the macaques' dependency on primary forest habitat as a safe retreat to sleep and socialize (Ruppert et al., 2014, A Holzner, unpublished data), confirming doubts on their ability to permanently persist in highly disturbed habitats (Caldecott, 1986). Using camera trapping, we provide first insights into the impact of forest degradation through tree felling on the occupancy of *M. nemestrina* in Peninsular Malaysia. Firstly, we used a dynamic occupancy modelling approach (MacKenzie et al., 2003) to

assess temporal changes in the macaques' distribution as well as factors potentially impacting dynamics in site occupancy in the highly disturbed Pasoh Forest Reserve (PFR), which was affected by partial clear cutting and selective logging from 2013 to 2017. Secondly, we investigated the macaques' spatial distribution within the Belum-Temengor Forest Complex (BTFC), focusing on differences between the undisturbed, totally protected Royal Belum State Park and the selectively logged Temengor Forest Reserve. Finally, we assessed potential differences in the macaques' age and sex structure in undisturbed as well as selectively logged forests within BTFC. This can inform about vital parameters of population dynamics, particularly breeding success and survival, and therefore be indicative of population health.

Methods

Study sites

Our study was conducted at two different sites in Peninsular Malaysia, which are characterized by different degrees of human disturbance. One site is located within the Pasoh Forest Reserve (PFR) in the state of Negeri Sembilan (102°31'0''E, 2°98'0''N). Large parts of the 140 km² sized PFR were logged between the 1950s and 1970s, today comprising regenerating lowland forest. Only its 4 km² sized core area still consists of virgin primary forest (Fletcher et al., 2012). Also today, PFR is subject to clear-felling and selective logging. It is surrounded by oil palm plantations from all sides. The second study site is located within the Belum-Temengor Forest Complex (BTFC) in the state of Perak (101°15'0''E, 101°46'0''E, 5°55'0''N-5°0'0''N). With a size of approximately 3,000 km², BTFC forms parts of the second-largest contiguous forest complex in Peninsular Malaysia. It comprises lowland, hill and upper dipterocarp, as well as montane forest (Rayan & Linkie, 2016). A highway (i.e. the Gerik-Jeli Highway) dissects the forest complex into two areas, i.e. the strictly protected Royal Belum State Park (hereafter 'Belum') in the north, and the Temengor Forest Reserve (hereafter 'Temengor'), where selective logging has been ongoing since the 1970s, in the south (Rayan & Linkie, 2016).

Camera trap setup

This study is based on camera trap data originally collected to assess habitat use of mainland clouded leopards (*Neofelis nebulosa*) in PFR (Tan et al., 2017), as well as density and habitat use

of tigers (*Panthera tigris*), occupancy of ungulates and interactions between large carnivores in BTFC (Rayan & Linkie, 2015, 2016, 2020). All necessary permits from the Perak State Parks Corporation, the Department of Wildlife and National Parks and the Forestry Department of Perak were acquired prior to data collection. Due to the non-invasive nature of observational studies based on camera trapping, no ethical approval was required.

Detection data of *M. nemestrina* from PFR were provided by the Tropical Ecology Assessment and Monitoring Network (TEAM Network 2019). In PFR, camera trapping was conducted from 2013 to 2017. Each camera trap was active for an average of 33 consecutive days per year. The camera setup covered an area of 120 km², including a grid of 60 cameras. The spacing between cameras was approximately 1.5 km. Camera images of macaques detected in BTFC were provided by D. Mark Rayan and WWF Malaysia. Here, camera trapping was conducted from 2009 to 2011. Camera traps were active for an average of 86 consecutive days between August 2009 and May 2010 in Temengor, and 82 consecutive days between August 2010 and April 2011 in Belum. The camera setup covered an area of approximately 400 km² in each habitat (Rayan & Linkie, 2015). A grid of 70 cameras was created in Belum and Temengor, respectively, with each grid cell covering 2 km x 2 km. To increase spatial coverage, the cameras were moved within the grid after three to four months of operation, resulting in 140 distinct camera locations. The sampling blocks within Belum and Temengor were chosen to represent the entire forest by taking into account the proportion of different vegetation types (Rayan & Linkie, 2015).

Figure 1 provides an overview on camera placements in PFR and BTFC. Camera traps (RECONYX and SONY P41) were separated by a minimum distance of 1 km from one another. As the approximate home range size of *M. nemestrina* is 1 km² (Ruppert et al., 2018; Holzner et al., 2019), a macaque group was unlikely to be detected by two different cameras, ensuring spatial independence between sites. Camera traps were active for 24 hours per day and set to take photos at 10-second intervals. They were fixed to trees at a height of approximately 50 cm above the ground. Ground trapping (as opposed to placing cameras higher up in the trees) was reasonable for this species, as *M. nemestrina* has previously been described as a predominantly terrestrial primate, spending on average 56% of its active time on the forest ground (Ruppert et al., 2018). GPS locations of the cameras were recorded using Garmin GPSMAP® 60CSX handheld GPS units.

Detection histories

Based on presence and absence data obtained from photographic records, we constructed detection histories for each camera site in PFR and BTFC. For repeated sampling occasions, we recorded a ‘1’ when macaques were detected and a ‘0’ when no macaques were detected even though a camera trap was active, either because they were truly absent from a particular site or because they were outside the detection range of a camera trap. Referring to previous studies (Tan et al., 2017; Semper-Pascual et al., 2020), we pooled daily detection/non detection records for each camera site into sampling occasions of seven (PFR) and 14 (BTFC) consecutive days, respectively, in order to minimize the risk of temporal interdependency among occasions. The periods of one and two weeks, respectively, were chosen to ensure a good model fit. As several camera traps within BTFC intermittently failed to record data for at least two sampling occasions and thus were excluded from analysis, the final datasets of Belum and Temengor included 129 and 125 camera sites, respectively. The total number of sampling occasions per year ranged between two and nine (mean $\pm$ standard deviation SD = 5.5 ± 2.0) in PFR and between two and eleven (mean $\pm$ SD = 7.0 ± 1.9) in BTFC.

Occupancy modelling

Using a maximum likelihood approach, occupancy models account for imperfect detection by linking a state model determining occupancy (ψ , i.e. the probability with which a species occurs at a specific site), with an observation model determining detection probability (p , i.e. the ability to detect a species correctly when it is present) based on repeated samples from the same site (MacKenzie et al., 2002). Variation in probabilities across sampling sites and observation periods can be modelled using site-specific (e.g. habitat variables) and observation-specific (e.g. the sampling effort) covariates.

