Title Page

There will be conflict – agricultural landscapes are prime, rather than marginal, habitats for Asian elephants

Authors

J. Antonio de la Torre[1,2], Ee Phin Wong[1,3], Alex M. Lechner[1,4], Natasha Zulaikha[1,3], Abdullah Zawawi[5], Pazil Abdul Patah[5], Salman Saaban[3,5], Benoit Goossens[6,7,8,9] & Ahimsa Campos-Arceiz[1,10,11 *]

Affiliations

[1] School of Environmental and Geographical Sciences, University of Nottingham Malaysia, Jalan Broga, 43500 Semenyih, Selangor, Malaysia;

[2] Programa Jaguares de la Selva Maya, Bioconciencia A.C., Ciudad de México;

[3] Management & Ecology of Malaysian Elephants, University of Nottingham Malaysia, Jalan Broga, 43500 Semenyih, Selangor, Malaysia;

[4] Centre for Water and Planetary Health, School of Geography, University of Lincoln, Brayford Pool, Lincoln, Lincolnshire. LN6 7TS;

[5] Department of Wildlife and National Parks, Km10, Jalan Cheras, 56100, Kuala Lumpur, Malaysia;

[6] Organisms and Environment Division, Cardiff School of Biosciences, Cardiff University, Sir Martin Evans Building, Museum Avenue, Cardiff CF10 3AX, UK;

[7] Danau Girang Field Centre, c/o Sabah Wildlife Department, Wisma MUIS, 88100 Kota Kinabalu, Sabah, Malaysia;

[8] Sabah Wildlife Department, Wisma Muis, 88100 Kota Kinabalu, Sabah, Malaysia;

[9] Sustainable Places Research Institute, Cardiff University, 33 Park Place, Cardiff CF10 3BA, UK;

[10] Southeast Asia Biodiversity Research Institute, Chinese Academy of Sciences, Nay Pyi Taw, Myanmar;

[11] Center for Integrative Conservation, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Menglun, Mengla, 666303, Yunnan, China.

Short title: Agricultural landscapes are vital for Asian elephants

Corresponding author: Ahimsa Campos-Arceiz, Southeast Asia Biodiversity Research Institute, Chinese Academy of Sciences, Yezin, Nay Pyi Taw 05282, Myanmar; Phone: +86 (0)135-7810-1064. ahimsa@xtbg.ac.cn

There will be conflict – agricultural landscapes are prime, rather than marginal, habitats for Asian elephants

Abstract

Misconceptions about species' ecological preferences compromise conservation efforts. Whenever people and elephants share landscapes, human-elephant conflicts (HEC) occur in the form of crop raiding, elephant attacks on people, and retaliatory actions from people on elephants. HEC is considered the main threat to the endangered Asian elephant (*Elephas maximus*). Much of HEC mitigation in Asia is based on *rescuing* elephants from conflict areas and *returning them to nature*, e.g., by means of 'problem elephant' translocation. Here, we used two independent and extensive datasets comprising elephant GPS telemetry and HEC incident reports to assess the relationship between elephant habitat preferences and the occurrence of HEC at a broad spatial scale in Peninsular Malaysia. Specifically, we assessed (a) the habitat suitability of agricultural landscapes where HEC incidents occur and (b) sexual differences in habitat preferences with implications for HEC mitigation and elephant conservation. We found strong differences in habitat use between females and males and that the locations of HEC incidents were areas of very high habitat suitability for elephants, especially for females. HEC reports suggest that in Peninsular Malaysia females are involved in more crop damage conflicts than males, while males are more prone to direct encounters with people. Our results show that human-dominated landscapes are prime elephant habitat, and not merely marginal areas that elephants use in the absence of other options. The high ecological overlap between elephants and people means that conflict will continue to happen when both species share landscapes. HEC mitigation strategies, therefore, cannot be based on elephant removal (e.g. translocation) and need to

be holistic approaches that integrate both ecological and human social dimensions to promote tolerated human-elephant coexistence.

Keywords: coexistence, *Elephas maximus*, human-elephant conflict, habitat use, Southeast Asia, translocation.

Introduction

Conserving large and potentially dangerous wildlife is a daunting task in the Anthropocene (Ripple et al., 2016), which is even harder if evidence-based principles are not applied. Unfortunately, conservation decision making is often based on assumptions and anecdotal sources, rather than scientific evidence (Sutherland et al., 2004). The situation is often aggravated by a lack of communication between conservation scientists and practitioners (Laurance et al., 2012). Here we argue that misconceptions about Asian elephant (*Elephas maximus*) ecological preferences drive key conservation interventions. These misconceptions need to be addressed to move towards effective elephant conservation and human-elephant conflict (HEC) mitigation strategies.

Elephants are the largest terrestrial animals in Asian ecosystems, where they play important and unique ecological functions (e.g., Campos-Arceiz & Blake, 2011; Terborgh et al., 2017). Once widely distributed throughout much of the continent, Asian elephants are now Endangered (Choudhury et al., 2008) and live in highly fragmented landscapes of tropical Asia. Where people and elephants share landscapes, HEC occurs in the form of crop raiding, elephant attacks on people, and retaliatory actions of people on elephants (e.g. Sukumar, 1990; Fernando et al., 2005; Palei et al., 2014; Goswami, Vasudev & Oli, 2014). HEC is now the main threat to Asian elephants (e.g. Leimgruber et al., 2003; Fernando &

Pastorini, 2011), as well as a grave social problem throughout the species range (Shaffer et al., 2019; Denninger Snyder & Rentsch, 2020). There is a wide range of strategies to prevent and mitigate HEC, including elephant physical exclusion (e.g. by means of electric fences and trenches), deterrence from agricultural fields (e.g. based on sound, light, or chili), early detection and warning systems, financial compensation schemes, and the removal of problem elephants by means of culling, domestication, or translocation (Shaffer et al., 2019; Denninger Snyder & Rentsch, 2020).

Elephant translocation is one of the most common strategies for HEC mitigation (Fernando et al., 2008a; Shaffer et al., 2019). It is considered a humane strategy (Massei et al., 2010) and consists of the relocation of ‘problem elephants’ from conflict areas to natural habitats with low potential for conflict. The narrative behind conflict-related translocation is powerful, i.e., “an elephant is *rescued* from a conflict area and released *back in nature*, thereby reducing the suffering of poor farmers”. This narrative assumes that elephants prefer to be “back in nature”, generally old-growth forests, and presents translocation as a win-win outcome. It is therefore not surprising that elephant translocation is popular in countries like India (Lahiri-Choudhury, 1983), Sri Lanka (Fernando et al., 2012), and Malaysia (Daim, 1995). In Peninsular Malaysia, where translocation is the main strategy for HEC mitigation, more than 600 elephants have been translocated since 1974 (Saaban et al., 2011). A recent population viability analysis in Endau Rompin, a landscape in southern Peninsular Malaysia, suggested that the local elephant population cannot sustain even low levels of removal for translocation (Saaban et al. 2020). Overall. the effectiveness of translocation to mitigate HEC has not been sufficiently evaluated but available information suggests it is not a long-term solution (Massei et al., 2010; Fernando et al., 2012, Saaban et al. 2020).

A key question that needs to be answered is: why do elephants come out of the forest in the first place? Elephants have extensive spatial needs to meet their resource requirements, and their movements and habitat use are complex. Asian elephants are considered to be forest edge specialists with preference for a combination of natural forest and secondary vegetation (e.g., English et al., 2014; Evans, Asner & Goossens, 2018; Wadey et al., 2018; de la Torre et al., 2019; Huang et al., 2020), which increases the likelihood of contact with people, and hence the risk of HEC (Campos-Arceiz, 2013).

Moreover, Asian elephants' habitat relationships and involvement in HEC are likely to differ with sex. Asian elephants are highly dimorphic and exhibit sexually distinct social (e.g., de Silva & Wittemyer, 2012), ranging (e.g. Fernando et al., 2008b), and crop raiding (e.g., Sukumar & Gadgil, 1988) behaviors. Females and their young offspring form matrilineal groups, while males are usually solitary or form loose associations with other males (bachelor groups) or female herds (e.g., Vidya & Sukumar, 2005). Despite known sexual differences in Asian elephant behavior, little is known about their intersexual differences in habitat use. Gaining a fine-scale understanding of how habitat preferences mediate female and male involvement in HEC is key to developing evidence-based HEC mitigation strategies tailored to the local circumstances.