Firstly, to assess temporal changes in the macaques’ distribution in the PFR, we fit the dynamic occupancy model described by MacKenzie et al. (2003). This assesses site occupancy dynamics over multiple seasons by estimating, besides detection (p) and first year occupancy (ψ), the probabilities of colonization (γ , i.e. the probability that a species is present at a previously unoccupied site) and extinction (ϵ , i.e. the probability that a species is absent at a previously occupied site, MacKenzie et al., 2003). We included the mean elevation per camera grid cell

(range = 94-664 m, mean $\pm$ SD = 295 $\pm$ 156 m) and the shortest distance to the forest edge (range = 5-2865 m, mean $\pm$ SD = 1076 $\pm$ 695 m) as potential predictors for first year ψ . Both altitude, as well as edge effects which are likely to affect microclimate and tree communities in areas near the forest border, are known to be important factors in predicting the distribution of wildlife species, including primates (McCain & Grytnes, 2010; Brodie, Giordano & Ambu, 2015). Further, a shorter distance of a camera site from the forest edge may facilitate human access and thus increase hunting pressure (Milner-Gulland & Bennett, 2003). Additionally, we modelled variation in γ and ε using a yearly site-specific covariate describing the occurrence and intensity of forest degradation through tree felling at a camera site during the past five years. Based on previous studies highlighting differences in species' responses depending on the severity of human activity (Gibson et al., 2011; Tobias, 2015), we distinguished between clear cutting, i.e. land use change resulting in the loss of the entire forest cover in a specific area, selective logging, i.e. the removal of a limited number of economically valuable trees for the timber industry, and no disturbance/tree felling. We considered the timespan of five years based on previous studies highlighting that primate populations may be critically affected also several years after logging took place (Shelton, 1985; Rao & Schaik, 1997). Finally, we included the survey effort, i.e. the number of days a camera trap was active during a sampling occasion (range = 1-7, mean $\pm$ SD = 6.0 $\pm$ 1.8 days), the sampling month (Jan, Feb, May-Dec) and the sampling year (2013-2017) as predictors for p in order to account for seasonal variation and the effects of abiotic factors on the macaques' activity (Takemoto, 2004; Hanya et al., 2018). Based on the six predictor variables, we constructed the full model and subsequently built candidate models with all possible combinations of predictor sets.

Secondly, to assess the macaques' spatial distribution within the BTFC, we fit a single-season occupancy model (MacKenzie et al., 2002). We are confident that our dataset, including sampling periods of a maximum length of five months, meets the closure assumption of occupancy modelling (i.e. that the occupancy status of a site does not change during the sampling, MacKenzie et al., 2002), as previous studies suggested home range areas of *M. nemestrina* to be stable even over several years (Ruppert et al., 2018; Holzner et al., 2019). As above, we included the mean elevation per grid cell (range = 323-1664 m, mean $\pm$ SD = 737 $\pm$ 302 m) as a potential predictor for ψ . To account for the effects of habitat degradation on ψ , we further modelled the habitat type (undisturbed Belum or selectively logged Temengor), and the

mean Normalized Difference Vegetation Index (NDVI, range = 0.45-0.85, mean $\pm$ SD = 0.78 $\pm$ 0.05, for details on computation see Rayan & Linkie, 2015). The NDVI estimates the density of green on a patch of land by measuring differences between visible and near-infrared reflectance of vegetation cover, thus having frequently been used as a proxy to describe the bio-structural changes in vegetation caused by land clearing and logging (Weier & Herring, 2000; Rayan & Linkie, 2015; Hamel et al., 2009). Additionally, we included the distance to the nearest human settlement, including indigenous villages and logging camps in the forest (range = 662-20643 m, mean $\pm$ SD = 8099 $\pm$ 4756 m), as this may be indicative of the intensity of human hunting of macaques at a camera site (Milner-Gulland & Bennett, 2003). Finally, to account for variation in p , we included the survey effort (range = 1-14 days, mean $\pm$ SD = 12.1 $\pm$ 3.6 days) and the sampling month (Jan-May, Aug-Dec) as observation-specific predictors into the model. As described above, we constructed the full model based on all six predictor variables and then built candidate models with all possible combinations of these predictors.

We fitted the occupancy models for PFR and BTFC, respectively, using the functions *colext* and *occu* from the package ‘unmarked’ (version 1.0.1, Fiske & Chandler, 2011) in R (version 3.4.4, R Core Team, 2018). To facilitate model interpretation and convergence, we standardized all continuous predictors before model fitting to a mean of zero and a standard deviation of one (Schielzeth, 2010). We drew inference using multi model inference based on Akaike's information criterion (AIC, Burnham & Anderson, 2002). Following recommendations of MacKenzie (2006), we first modelled detection, identifying a suitable covariate structure for p while holding ψ and, in the dynamic model of PFR, γ and ε at the most general model including all covariates. Having identified the most parsimonious model structure for p , we kept this constant and modelled occupancy, colonization and extinction, respectively. We assessed the role of our covariates on ψ , γ and ε by ranking all candidate models according to their AIC corrected for small sample sizes (AIC_c, Burnham & Anderson, 2002). We considered top-ranked models as those with $\Delta\text{AIC}_c \leq 2$ (Burnham & Anderson, 2002). Model estimates were obtained by averaging over all candidate models using the zero method (Nakagawa & Hauber, 2011). We tested the goodness of fit of the global models by comparing the observed Chi-square statistics to respective reference distributions calculated from 1000 parametric bootstraps (MacKenzie & Bailey, 2004). This indicated no lack of fit for both models (both $P > 0.05$, further details and R functions used in Supplemental Methods).

273

274 *Assessment of the macaques' age and sex structure*

275 To gain deeper insight into the viability of *M. nemestrina* in selectively logged forests, we
 276 compared age and sex ratios in the macaque populations in Belum and Temengor, respectively,
 277 based on camera trap images. Due to limitations in data availability for PFR, this assessment was
 278 restricted to BTFC. Each individual detected was identified as adult male, adult female, subadult,
 279 juvenile or infant according to its body size and sexual characteristics (e.g. anogenital swelling or
 280 elongated nipples in females, and prominent testes in males, Bullock et al., 1972), or individual
 281 behaviour (e.g. juveniles ranging in frequent proximity to their mother or infants nipple holding).
 282 Individuals that were partly hidden from view and thus could not be clearly assigned to either of
 283 these categories were marked as 'unknown'. We then summed the number of independent
 284 detections in each age and sex class, separately for each of the two habitats. Following O'Brien
 285 et al. (2003) and Kafley et al. (2019), we defined independent detections as (1) consecutive
 286 photographs of identifiable different individuals based on their unique characteristics, (2)
 287 consecutive photographs of individually unrecognizable macaques of the same age and sex class
 288 taken more than 30 minutes apart, or (3) non-consecutive photographs of individuals of the same
 289 age and sex class. As described above, spatial independence between camera sites was assumed
 290 due to the generally small home range size of approximately 1 km² of *M. nemestrina* (Ruppert et
 291 al., 2018; Holzner et al., 2019). The identification of individuals in images across cameras was
 292 not possible in the framework of this study. We assessed differences in the macaques' age and
 293 sex structure between Belum and Temengor using a Chi-square test for independence.

294

295 **Results**

296 *Detection of macaques in PFR and BTFC*

297 Within **Pasoh Forest Reserve** (PFR), we detected *M. nemestrina* during 42.3% of in total 1636
 298 independent sampling occasions. The naïve occupancy, i.e. the proportion of camera sites with at
 299 least one detection (MacKenzie et al., 2006), ranged between 0.80 and 0.93 during the five-year
 300 sampling period, with the highest rate recorded in 2013. In the Belum-Temengor Forest Complex
 301 (BTFC), macaques were present during 13.3% of 1774 sampling occasions. The naïve

occupancy was 0.53 in the undisturbed forest of Belum and 0.39 in the selectively logged forest of Temengor.

Based on AIC, camera trapping effort and the sampling date significantly contributed to explaining the variation in the detection probability of *M. nemestrina* (Table 1). Specifically, detection was positively correlated with the number of trapping days at both study sites, i.e. PFR and BTFC (model estimate $\pm$ standard error (PFR/BTFC) = 0.51 ± 0.06 / 0.61 ± 0.12), and varied between sampling year and sampling month, respectively, indicating the presence of seasonal effects (details in Table S2). The mean estimated detection probability across all camera sites was 0.48 (SD = 0.15) in PFR and 0.23 (SD = 0.11) in BTFC.

Temporal changes in macaque site occupancy in the highly disturbed PFR

Using a dynamic occupancy modelling approach, we aimed at predicting temporal changes in macaque site occupancy as well as their potential causes in PFR. The initial occupancy probability of *M. nemestrina* in PFR was estimated to be 0.95 (standard error (SE) = 0.03), when fixing elevation and the distance to the forest edge at their mean values. Macaque site occupancy in subsequent years was found to decrease by 10% from 0.95 in 2013 to 0.85 in 2017 (Fig. 2).

Further, we assessed the role of environmental and anthropogenic factors in predicting occupancy, colonization and extinction in PFR. Accordingly, only the top-ranked model, including forest degradation (arising from tree felling through clear cutting or selective logging) as predictor for extinction, received substantial support ($\Delta AICc \leq 2$, Table 2). In line with this, model-averaged coefficients corroborated the effect of forest degradation on the local extinction probability of *M. nemestrina* in PFR (Table 3). Specifically, the probability that the macaques were absent at a previously occupied camera site was found to be approximately six-fold higher in areas affected by clear cutting compared to undisturbed forest patches (Fig. 3). No significant effect could be found for selective logging, yet large confidence intervals indicate high variability in the response of *M. nemestrina* to this less intensive form of habitat degradation, likely relating to different practices and intensities of selective timber harvesting (Fig. 3). Further, low model-averaged coefficients and 95% confidence intervals including zero suggest that both elevation and the distance of a camera site to the forest edge did not significantly affect macaque site occupancy in PFR (Table 3).

Macaques' spatial distribution in undisturbed and selectively logged forests within BTFC

To better understand the effects of selective logging on *M. nemestrina*, we assessed the macaque distribution as well as the covariate structure that best explains variation in occupancy probabilities within BTFC. Unlike in PFR, we found evidence that elevation had a strong effect on site occupancy in BTFC, as indicated by its inclusion in the top-ranked model ($\Delta AIC_c \leq 2$, Table 2). Specifically, occupancy probability was found to significantly decrease with increasing elevation (Table 3, Fig. 4). Note that elevation was on average lower in PFR than BTFC, and only included a small portion of the variation found in BTFC (see Methods). Further, low model-averaged coefficients and comparatively large 95% confidence intervals suggest that occupancy did not significantly differ between habitats. Predicted occupancy probabilities in the strictly protected forest of Belum and the selectively logged forest of Temengor were 0.59 (SE = 0.08) and 0.58 (SE = 0.09), respectively, when fixing all other covariates at their mean values. Similarly, the NDVI and distance to the closest human settlement had no effect on macaque site occupancy (Table 3).

Macaques' age and sex structure in BTFC

To explicitly examine the viability of *M. nemestrina* in selectively logged forests, we investigated whether the macaques' age and sex structure differed between intact and partially degraded habitats within BTFC. We detected a total of 614 and 695 individual macaques in Belum and Temengor, respectively, 96% of which could be unambiguously assigned to an age-sex class. Chi-square test of independence did not reveal significant differences in the age-sex ratio between the undisturbed forest of Belum and the selectively logged forest of Temengor ($\chi^2 = 0.45$, $df = 4$, $p = 0.98$). In both habitats, approximately 60% of detected individuals were adults, while 40% of detections were immatures including subadults, juveniles and infants (Fig. 5).

Discussion

Globally, increasing human encroachment into natural habitats is a major cause of biodiversity loss (Marques et al., 2019), yet previous studies have highlighted the high variability in species'

ability to cope with anthropogenic impact (Brodie, Giordano & Ambu, 2015). This study provides first insights into the temporal and spatial distribution of *M. nemestrina* across intact and degraded forest habitats in Peninsular Malaysia, focusing on the effects of tree felling on macaque occupancy over time. Specifically, clear cutting significantly increased the probability that *M. nemestrina* became locally extinct at a previously occupied site, likely accounting for the considerable decline in site occupancy observed in PFR during our five-year study period from 2013 to 2017. In contrast, selective logging did not predict dynamics in site occupancy within PFR, which is consistent with our findings from BTFC where occupancy probabilities did not depend on whether a site was located in the undisturbed forest of Belum or the selectively logged forest of Temengor. In line with this, there were no differences in the macaques' age and sex structure between Belum and Temengor, suggesting that degraded habitat, such as selectively logged forest, may under certain conditions allow macaques to maintain viable populations.