The effective mitigation of HEC, and hence Asian elephant long-term survival, requires a deeper understanding of the drivers of this conflict. In this paper we aim to assess the relationship between elephant habitat preferences and the occurrence of HEC at a broad spatial scale in Peninsular Malaysia. Our specific objectives are to assess: (a) the habitat suitability of agricultural landscapes where HEC incidents occur and (b) sexual differences in habitat preferences with implications for HEC mitigation and elephant conservation. We implemented this analysis using one of the largest datasets of GPS telemetry of any terrestrial mammals in mainland Southeast Asia and an extensive dataset of HEC incidents compiled by the Department of Wildlife and National Parks of Peninsular Malaysia (DWNP).

Materials and Methods

Study area

Peninsular Malaysia extends 780 km from latitude 1°15' north of the Equator. Its terrain is hilly with several mountain ranges in a north-south alignment and an altitudinal range from sea level to 2,187 m a.s.l. Peninsular Malaysia is covered by approximately 57,900 km^2 of forest (PMDWNP, 2013) in which the dominant forest types are lowland dipterocarp, hill dipterocarp, and montane forest. The main crops in Malaysia are oil palm (*Elaeis guineensis*) and rubber (*Hevea brasiliensis*) plantations (Petersen et al. 2016). Our study area included all the extension of the three Managed Elephant Ranges (MERs; Fig. 1) defined in the National Elephant Conservation Action Plan (NECAP), covering an area of ~ 73,100 km^2 in which wild elephants are expected to roam in the foreseeable future (PMDWNP, 2013).

Data acquisition and curation of GPS and HEC data

We used GPS telemetry data of 48 Asian elephants monitored between 2011 and 2018, including 16 resident (ten females and six males) and 32 translocated (six females and 26 males) individuals with a total of 200,891 localizations (Appendix S1). By 'translocated' we refer to elephants relocated from human-elephant conflict areas to protected areas by the DWNP (Saaban et al., 2011); while 'resident' elephants were individuals sedated, collared, and released at the same location within a few hours. We used Inmarsat and Iridium satellite GPS collars (10D cells, Africa Wildlife Tracking, Pretoria, South Africa), programmed to record a location every one or two hours. Since approximately 40% of the entire estimated population of elephants (>600 out of ~1,500 individuals; Saaban et al., 2011) have been translocated in Peninsular Malaysia since 1974, we used the data of both translocated and non-translocated elephants in our analyses.

Additionally, we used DWNP's database of HEC incidents, compiled based on individual citizens self-motivated reports. This database included localizations of 5,616 HEC reports obtained from 2006 to 2016. Each HEC report contained information on the type of conflict such as crop raiding, property damage, human damage, or just elephants roaming near a human settlement. Human damage reports mostly corresponded to scared people, but also included nine cases which resulted in injury, and two fatalities. Additionally, HEC reports included the incident's date and location (GPS point taken by DWNP officers within two days from the report made), and the number of elephants involved in the incident. We assigned new categories to the data fields and categories originally recorded by DWNP. Because most of the reports included an estimated number of elephants involved in the incidents, we classified this information as a) solitary (1 elephant); b) small groups (2-5 elephants); c) large groups (≥ 6 elephants); and d) no information. In our analysis we assumed that reports of solitary elephants (n=1,299) are related to male elephants and that large group reports (n=2,100) were associated with female groups (Vidya & Sukumar, 2005; Srinivasaiah et al., 2019).

Environmental covariates

We compiled a geospatial dataset representing habitat covariates for elephants in Peninsular Malaysia (Table 1). This dataset included variables associated with the land use (e.g., proportion of primary forest) and distance to forest and plantation (oil palm and rubber) edges, as well as terrain covariates (elevation and slope). We also used covariates that capture important information about the vegetation, forest structure, and/or moisture content, for which we used Google Earth Engine (GEE) to derive a multidate (year 2018) cloud free mosaic surface reflectance product using Landsat 8 for Peninsular Malaysia. From this mosaic we calculated the Enhanced Vegetation Index (EVI) and Normalized Difference Vegetation Index (NDVI) to test if elephant movements were related to vegetation greenness. Additionally, we calculated the Normalized Difference Water Index (NDWI) and Tasseled Cap Wetness Index (hereafter 'wetness') to evaluate if the movements were related to wetness and moisture content of the natural and cultivated vegetation. These two covariates are also proxies of the forest quality and their values reflect changes in vegetation structure. Additionally, we calculated the Euclidian distance to different landscape attributes such as forest edge, plantations, water sources and paved roads, and generated raster layers of these covariates (Table 1). To evaluate the influence of anthropogenic activities we used the mean of nightlight and distance to main roads covariates (see Table 1 for details and sources of spatial covariates).

We represented all these explanatory variables as raster layers of 30 m resolution. We used 30 m as resolution because that was the original resolution of most of the landscape covariates in our analyses, and finer-grained geospatial data are superior than coarse scales to model habitat use and movements from data obtained by GPS telemetry (Zeller et al., 2017). Land use covariates were obtained in raster format with an original resolution of 250 m (Miettinen et al. 2015), resampled to 30 m resolution using the nearest neighbour method. Each land use class was then converted to a binary raster (i.e. presence versus absence). The mean of nightlight was obtained using GEE with an original resolution of 500 m, and then resampled to 30 m using the bilinear method, as it is a continuous dataset.

Given that multi-scale models tend to yield better predictions than single scale models (Zeller et al., 2014; 2016), we calculated some of the covariates at five spatial scales using different circular moving windows with radii of 210, 750, 1,140, 3,990, and 7,560 m, which represent the mean distance travelled by the tracked elephants in 2 h, 12 h, 24 h, one week, and one month, respectively. We selected the 2 h scale because it matched the steps in our step selection function models (see below), and the 12 and 24 h because they represented half and a full circadian cycles. The one-month scale approximated the minimum home range crossing time of the elephants tracked (Wadey, 2020), and the one-week scale was chosen as an intermediate scale between the three fine and the coarse scales. The covariates evaluated at multiple scales include elevation, slope, nightlight, the land use descriptors (calculated as coverage of each land use class), and the distance to water, forest, plantations, and roads (Table 1).

Habitat suitability for Asian elephants and its relationship with HEC

We evaluated elephant habitat suitability using step selection function models (SSF; Fortin et al., 2005; Thurfjell, Ciuti & Boyce, 2014). SSF are statistical models deployed to estimate resource selection by animals moving through the landscape (Thurfjell, et al., 2014). We removed all the localizations obtained during the first 15 days of each individual's tracking, to reduce the potential effects of the capture and release on its movements. Since the tracked elephants were monitored using different fix acquisition schedules (either 1 or 2 hours), we resampled the data to constant 2 ± 0.16 hour intervals, and then calculated the distance of each step between consecutive GPS fixes and filtered the data, retaining only steps that measured 50 m or more. This distance threshold was chosen for steps to represent resource use and displacement behaviors of elephants (Zeller et al., 2016). We simulated nine “available” steps for each “used” step; since our GPS telemetry dataset has a large number of locations per individual, a low ratio of simulated to used steps is sufficient for parameter estimation (Thurfjell et al., 2014). Step lengths were drawn from the empirical movement data using a Gamma distribution with rate and shape parameters estimated from the empirical data of step lengths distribution of all tracked elephants. Turning angles were also drawn from the empirical data for the collared elephants using a von Mises distribution. We used the *amt* package (Signer, Fieberg, & Avgar, 2019) in R version 4.0.2 (R Core Team, 2020) to generate the random steps.

For each used and available step, we calculated the values of the habitat covariates at the end point of the steps. We constructed several SSF models with different combinations of habitat covariates using a conditional logistic regression framework with the “amt”package (Sigher et al., 2019). We then identified the best SSF using the Akaike Information Criterion (AIC; Burnham & Anderson, 2002). To implement the SSFs, our first step was to evaluate the most informative scale (210, 750, 1,140, 3,990 or 7,560 m) for each variable using univariate models; we compared them contrasting their AIC values and likelihood explained. Later, we ran multivariate models using the most informative scale of the variables assessed. We tested all explanatory variables for multicollinearity using the Pearson’s correlation matrix, and we did not include in the same candidate model variables that were correlated at $|r| > 0.5$ (Zeller et al., 2014). We selected the best-fitting models using AIC, calculated model averages for all models within $\Delta AIC < 2$ from the best model (Burnham & Anderson, 2002), and estimated the importance of predictor variables by the

Sum of Weights (*SW* = 1; Galipaud et al., 2014). These analyses were implemented using MuMIn R package (Bartoń, 2019).