Despite increasing the interval of sampling occasions in BTFC from seven to 14 days, detection was more than twice as likely in PFR than BTFC. As pointed out by previous research (Neilson et al., 2018), the comparatively higher detection probability in PFR (i.e. a relatively small forest surrounded by oil palm plantations) may have various reasons, such as small home range areas frequently reported for primate groups ranging in anthropogenic environments (McLennan, Spagnoletti & Hockings, 2017), high group densities (Parsons et al., 2017), or increased movement on the ground due to canopy gaps in degraded forests (Ancorenaz et al., 2014). Another crucial factor in determining variation in the detection of wildlife may be seasonality. Based on our results, the date of sampling was identified as an important predictor for detection probability. Prolonged rainfall during the monsoon season may decrease the macaques' overall activity and/or terrestriality (Takemoto, 2004; Hanya et al., 2018), thus resulting in a lower probability of being detected by the camera traps on the ground. Whereas camera trapping was performed from August until May in BTFC, in PFR more than 87% of sampling days took place during the commonly dryer period between May and August, likely resulting in lower variability and a higher detection probability in PFR compared to BTFC. Overall, these results confirm previous findings which stressed the importance to account for imperfect detection during the data collection when studying the occurrence or distribution of wild animals (MacKenzie, 2006).

As one of the world's leading palm oil producers, Malaysia continues to be affected by deforestation, which has dramatic consequences for many tropical species that rely on primary

rainforest (Vijay et al., 2016; Estrada et al., 2017). Our results provide evidence that southern pig-tailed macaques are particularly threatened by intensive forest clearance. Clear cutting for the purpose of converting natural forest, whether primary or selectively logged, into other land use forms, including agricultural land, is likely to dramatically reduce the suitability of a habitat for these macaques. In degraded forests, wildlife may suffer from habitat fragmentation, reduced food availability and a high human hunting pressure facilitated by the increased accessibility to the remaining forest patches (Johns, 1985; Tilker et al., 2019). Selectively logged forests, on the other hand, may sustain viable macaque populations under certain conditions. Previous studies suggested that species characterized by a more generalist diet and thus a lower degree of frugivory may thrive in partially logged habitats (Johns & Skorupa, 1987; Vetter et al., 2011). Although the main component of *M. nemestrina*'s natural diet are fruits (ca. 75%, Caldecott, 1986) they feed on a wide range of other foods, such as insects, leaves, mushrooms and small mammals (Ang et al., 2020). Southern pig-tailed macaques inhabiting a forest-oil palm matrix at the west coast of Peninsular Malaysia were reported to complement their natural forest diet with cultivated oil palm fruits and plantation rats (Ruppert et al., 2018; Holzner et al., 2019), suggesting that macaques may indeed be able to adapt their diet to changing environmental conditions, as also found for other Malaysian primates (Johns, 1985). Overall, our data indicate that previously selectively logged forests may constitute a valuable habitat for *M. nemestrina* and therefore should be protected and regenerated instead of opened for more land development. Ultimately, it is imperative to clearly differentiate between these partially degraded, but for the protection of biodiversity very important forests (Johns, 1985; Leong & Powell & Lindsell, 2015) and inhabitable monoculture plantations. Frequently, the latter are likewise defined as 'forest' (e.g. Peninsular Malaysia's National Forestry Act of 1984) and thus continue to legally replace selectively logged areas, i.e. potential primate habitats, in many forest reserves after the high-value forest timber had been extracted (Aziz, Lurance & Clements, 2010).

Nevertheless, it is crucial to stress here that the effects of selective logging on the macaques' ability to occupy and persist in a habitat strongly depend on the intensity of human activity, including secondary threats such as hunting pressure by humans. As demonstrated by Tilker et al. (2019), intensive hunting may be an even more immediate threat to tropical wildlife than moderate habitat degradation. Both the distance to human settlements and the distance to the forest edge were not included in our top-ranked occupancy models, indicating that hunting

activities by indigenous tribes, local residents and logging workers may have been rather low at our study sites. In BTFC, this may be closely linked to low densities of settlements which entail far distances of on average 8 km to camera sites. Furthermore, based on our analyses, we can infer primarily macaque occupancy, yet not necessarily abundance. Although MacKenzie and Nichols (2004) proposed that occupancy may serve as a surrogate for abundance estimation and some earlier studies found strong associations between occupancy and density in carnivorous species (Clare, Anderson & MacFarland, 2015; Linden et al., 2017), this relationship remains unknown for *M. nemestrina*. Therefore, in order to provide in-depth information on whether or not selective logging affects the long-term viability of *M. nemestrina*, more detailed studies including larger data sets are needed.

With low to moderate human disturbance, elevation in particular appears to be an important factor in predicting whether macaques occur at a given site. This is unsurprising, as elevation defines different floristic zones and thus determines food availability for the predominantly frugivorous southern pig-tailed macaques (Saw, 2010). Our result is consistent with previous findings reporting the highest density of southern pig-tailed macaque groups in lowland and dipterocarp hill forest, as compared to montane forest (Ang et al., 2020). Accordingly, McCain & Grytnes (2010) found a general trend of declining species richness with increasing elevation across multiple taxa, including small mammals, reptiles, or amphibians. However, PFR lacks this correlation between elevation and macaque site occupancy, potentially due to low variation between camera sites and generally lower altitudes not exceeding 670 m. In BTFC, on the other hand, altitudes reached up to 1600 m. Ultimately, this may explain the general discrepancy between occupancy estimates in PFR and BTFC.

There are no current population assessments of *M. nemestrina* in its range but general estimates are primarily based on assumptions inferred from knowledge available from other primates occupying the same or similar habitats (Ang et al., 2020). Here, we add to these findings by providing thorough insight into the macaques' ability to persist in human-impacted habitats and quantifying the effect of tree felling activities on the distribution of *M. nemestrina*. We confirm how population monitoring through camera trapping can contribute to understanding the response of an elusive and threatened Malaysian primate to ecological and anthropogenic factors, and hence to informing conservation efforts. The present study stresses the high sensitivity of *M. nemestrina* to severe human encroachment, such as forest clearance for the cultivation of

monocultures. This confirms previous findings emphasizing the macaques' dependency on primary forest habitat to be able to perform the full range of their natural behavioural repertoire (A Holzner, unpublished data). This includes the formation of strong social relationships which are critical characteristics of group-living animals owing to their crucial link to individual fitness (Cameron, Setsaas & Linklater, 2009; Schülke et al., 2010; Ellis et al., 2019) and offspring survival (Silk, Alberts & Altmann, 2003). To counteract population declines at accelerated rates, as shown for many wildlife species around the globe (WWF, 2020), conservation actions need to focus on the maintenance (and if necessary, restoration) of primary and secondary forest habitats, including partially degraded forest that can provide valuable habitat for various species, such as *M. nemestrina*. Specifically, the protection of selectively logged forest against conversion into other land use forms, e.g. monoculture plantations, targeted restoration efforts of degraded habitats, and the reconnection of isolated forests through the establishment of wildlife corridors in fragmented habitats are important conservation measures. This may facilitate natural dispersal between wildlife populations, which is inevitable to ensure the long-term survival of this and other species.

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Author contributions

Conceptualization, N.R., H.K., A.W. and A.H.; Investigation (data provision), D.M.R, J.M. and C.K.W.T.; Formal Analysis, A.H., L.C. and L.K.; Visualization, A.H.; Writing – Original Draft, A.H.; Writing – Review & Editing, all authors; Funding acquisition, N.R., A.H. and D.M.R.

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Figure 1

Study sites in Peninsular Malaysia.

The maps indicate the camera trap distribution in Belum-Temengor Forest Complex (left) and Pasoh Forest Reserve (right). Adapted from Darmaraj (2012).

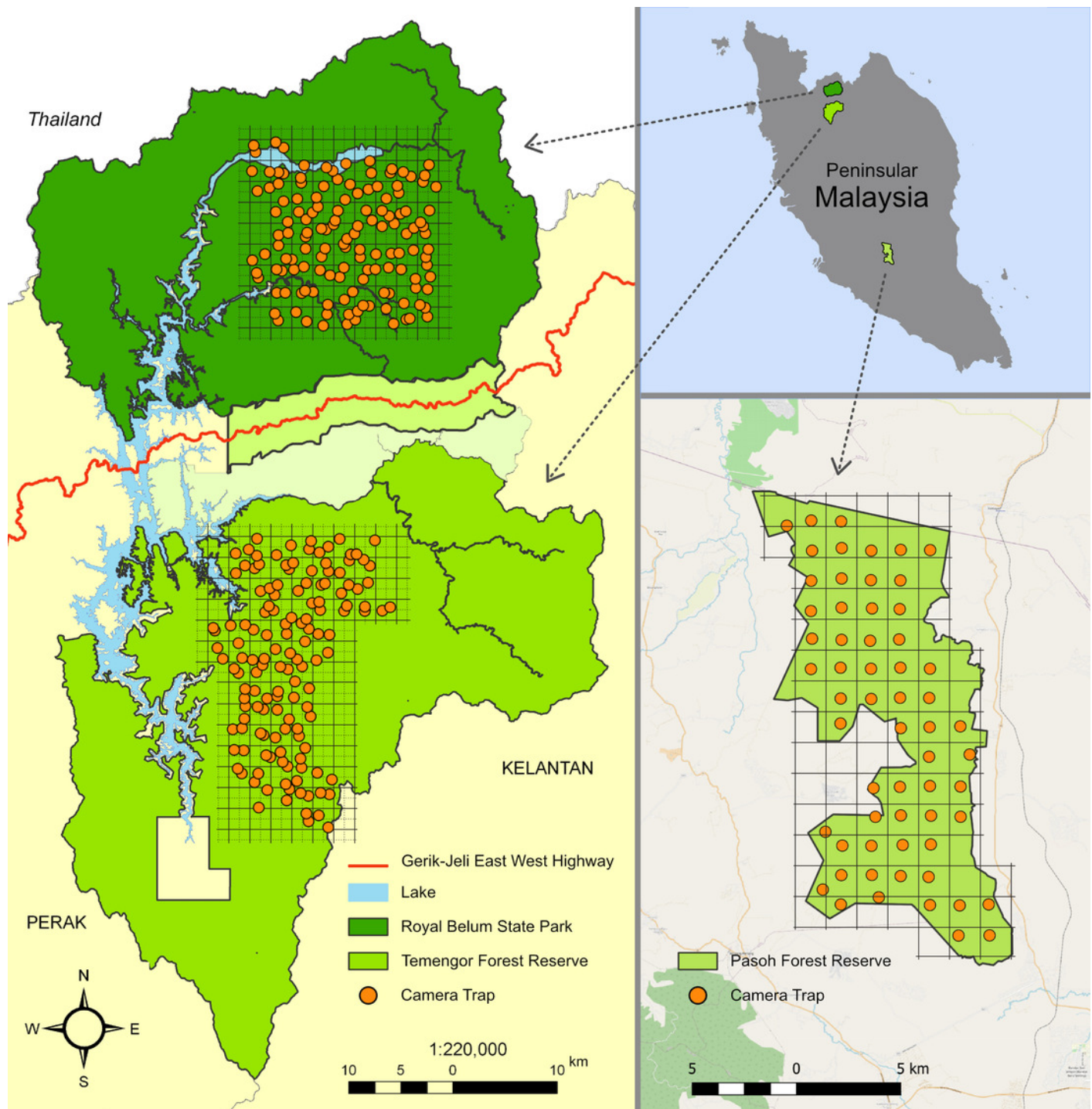


Figure 2

Dynamics in *Macaca nemestrina* occupancy in Pasoh Forest Reserve from 2013 to 2017.

Shown are smoothed site occupancy estimates, i.e. the predicted proportion of sampled sites that are occupied, and their standard errors (N = 60). The bars indicate the cumulative proportion of sites at which clear cutting occurred.