We built separate SSF models at population-level for females and males and used the best models by sex to predict habitat suitability for female and male elephants across our entire study area. The resulting habitat suitability layer characterizes each cell with continuous values between 0 and 1, representing the suitability of the landscape to elephants. To evaluate model performance, we retained 10% of the GPS fixes from every elephant and performed a 10-fold cross-validation using methods recommended by Johnson et al. (2006). For the best female and male elephant models, we classified suitability probabilities into 10 bins that ranged from 1=low to 10=high. We counted our retained evaluation fixes in each bin to evaluate if we would find a large number of fixes in the higher suitability bins that were normalized by area and, similarly to Zeller et al. (2014; 2016), we quantified the quality of the model applying the concordance correlation coefficient (CCC) to the relationship of evaluation fixes in each bin versus bins that were normalized by area (Lin, 1989). According to Johnson et al. (2006), the predicted observation of a good model should fall close to the expected observation on a line originating at 0 with a slope of 1. The CCC statistic measures how correlated two points are based on their deviance from this 45-degree line, and higher values of squared CCC are indicative of a good model. We used R's *DescTools* package to perform the CCC analysis (Signorell, 2007).

We extracted habitat suitability values from our best model maps (both for females and males) at each HEC report location and compared them with habitat suitability values of 10,000 random localizations within the MERs to assess if HEC locations had higher suitability values than expected by chance. Additionally, we repeated this comparison using a resampling procedure randomly selecting 5,000 samples from each population and contrasting them with their 95% confidence intervals. We also evaluated the relationship of the HEC locations with habitat suitability of female and male elephants. Finally, we used a G-test of independence to evaluate if the proportions among the four main HEC categories (i.e., crop damage, human damage, property damage, and roaming) were different between male elephants (solitary) and female elephants (groups of six or more elephants). We implemented this analysis in R using the *RVAideMemoire* package (Hervé, 2019).

Results

Habitat suitability models

The SSF models revealed important differences in habitat use between male and female elephants (Table 2; Fig. 2; Appendices 3 & 4). Overall, both males and females preferred disturbed vegetation such as forest gaps, secondary forests, and areas of regrowth and new plantations (positive effect of 'wetness' and 'percentage of regrowth and new plantations'). 'Wetness^2'(quadratic term of wetness) shows that elephants preferred intermediate values of forest openness, while the negative effect of 'distance to forest' shows that elephants preferred open vegetation but generally close to mature forest ('distance to forest'; mean = 0.14, range 0 - 11.92 km in females; mean = 0.43, range 0 - 15.55 km in males). Both males and females were attracted to the proximity of plantations ('distance to plantations'; mean = 1.41, range 0 - 19.60 km in females; mean = 4.78, range 0 - 32.79 km in males) and to areas of new plantations ('percentage of regrowth and new plantations') but avoided areas with high coverage of plantations ('percentage of plantations'). Both males and females clearly avoided areas with steep and rugged terrain (slope), and 'elevation^2' (quadratic term of elevation) shows that both sexes preferred lowland areas and the higher sites in the mountain ranges such as ridges, though this relationship was stronger in males (Table 2).

Males, in contrast to females, were attracted to areas with water availability (distance to water, percentage of water). Both sexes also differed in their response to human disturbance, with males using more open areas (percentage of open areas) and females more actively avoiding areas close to towns and villages (mean nightlight). Further, males were attracted to the proximity of primary roads (distance to roads; Table 2). Female and male elephants also responded in different way to the scales of some landscape covariates (Appendix 3; Table S4). Females' response to landscape variables related to plantations and secondary forest (percentage of regrowth and new plantations, percentage of plantations and distance of plantations) was stronger at finer scales (30 – 750 m); while they responded more strongly at coarse scale (3,990 m) to variables such as distance to forest, distance to water, and mean nightlight. Males, on the other hand, showed stronger response at finer scales (30-750 m) to variables related to land use (percentage of regrowth and new plantations, plantations, water, open areas) and distances to landscape attributes (distance to forest, plantations, water, roads). Male response to mean nightlight was strongest at the intermediate scale (1,140 m).

Males' most suitable habitats were predicted in lowland areas, while females preferred both lowlands and, to a lesser extent, high elevation areas where most of the primary forest occurs (Fig. 2). Habitat suitability models showed good performance, with squared CCC values of 0.96 for females' model and 0.78 for males', indicating that our models have high potential for predicting the habitat use of elephants across Peninsular Malaysia.

Habitat suitability and HEC occurrence

Contrasting the location of HEC reports with the habitat suitability maps we found that HEC cases in Peninsular Malaysia are related with areas of high habitat suitability for both females (95% CI 0.902 – 0.907 vs 0.845 – 0.853) and males (95% CI 0.792 – 0.800 vs 0.600 – 0.612; Fig. 3). Most of the HEC locations concur with sites of high habitat suitability for both female and male elephants ($R^2 = 0.13$, $p < 0.0001$; Fig. 3a).

Most (61%; n=3,399) of the HEC reports in our database were attributed to large elephant groups (Fig. 4) and associated with higher female habitat suitability values (Fig. 3b), suggesting that female groups might be more prone to cause conflicts in Peninsular Malaysia. On the other hand, human damage reports were more often (53%, n=489) associated with solitary individuals, suggesting that males might be more prone to direct encounters with people (G = 56.8.9, *d.f.* = 3, $P < 0.0001$; Fig. 3).

Discussion

Our analyses showed that in Peninsular Malaysia the areas of HEC incidents are of very high habitat suitability for Asian elephants, especially females. These findings have important implications for HEC mitigation.

To our best knowledge, this is the first evaluation of sexual differences in habitat use by Asian elephants. Both sexes preferred disturbed vegetation such as forest gaps, but always in close proximity to mature forest, and both sexes were attracted to areas near plantations (i.e., high human disturbance). These results are consistent with previous studies on Asian elephant habitat selection (Sitompul et al., 2013; Evans, Asner, & Goossens, 2018; Krishnan et al., 2019; Evans et al., 2020). Females, however, used both lowlands and, to a lesser extent, the higher elevation ranges where most of the primary forests occur. Males spent more time in lowland areas, in sites nearby plantations, and in highly disturbed human-dominated landscapes. Females' selection of primary forests and more remote areas in higher elevation ranges may be driven by avoidance of human disturbance to protect their offspring (Kumar & Singh, 2010; Kumar, Mudappa & Raman, 2010). As expected from their social behavior, Asian elephant males are more tolerant to human disturbances than females (Sukumar & Gadgil, 1988; Srinivasaiah et al., 2019).

Adult Asian elephant females and their infants form matrilineal groups, while males disperse from their natal group when they reach the puberty (Vidya & Sukumar, 2005). Females' social behavior is likely to be a strategy to improve the survival of their offspring through intra-group cooperation (e.g., allomothering, knowledge sharing) and by choosing habitats and movement paths suitable for their infants (Vidya & Sukumar, 2005). Males, on the other hand, can adopt a high-risk foraging strategy venturing into higher-risk areas and feeding on nutritious crops to improve their reproductive fitness (Sukumar & Gadgil, 1988; Srinivasaiah et al., 2019).

Female and male elephants also responded differently to landscape covariates and spatial scales. Given Asian elephant complex behavior (Mumby & Plotnik 2018) and their high individual variability in habitat preferences (Wadey et al. 2018), we do not discuss the details of these differences. Although both models performed relatively well, females' model outperformed that of males. The high prevalence of translocation among males could affect the performance of their model. Differences in model performance could also influence the relationship between habitat preference and HEC locations, creating a positive bias for females. Such potential bias, however, would not affect our general conclusions since most of the HEC incidents occurred in locations of high habitat suitability for both females and males.

Contrary to the situation in other countries (e.g., Sukumar & Gadgil, 1988; Fernando et al., 2005; Campos-Arceiz et al., 2009), HEC reports indicate that in Peninsular Malaysia females are more likely to be involved in crop damage conflicts than males (Fig. 4). This suggests that crop raiding in Malaysia – which largely involves oil palm and rubber plantations – is perceived as relatively low risk by elephants, at least in comparison with crop raiding in small-scale seasonal crops, often guarded by farmers, such as paddy fields in South Asia. Male elephants in Peninsular Malaysia were more prone to direct encounters with local people, which is likely to reflect their higher tolerance for risk and movement near villages and roads.

We assumed that HEC reports of solitary elephants are associated with male elephants, and large groups (≥ 6 elephants) are associated with female groups. We acknowledge however that Asian elephants' group cohesion is poorly understood, and female groups do exhibit fission-fusion dynamics, whereby social affiliates sometimes split up into smaller aggregations (De Silva, Ranjeewa, & Kryazhimskiy, 2011). To cope with such caveat, we excluded HEC incidents caused by small groups (2-5 elephants), which are likely to include both male bachelor groups and temporarily split up females. Another potential caveat is that we implemented the SSF models at population level, which could lead to an overgeneralization of resource selection and spatial bias in the habitat suitability maps. These biases are more problematic with small sample sizes (Bastille-Rousseau & Wittemyer, 2019; Osipova et al., 2019). The predictive power of our models is likely to be adequate because of our large sample size (16 females and 32 males) and the wide geographical distribution of our sample (across most of Peninsular Malaysia; Osipova et al., 2019).

The strong positive correlation between Asian elephants' use of space and the occurrence of HEC incidents indicates that the human-dominated landscapes where HEC occurs in Peninsular Malaysia are also areas of high habitat suitability for elephants. In other words, disturbed human-dominated landscapes are prime elephant habitat, and not merely marginal areas that elephants use when they have no other option, as the narrative often suggests. If moderately-disturbed human-dominated landscapes near large forest patches are prime elephant habitats, translocating conflict elephants to areas of continuous old-growth forest (i.e., less preferred habitats) is unlikely to be a long-lasting solution against HEC, since elephants are likely to move to the forest fringes where conflict will take place again (Fig. 5). Translocation may have other negative consequences, including social disruption and potentially aggravating the severity of HEC due to elephants' disorientation and lack of familiarity with release areas (Fernando et al., 2012). For small elephant populations, the regular removal of individuals can compromise their long-term population viability (Saaban et al. 2020).

We argue that the high ecological overlap between elephants and people (as manifested in the overall use of space) means that elephants will always tend to come into conflict with people when sharing landscapes. The strategy to address HEC, therefore, cannot be based on elephant removal and needs to be a holistic approach that integrates both ecological and human social dimensions (Madden and McQuinn, 2014; Shaffer et al. 2019) to promote tolerated human-elephant coexistence, a situation in which people and elephants share space to some extent, but without either side incurring severe costs.

In Peninsular Malaysia we advocate for an integrated strategy that includes: (1) land use planning, i.e., protecting natural habitats and avoiding the development of new plantations in areas of high HEC potential (Adams et al., 2017; Neupane, Johnson, &

Risch, 2017); (2) using small-scale exclusionary measures such as electric fences and trenches to maintain elephants out, not in, e.g., to prevent elephants from entering plantations rather than trying to prevent them from leaving protected areas (Kioko et al., 2008; Shaffer et al., 2019); (3) implementing mechanisms for fair financial compensation, such as insurance schemes (Chen et al., 2013); (4) promoting tolerance to elephants and low-intensity HEC (Gunaryadi, Sugiyo, & Hedges, 2017; Saif et al., 2019); and (5) removing elephants only in cases of very high intensity of conflict or where elephants are not wanted in the broad-scale landscape (e.g., outside MERs in Peninsular Malaysia). Importantly, stakeholders need to have a sense of ownership and shared responsibility (Denninger Snyder & Rentsch, 2020), as is currently being promoted by Peninsular Malaysia's Department of Wildlife and National Parks.

Science deficiencies can be very costly in conservation practice (e.g., Karanth et al., 2006). Addressing misconceptions about Asian elephant ecological preferences and shifting the paradigm of HEC management is necessary for the effective conservation of Asian elephants, the largest animals roaming Asian landscapes.

Acknowledgements

We are very grateful to the Department of Wildlife and National Parks (DWNP), especially its Director General Dato' Abdul Kadir bin Abu Hashim, for the research permits, access to the human-elephant conflict database, and the elephant GPS-collaring and tracking. Field activities were financed by Yayasan Sime Darby (M0005.54.04), Wildlife Reserves Singapore (S0002.54.02), US Fish & Wildlife Service (ASE-0525), and Marinescape (M0004.54.04). JAdlT was financed by a CONACYT-Mexico postdoctoral fellowship (711042). We are grateful to all people who provided assistance during elephant collaring

and tracking activities. The data used in this article can be shared upon request to the authors.

References

Adams, T. S. F., Chase, M. J., Rogers, T. L., & Leggett, K. E. A. (2017). Taking the elephant out of the room and into the corridor: Can urban corridors work? *Oryx* **51**, 347–353.

Bartoń, K. (2019). MuMIn: Multi-model inference. R Packag. version 1.43.6.

Bastille-Rousseau, G., & Wittemyer, G. (2019). Leveraging multidimensional heterogeneity in resource selection to define movement tactics of animals. *Ecol. Lett.* **22**, 1417–1427.

Burnham, K.P. & Anderson D.R. (2002). *Model Selection and Multimodel Inference: a Practical Information-theoretic Approach*, 2nd edn. Springer-Verlag, New York. Page New York Springer.

Campos-Arceiz, A. (2013). The dangerous myth of the Noble Beast. *Gajah* **38**,5.

Campos-Arceiz, A. & Blake, S. (2011). Megagardeners of the forest–the role of elephants in seed dispersal. *Acta Oecol.* **37**, 542-553.

Campos-Arceiz, A., Takatsuki, S., Ekanayaka, S.K. & Hasegawa, T. (2009). The Human-Elephant Conflict in Southeastern Sri Lanka: Type of Damage, Seasonal Patterns, and Sexual Differences in the Raiding Behavior of Elephants. *Gajah* **31**, 5-14.

Chen, S., Yi, Z.F., Campos-Arceiz, A., Chen, M.Y. and Webb, E.L. (2013). Developing a spatially-explicit, sustainable and risk-based insurance scheme to mitigate human–wildlife conflict. *Biol. Conserv.***168**, 31-39.

Choudhury, A., Lahiri Choudhury, D.K., Desai, A., Duckworth, J.W., Easa, P.S., Johnsingh, A.J.T., Fernando, P., Hedges, S., Gunawardena, M., Kurt, F., Karanth, U., Lister, A., Menon, V., Riddle, H., Rübel, A. & Wikramanayake, E. (2008). Elephas maximus. *The IUCN Red List of Threatened Species 2008*: e.T7140A12828813. https://dx.doi.org/10.2305/IUCN.UK.2008.RLTS.T7140A12828813.en. Downloaded on 06 May 2020.

Daim, M.S. (1995). Elephant translocation: the Malaysian approach. *Gajah*, **14**, 43-48.

de la Torre, J.A., Lechner, A.M., Wong, E.P., Magintan, D., Saaban, S. and Campos-Arceiz, A. (2019). Using elephant movements to assess landscape connectivity under Peninsular Malaysia's central forest spine land use policy. *Conserv. Scien. Pract.* 1:e133. doi.org/10.1111/csp2 .133

de Silva, S. & Wittemyer, G. (2012). A comparison of social organization in Asian elephants and African savannah elephants. *Int. J. Primatol*. **33**, 1125-1141.

Denninger Snyder, K., & Rentsch, D. (2020). Rethinking assessment of success of mitigation strategies for elephant-induced crop damage. *Conserv. Biol.* **34**, 829–842.

English, M., Ancrenaz, M., Gillespie, G., Goossens, B., Nathan, S., Linklater, W. (2014). Foraging site recursion by forest elephants *Elephas maximus borneensis*. Curr. Zool. **60**, 551–559.

Evans, L.J., Asner & G.P, Goossens, B. (2018). Protected area management priorities crucial for the future of Bornean elephants. *Biol. Conserv.* **22**, 365–373.

Evans, L. J., Goossens, B., Davies, A. B., Reynolds, G., & Asner, G. P. (2020). Natural and anthropogenic drivers of Bornean elephant movement strategies. *Glob. Ecol. Conserv.* **22**, e00906.