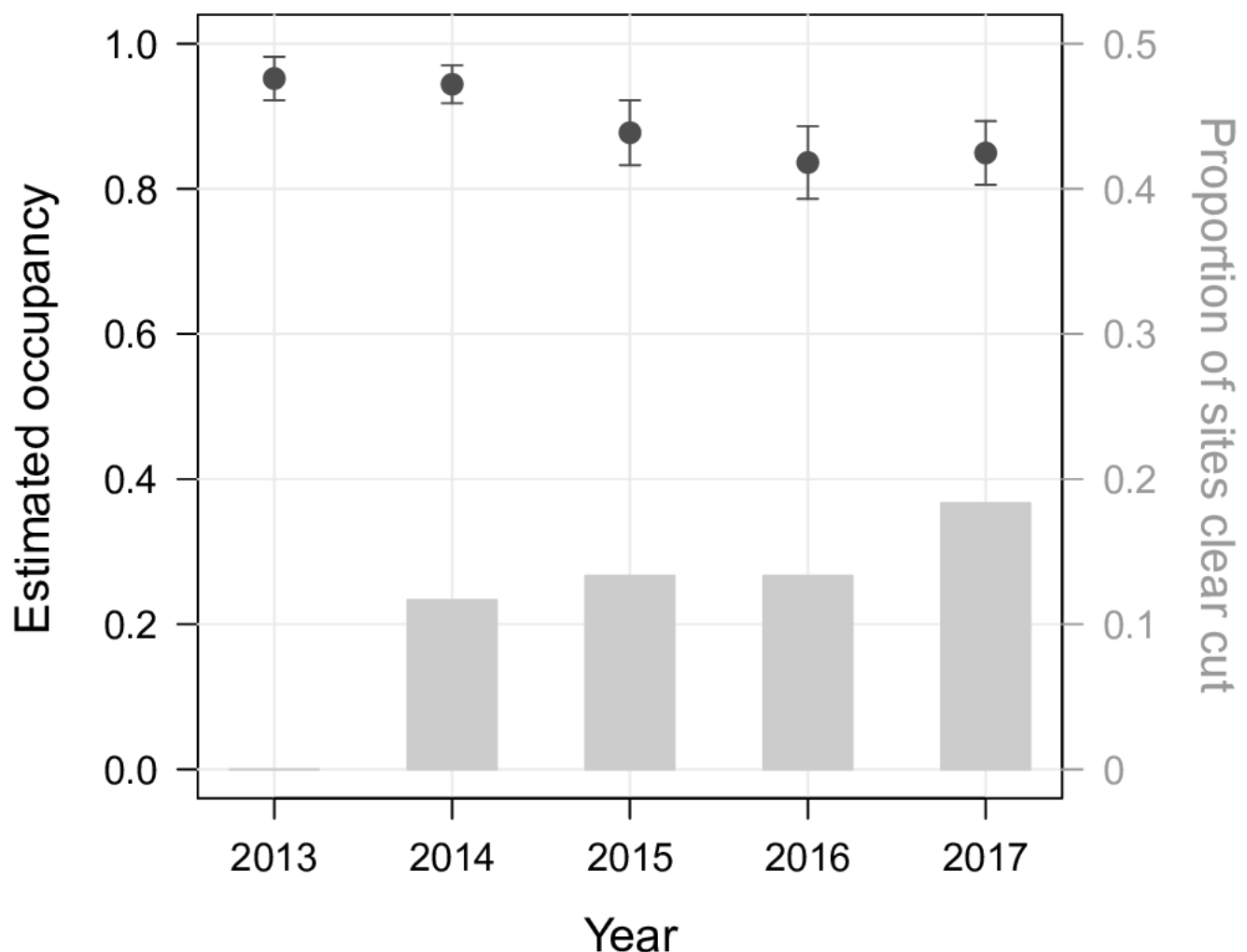


Figure 3

Effect of forest degradation on the local extinction probability of *Macaca nemestrina* in Pasoh Forest Reserve.

The filled circles show the fitted model and the whiskers its 95% confidence interval, conditional on all other predictors being fixed at their mean values (N = 60).