Fernando, P., Kumar, M.A., Williams, A.C., Wikramanayake, E., Aziz, T. & Singh, S.M., (2008a). *Review of human-elephant conflict mitigation measures practiced in South Asia*. Gland, Switzerland: WWF. 45 pp.

Fernando, P., Wikramanayake, E.D., Janaka, H.K., Jayasinghe, L.K.A., Gunawardena, M., Kotagama, S.W., Weerakoon, D. & Pastorini, J. (2008b). Ranging behavior of the Asian elephant in Sri Lanka. *Mamm. Biol.*, **73**, 2-13.

Fernando, P., Leimgruber, P., Prasad, T. & Pastorini, J. (2012). Problem-elephant translocation: translocating the problem and the elephant? *PLoS ONE*, **7**, e50917.

Fernando, P. & Pastorini, J. (2011). Range-wide status of Asian elephants. *Gajah* **35**, 15-20.

Fernando, P., Wikramanayake, E., Weerakoon, D., Jayasinghe, L.K.A., Gunawardene, M. & Janaka, H.K. (2005). Perceptions and patterns of human–elephant conflict in old and new settlements in Sri Lanka: insights for mitigation and management. *Biodivers. Conserv.*, **14**, 2465-2481.

Fortin, D., Beyer, H.L., Boyce, W.M., Smith, D.W., Duchesne, T., Mao, J.S., 2005. Wolves influence elk movements: behavior shapes a trophic cascade in Yellowstone National Park. *Ecology* **86**, 1320–1330.

Galipaud, M., Gillingham, M. A. F., David, M., & Dechaume-Moncharmont, F. X. (2014). Ecologists overestimate the importance of predictor variables in model averaging: A plea for cautious interpretations. *Methods Ecol. Evol*. **5**, 983–991.

Goswami, V.R., Vasudev, D. & Oli, M.K. (2014). The importance of conflict-induced mortality for conservation planning in areas of human–elephant co-occurrence. *Biol. Conserv.* **176**, 191-198.

Gunaryadi, D., Sugiyo, & Hedges, S. (2017). Community-based human-elephant conflict mitigation: The value of an evidence-based approach in promoting the uptake of effective methods. *PLoS One* **12**, 1–13.

Hervé, M. (2019). RVAideMemoire: Testing and Plotting Procedures for Biostatistics. https://CRAN.R-project.org/package=RVAideMemoire.

Huang, C., Li, X., Hu, W. & Jiang, X. (2020). Predicting indirect effects of transportation network expansion on Asian elephants: Implications for environmental impact assessments. *Biotropica* **52**, 196-202.

Johnson, C. J., Nielsen, S. E., Merrill, E. H., McDonald, T. L., & Boyce, M. S. (2006). Resource selection functions based on use–availability data: Theoretical motivation and evaluation methods. *J. Wildl. Manage.* **70**, 347–357.

Karanth, K.U., Nichols, J.D., Seidenstricker, J., Dinerstein, E., Smith, J.L.D., McDougal, C., Johnsingh, A.J.T., Chundawat, R.S. & Thapar, V. (2003). Science deficiency in conservation practice: the monitoring of tiger populations in India. *Anim. Conserv.* **6**, 41-146.

Kioko, J., Muruthi, P., Omondi, P., & Chiyo, P. I. (2008). The performance of electric fences as elephant barriers in Amboseli, Kenya. *African J. Wildl. Res.* **38**, 52–58.

Krishnan, V., Kumar, M. A., Raghunathan, G., & Vijayakrishnan, S. (2019). Distribution and Habitat Use by Asian Elephants (Elephas maximus) in a Coffee-Dominated Landscape of Southern India. *Trop. Conserv. Sci.* **12**, 1–12.

Kumar, M. A., & Singh, M. (2010). Behavior of Asian elephant (*Elephas maximus*) in a land-use mosaic: Implications for human-elephant coexistence in the Anamalai Hills, India. *Wildl. Biol. Pract.* **6**, 69–80.

Kumar, M. Ananda, Mudappa, D., & Raman, T. R. S. (2010). Asian elephant *Elephas maximus* habitat use and ranging in fragmented rainforest and plantations in the Anamalai Hills, India. *Trop. Conserv. Sci.* **3**, 143–158.

Lahiri-Choudhury, D.K. (1993). Problems of wild elephant translocation. *Oryx* 27, 53-55.

Laurance, W.F., Koster, H., Grooten, M., Anderson, A.B., Zuidema, P.A., Zwick, S., Zagt, R.J., Lynam, A.J., Linkie, M. & Anten, N.P. (2012). Making conservation research more relevant for conservation practitioners. *Biol. Conserv.* **153**, 164-168.

Leimgruber, P., Gagnon, J.B., Wemmer, C., Kelly, D.S., Songer, M.A. & Selig, E.R. (2003). *November. Fragmentation of Asia's remaining wildlands: implications for Asian elephant conservation*. In Animal conservation forum **6**, 347-359. Cambridge University Press.

Lin, L. I.-K. (1989). A Concordance Correlation Coefficient to Evaluate Reproducibility. *Biometrics* **1**, 255–268.

Madden, F. & McQuinn, B. (2014). Conservation's blind spot: The case for conflict transformation in wildlife conservation. *Biol. Conserv.* **178**, 97-106.

Massei G., Guy R.J., Gurney J. & Cowan D.P. (2010). Can translocations be used to mitigate human-wildlife conflicts? *Wild. Res.* **37**, 428-439.

Miettinen J., Shi, C., Liew, S.C. (2016). 2015 Land cover map of Southeast Asia at 250 m spatial resolution. *Remote Sens. Lett.* **7**, 701-710.

Mumby, H.S. and Plotnik, J.M., 2018. Taking the elephants' perspective: Remembering elephant behavior, cognition and ecology in human-elephant conflict mitigation. Frontiers in Ecology and Evolution, 6, p.122.

Neupane, D., Johnson, R. L., & Risch, T. S. (2017). How do land-use practices affect human-elephant conflict in nepal? *Wildlife Biol.* **2017**. doi.org/10.2981/wlb.00313

Neupane, D., Kwon, Y., Risch, T. S., Williams, A. C., & Johnson, R. L. (2019). Habitat use by Asian elephants: Context matters. *Glob. Ecol. Conserv.* **17**, e00570.

Osipova, L., Okello, M. M., Njumbi, S. J., Ngene, S., Western, D., Hayward, M. W., & Balkenhol, N. (2019). Using step-selection functions to model landscape connectivity for African elephants: Accounting for variability across individuals and seasons. *Anim. Conserv.* **22**, 35–48.

Palei, N.C., Palei, H.S., Rath, B.P. & Kar, C.S. (2014). Mortality of the Endangered Asian elephant *Elephas maximus* by electrocution in Odisha, India. *Oryx* **48**, 602-604.

Petersen, R., Aksenov, D., Esipova, E., Goldman, E., Harris, N., Kuksina, N., Kurakina, I., Loboda, T., Manisha, A., Sargent, S., & Shevade, V. (2016). Mapping Tree Plantations with Multispectral Imagery: Permiminary Results for Seven Tropical Countries. *Tech. Note - World Resour. Inst.* January 1-18.

PMDWNP. (2013). *National Elephant Conservation Action Plan - Blue Print to Save Malaysian Elephants*. Department of Wildlife and National Parks Peninsular Malaysia, Kuala Lumpur, Malaysia.

R Core Team (2020). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Ripple, W.J., Chapron, G., López-Bao, J.V., Durant, S.M., Macdonald, D.W., Lindsey, P.A., Bennett, E.L., Beschta, R.L., Bruskotter, J.T., Campos-Arceiz, A. & Corlett, R.T. (2016). Saving the world's terrestrial megafauna. *Bioscience* **66**, 807-812.

Saaban, S., Othman, N.B., Yasak, M.N.B., Burhanuddin, M.N., Zafir, A. & Campos-Arceiz, A. (2011). Current status of Asian elephants in Peninsular Malaysia. *Gajah* **35**, 67-75.

Saaban, S., Yasak, M.N., Gumal, M., Oziar, A., Cheong, F., Shaari, Z., Tyson, M. and Hedges, S., 2020. Viability and management of the Asian elephant (Elephas maximus) population in the Endau Rompin landscape, Peninsular Malaysia. PeerJ, 8, p.e8209.

Saif, O., Kansky, R., Palash, A., Kidd, M., & Knight, A. T. (2019). Costs of coexistence: Understanding the drivers of tolerance towards Asian elephants Elephas maximus in rural Bangladesh. *Oryx*. doi.org/10.1017/S0030605318001072

Shaffer, L.J., Khadka, K.K., Van Den Hoek, J. & Naithani, K.J. (2019). Human-elephant conflict: A review of current management strategies and future directions. *Front. Ecol. Evol.* **6**, 235. doi: 10.3389/fevo.2018.00235

Signer, J., Fieberg, J., & Avgar, T. (2019). Animal movement tools (amt): R package for managing tracking data and conducting habitat selection analyses. *Ecol. Evol.* **9**, 80–890.

Signorell, A., 2017. *DescTools: Tools for descriptive statistics*. R package version 0.99.20. CRAN. https://doi.org/10.1016/j.foreco.2014.09.033

Sitompul, A. F., Griffin, C. R., Rayl, N. D., & Fuller, T. K. (2013). Spatial and temporal habitat use of an Asian elephant in Sumatra. *Animals* **3**, 670–679.

Srinivasaiah, N., Kumar, V., Vaidyanathan, S., Sukumar, R. (2019). All-Male Groups in Asian Elephants: A Novel, Adaptive Social Strategy in Increasingly Anthropogenic Landscapes of Southern India. *Sci. Rep.* **9**, 8678. http://dx.doi.org/10.1038/s41598-019-45130-1.

Sukumar, R. (1990). Ecology of the Asian elephant in southern India. II. Feeding habits and crop raiding patterns. *J. Trop. Ecol.* **6**, 33-53.

Sukumar, R. & Gadgil, M. (1988). Male-female differences in foraging on crops by Asian elephants. *Anim. Behav.* **36**, 1233-1235.

Sutherland, W.J., Pullin, A.S., Dolman, P.M. & Knight, T.M. (2004). The need for evidence-based conservation. *Trends Ecol. Evol.* **19**, 305-308.

Terborgh, J., Davenport, L.C., Ong, L. & Campos-Arceiz, A. (2018). Foraging impacts of Asian megafauna on tropical rain forest structure and biodiversity. *Biotropica* **50**, 84-89.

Thurfjell, H., Ciuti, S., Boyce, M.S. (2014). Applications of step-selection functions in ecology and conservation. Mov. Ecol. **2**:4, https://doi.org/10.1186/2051-3933-2-4

Vidya, T.N.C. & Sukumar, R. (2005). Social organization of the Asian elephant (*Elephas maximus*) in southern India inferred from microsatellite DNA. *J. Ethol.* **23**, 205–210.

Wadey, J. (2020). *Movement ecology of Asian elephants in peninsular Malaysia*. PhD thesis, University of Nottingham Mayasia.

Wadey, J., Beyer, H.L., Saaban, S., Othman, N., Leimgruber, P., Campos-Arceiz, A. (2018). Why did the elephant cross the road? The complex response of wild elephants to a major road in Peninsular Malaysia. *Biol. Conserv.* **218**, 91–98.

Zeller, K.A., McGarigal, K., Beier, P., Cushman, S. A., Vickers, T. W., & Boyce, W. M. (2014). Sensitivity of landscape resistance estimates based on point selection functions to scale and behavioral state: pumas as a case study. *Landsc. Ecol.* **29**, 541–557.

Zeller, K.A., McGarigal, K., Cushman, S.A., Beier, P., Vickers, T.W., Boyce, W.M. (2016). Using step and path selection functions for estimating resistance to movement: pumas as a case study. *Landsc. Ecol.* **31**, 1319–1335.

Zeller, K. A., McGarigal, K., Cushman, S. A., Beier, P., Vickers, T. W., & Boyce, W. M. (2017). Sensitivity of resource selection and connectivity models to landscape definition. *Landsc. Ecol.* **32**, 835–855.

Table 1. List of environmental variables evaluated to modelling the movement probability of Asian elephants across the Peninsular Malaysia landscape. With these environmental variables we generated raster layers at 30 m of resolution to implement the analyses. GEE refers to products derived using the Google Earth Engine cloud-based platform which includes a data repository, and also methods for processing and exporting data.

Type	**Variable name**	**Initial data resolution**	**Description**	**Source**
Natural	Proportion of primary forest	250 m	Evergreen forest, predominantly primary (including degraded) forests estimated to have >60% canopy cover. May include also secondary forests that have reached structural characteristics similar to primary forest.	Miettinen et al. (2015)
	Proportion of regrowth/plantation	250 m	Natural regrowth and plantations as well as open canopy (<60%) evergreen forest with regrowth. Typically, young secondary forest and dense shrub as well as closed canopy industrial and small-holder plantations.	Miettinen et al. (2015)
	Proportion of open areas	250 m	Clearances and other open areas covered by annual crops, sparse fern/grass or low shrub. Typically, agricultural areas, areas undergoing land cover change or extremely degraded areas. These areas may also have scattered trees (<25% canopy cover).	Miettinen et al. (2015)
	Proportion of mosaic areas	250 m	Mosaic of open and vegetated, typically consists of tree gardens, agricultural fields, clearances, forest, regrowth or plantations. Sparse/patchy shrub vegetation (e.g., new plantation area), and evergreen savannah-type vegetation with patches of trees may also fall into this class.	Miettinen et al. (2015)
	Proportion of water bodies	250 m	Inland water bodies, include lakes and main rivers	Miettinen et al. (2015)

	Proportion of large-scale palm oil plantations	250 m	Contiguous closed canopy palm plantations larger than 1 km2. Most of them are oil palm, but some coconut and sago are also included.	Miettinen et al. (2015)
	Distance to water sources	Vector data	Euclidian distance to rivers, streams, drainages and lakes	Open Street Maps
	Elevation	30 m	Digital Elevation Data 30m Shuttle Radar Topography Mission (SRTM) V3 product (SRTM Plus) NASA JPL.	SRTM (GEE)
	$Elevation^2$	30 m	Quadratic term of Elevation covariate.	
	Slope	30 m	Slope derived from Digital Elevation Data	SRTM (GEE)
	Enhanced Vegetation Index	30 m	Optimized vegetation index used as a measure of primary productivity or live green vegetation, which is indicative of food abundance. Derived from Landsat cloud free multi-date mosaic (GEE).	Landsat (GEE)
	Normalized Difference Vegetation Index	30 m	Optimized vegetation index used as a measure of primary productivity or live green vegetation. Derived from Landsat cloud free multi-date mosaic (GEE).	Landsat (GEE)
	Normalized Difference Water Index	30 m	Index used to evaluate measure water content of leaves in green vegetation. Indicative of forest humidity and maturity. Derived from Landsat cloud free multi-date mosaic (GEE).	Landsat (GEE)
	Wetness	30 m	Tassled cap wetness index. Indicator for soil and canopy moisture. Recommended method to classify forest maturity and to classify the forest in a continuous scale between open (grasslands and early succession habitats) and closed (mature and old growth forest) habitats. Derived from Landsat cloud free multi-date mosaic (GEE).	Landsat (GEE)
	$Wetness^2$	30 m	Quadratic term of Wetness covariate.	
Anthropogenic	Distance to forest edge	250 m	Euclidian distance to the forest edge	Miettinen et al. (2015)

	Distance to mono-cultures edge	30 m	Euclidian distance to the mono-cultures edges	Petersen et al. (2016)
	Mean of nightlight	500 m	Mean monthly average radiance night-time lights derived from the Visible Infrared Imaging Radiometer Suite (VIIRS) Day/Night Band (DNB) for 2015. Indicative of human perturbation across the landscape.	VIIRS (GEE)
	Distance to motorway and primary roads	Vector data	Euclidian distance to the mono-cultures edges	Open Street Maps

Table 2. Landscape variables that have an effect in a probability of movement of female and male Asian elephants in Peninsular Malaysia (See Table 1 for variable definitions).