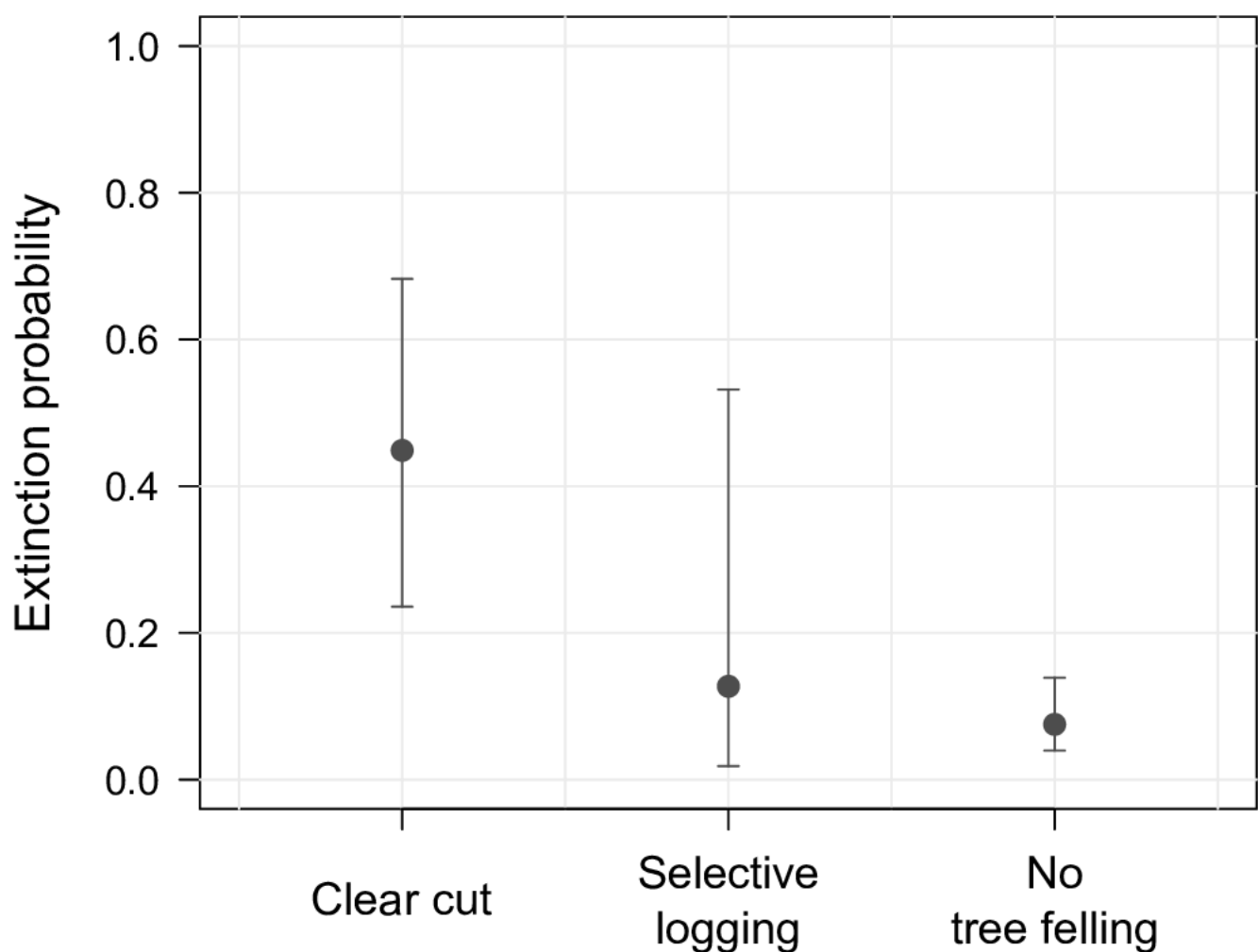


Figure 4

Effect of elevation on site occupancy of *Macaca nemestrina* in Belum-Temengor Forest Complex.

The solid line shows the fitted model and the shaded areas its 95% confidence interval, conditional on all other predictors being fixed at their mean values (N = 254). The dashed lines indicate the mean elevation at the two study sites, i.e. Belum-Temengor Forest Complex (BTFC) and Pasoh Forest Reserve (PFR).

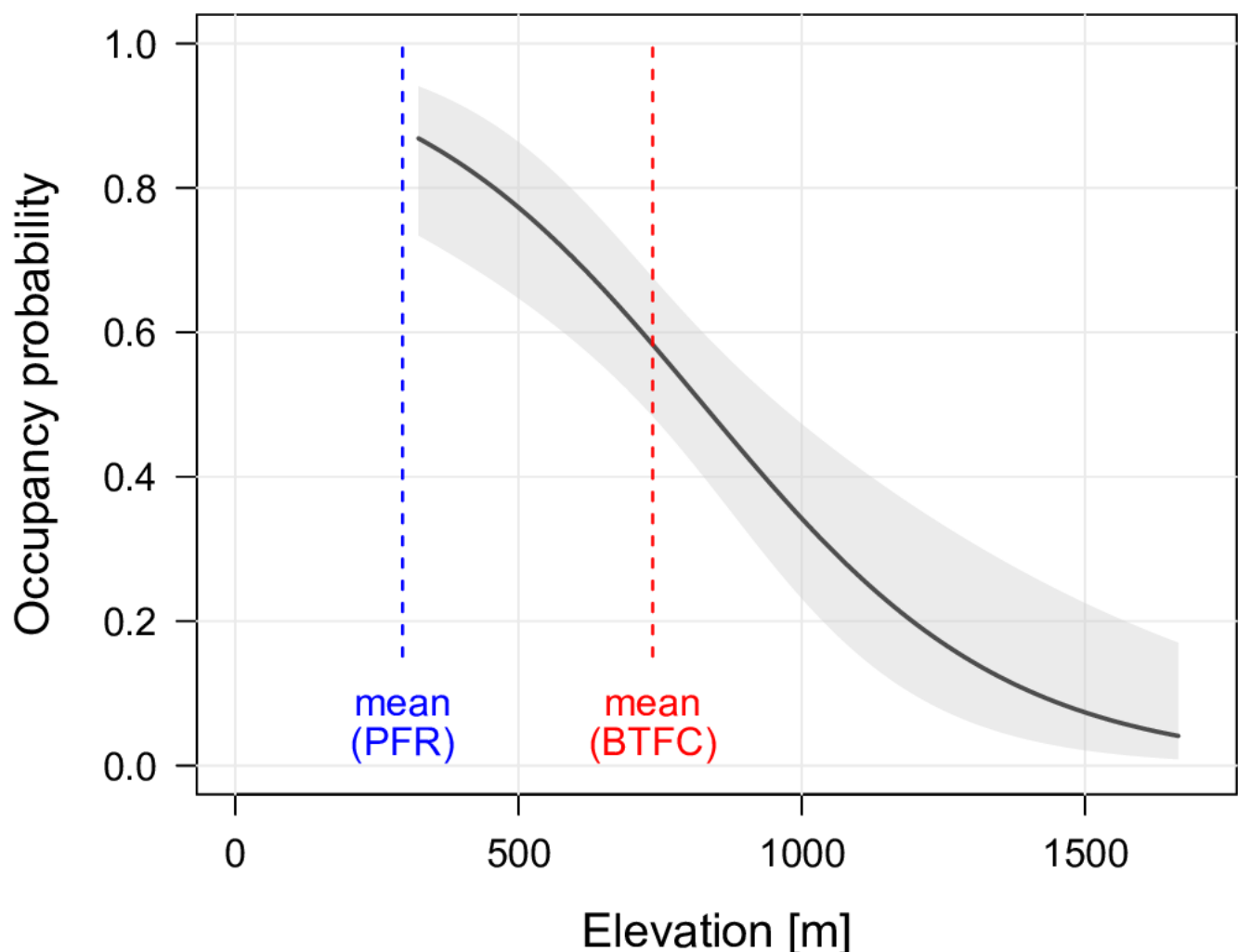


Figure 5

Age-sex structure of *Macaca nemestrina* in the Belum-Temengor Forest Complex.

Pie charts indicate the proportion of independent detections of each age-sex category, separately for the Royal Belum State Park (Belum, N = 594) and the Temengor Forest Reserve (Temengor, N = 663).