Sex	**Variable**	**Standardized coefficient**	**Standard error**	**z value**	**Level of significance *(P)* ***
Female	Wetness	0.880712	0.046046	19.987	99 %
	Elevation (30)	-0.687408	0.105088	-6.546	99 %
	Wetness^2	-0.646865	0.044633	-15.267	99 %
	Elevation^2	0.545791	0.093791	5.822	99 %
	Distance to forest (3,990 m)	-0.420058	0.158529	-2.655	99 %
	Distance to water (3,990 m)	0.345286	0.203501	1.948	insignificant
	Slope (30)	-0.172486	0.007619	-22.656	99 %
	Mean of nightlight (3,990 m)	-0.181316	0.307862	-3.484	99 %
	Percentage of regrowth and new plantations (750 m)	0.140288	0.027082	5.255	99 %
	Distance to plantations (30 m)	-0.135735	0.084545	-1.635	insignificant
	Percentage of plantations (750 m)	-0.059036	0.021255	-2.788	99 %
Male	Elevation (30)	-0.922531	0.085517	10.788	99%
	Wetness	0.886938	0.057096	15.534	99 %
	Elevation^2	0.658390	0.085517	8.096	99 %
	Wetness^2	-0.566196	0.051464	11.002	99 %
	Distance to roads (30 m)	-0.440359	0.419286	1.050	insignificant
	Distance to forest (30 m)	-0.304602	0.048618	6.265	99 %
	Distance to plantations (750 m)	-0.297368	0.166870	1.782	insignificant
	Slope (30)	-0.175006	0.008159	21.449	99 %
	Distance to water (210 m)	-0.168948	0.048120	3.511	99 %
	Percentage of regrowth and new plantations (750 m)	0.153568	0.020196	7.604	99 %
	Percentage of plantations (210 m)	-0.046446	0.166870	3.495	99 %
	Percentage of water (210 m)	0.034930	0.016049	2.176	95 %
	Percentage of open areas (210 m)	0.016974	0.011004	1.542	insignificant

Mean of nightlight (1,140 m)	-0.004755	0.017798	0.267	insignificant

* Level of significance: insignificant (> 0.5), 95% (< 0.5 and > 0.01), 99% (< 0.01).

Figure 1. Study area in Peninsular Malaysia which included the complete extension of the Managed Elephant Ranges (MER) and the main Protected Areas in the region.

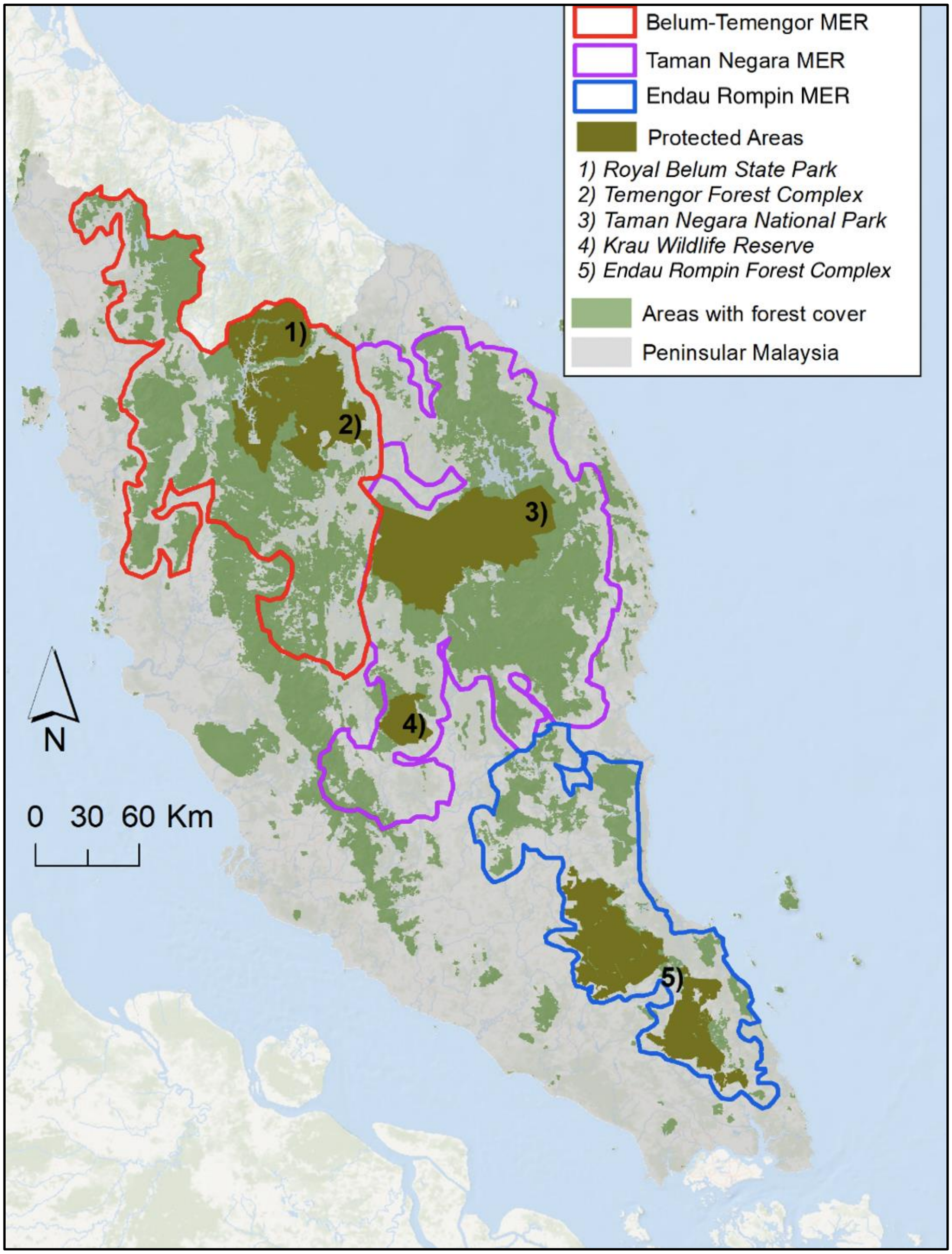


Figure 2. Probability of habitat use of A) female and B) male Asian elephants in Peninsular Malaysia. Probability habitat use is only included for the NECAP three Managed Elephant Ranges (MERs).