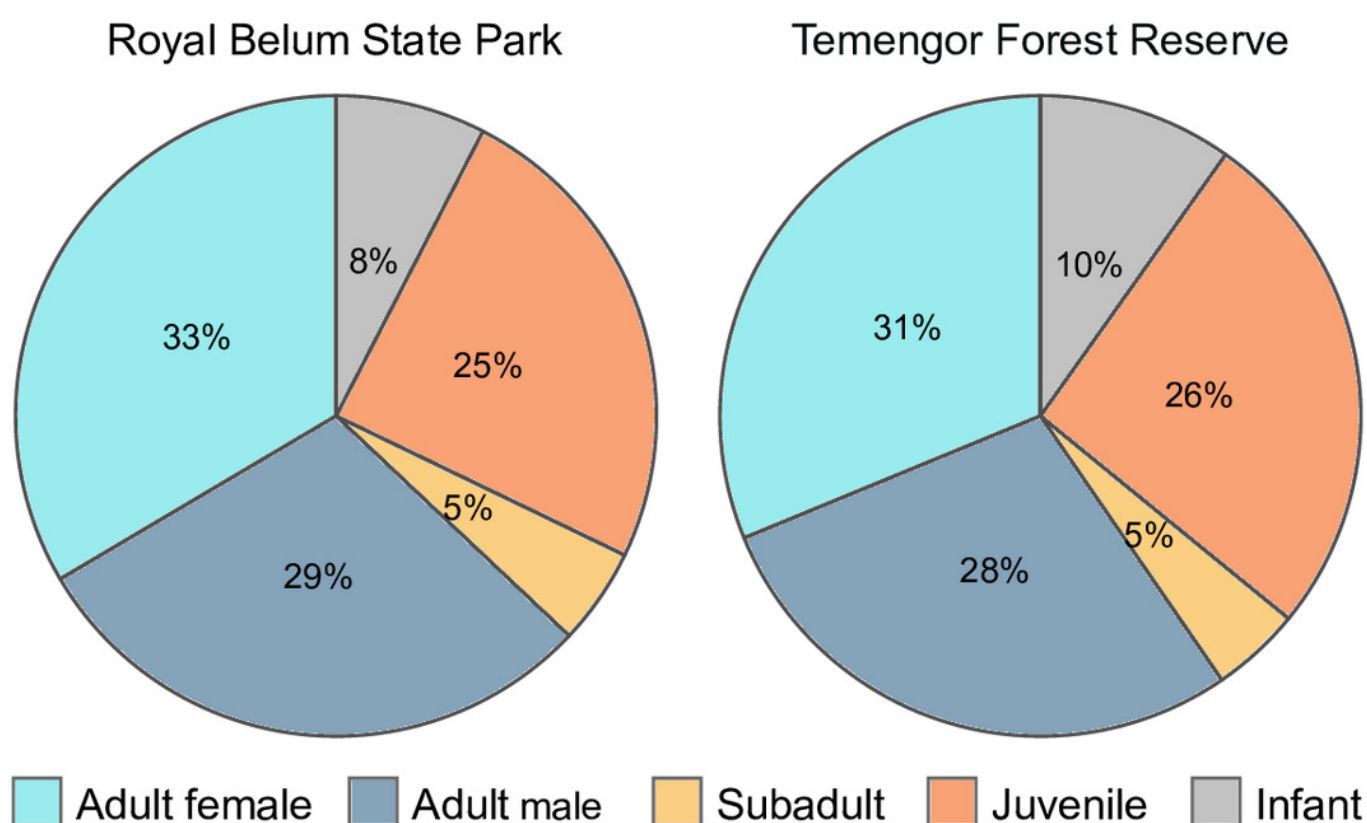


Table 1(on next page)

Top-ranked *Macaca nemestrina* detection models ($\Delta AIC_c \leq 2$) for Pasoh Forest Reserve (PFR) and Belum-Temengor Forest Complex (BTFC) with global occupancy models.

Shown are Akaike's Information Criterion corrected for small samples (AIC_c), differences in AIC_c between each model and the respective best model (ΔAIC_c), the probability of each model to the best model, i.e. the Akaike weights ($wAIC$), and the number of parameters (K , details on model selection and model averaged estimates for all covariates in Tables S1 and S2).

Site	Top-ranked models	AIC _c	ΔAIC _c	wAIC	K
<i>PFR</i>	p (effort + sampling year)	2069.5	0	1	15
<i>BTFC</i>	p (effort + sampling month)	1238.6	0	0.995	16

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Table 2 (on next page)

Top-ranked *Macaca nemestrina* occupancy models ($\Delta AIC_c \leq 2$) for Pasoh Forest Reserve (PFR) and Belum-Temengor Forest Complex (BTFC) with best respective detection models.

Shown are Akaike's Information Criterion corrected for small samples (AIC_c), differences in AIC_c between each model and the respective best model (ΔAIC_c), the probability of each model to the best model, i.e. the Akaike weights ($wAIC$), and the number of parameters (K , details on model selection in Table S3).

Site	Top-ranked models	AIC _c	ΔAIC _c	wAIC	K
<i>PFR</i>	ψ (.) γ (.) ε (forest degradation)	2056.4	0	0.633	11
<i>BTFR</i>	ψ (elevation)	1232.1	0	0.415	13

1

Table 3(on next page)

Effect of covariates on *Macaca nemestrina* occupancy, colonization and extinction in Pasoh Forest Reserve (PFR) and Belum-Temengor Forest Complex (BTFC).

Shown are model averaged estimates (zero method), standard errors (SE) and lower and upper 95% confidence intervals (CI). Predictors included into the respective top models ($\Delta AIC_c \leq 2$) are indicated in bold.

Site	Parameter	Covariate	Estimate	SE	lower CI	upper CI
<i>PFR</i>	Occupancy ψ	distance to edge ^a	-0.03	0.29	-1.47	1.14
		elevation ^a	-0.04	0.29	-1.51	1.12
	Colonization γ	forest degradation (no vs. clear cut) ^b	0.02	0.33	-2.58	3.58
		forest degradation (no vs. selective) ^b	-0.01	0.34	-3.52	2.81
	Extinction ε	forest degradation (no vs. clear cut)^b	2.25	0.69	1.13	3.48
		forest degradation (no vs. selective)^b	0.60	1.06	-1.47	2.70
<i>BTFC</i>	Occupancy ψ	habitat (Belum = 0, Temengor =1)	-0.001	0.23	-0.90	0.90
		NDVI ^a	0.02	0.10	-0.28	0.45
		distance to settlement ^a	-0.01	0.11	-0.46	0.35
		elevation^a	-1.17	0.23	-1.62	-0.73

^a z-transformed to mean = 0 and SD = 1 prior to model fitting; original means $\pm$ SDs were: distance to edge: 1076 $\pm$ 695 m, elevation (*PFR*): 295 $\pm$ 156 m, NDVI: 0.78 $\pm$ 0.05, distance to settlement: 8099 $\pm$ 4756 m, elevation (*BTFC*): 737 $\pm$ 302 m.

^b Reference level is 'no tree felling'.