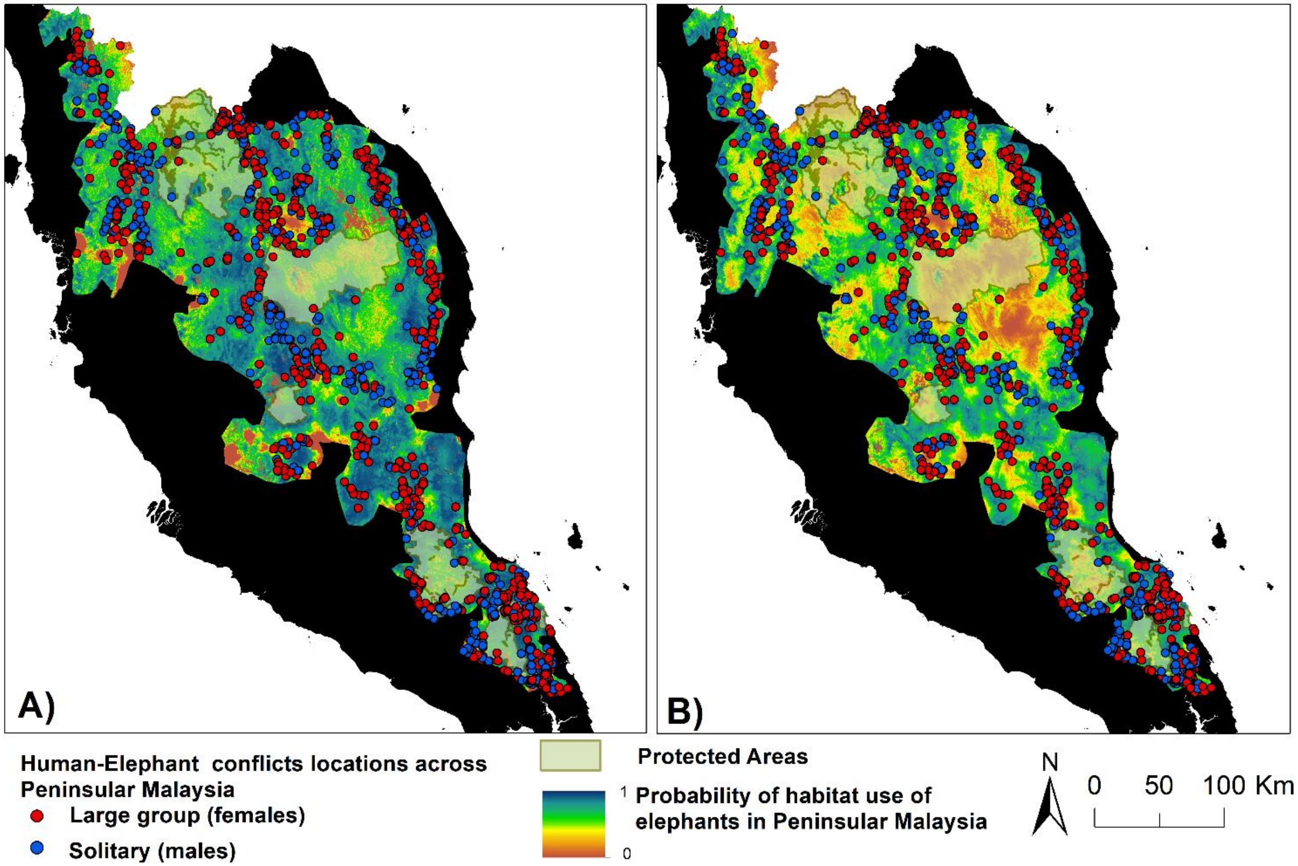


Figure 3. Relationship (a) between the locations of the human-elephant conflict (HEC) reports in Peninsular Malaysia and habitat suitability of female and male Asian elephants ($R^2 = 0.13$, $p < 0.0001$); (b) of HEC reports with female and male elephants' habitat suitability; (c) of female elephants' habitat suitability with the type of conflict documented in the HEC reports for the large groups; and (d) of male elephants' habitat suitability with the type of conflict documented in the HEC reports for solitary elephants. Size groups include solitary individuals which are more likely to be males, and large groups (six or more elephants) which are more likely to be groups of females.

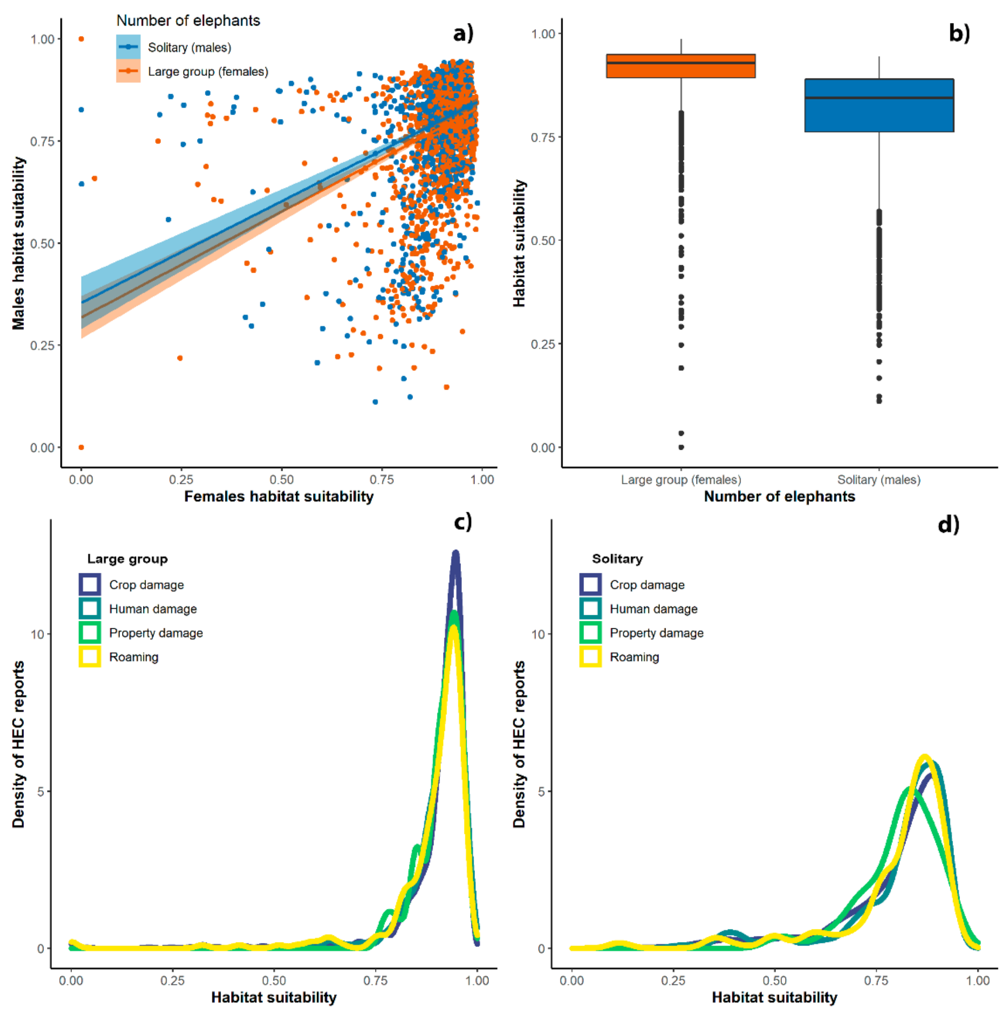


Figure 4. Frequency of HEC report types and their relationship with the number of elephants documented in each incident. The size groups include solitary individuals which are more likely to be males, and groups with 6 elephants or more which are more likely to be groups of females. Type of conflicts included: crop damage (n=2,393), human damage (n=489), property damage (n=74), roaming (n=443).

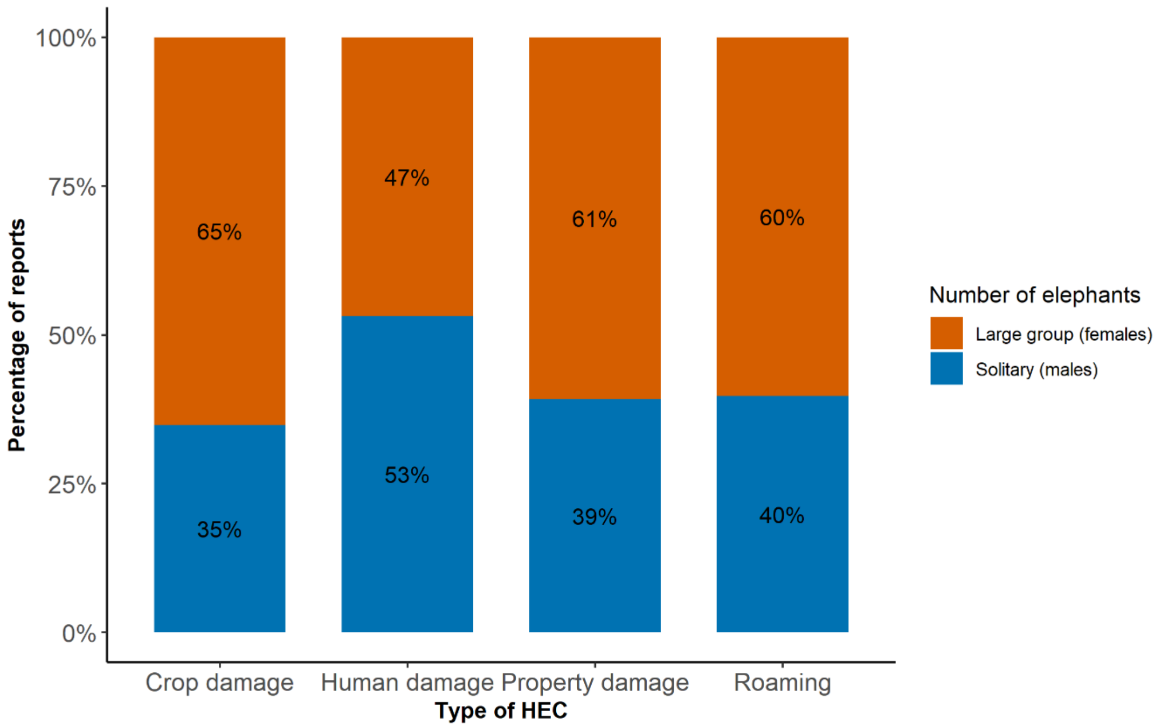
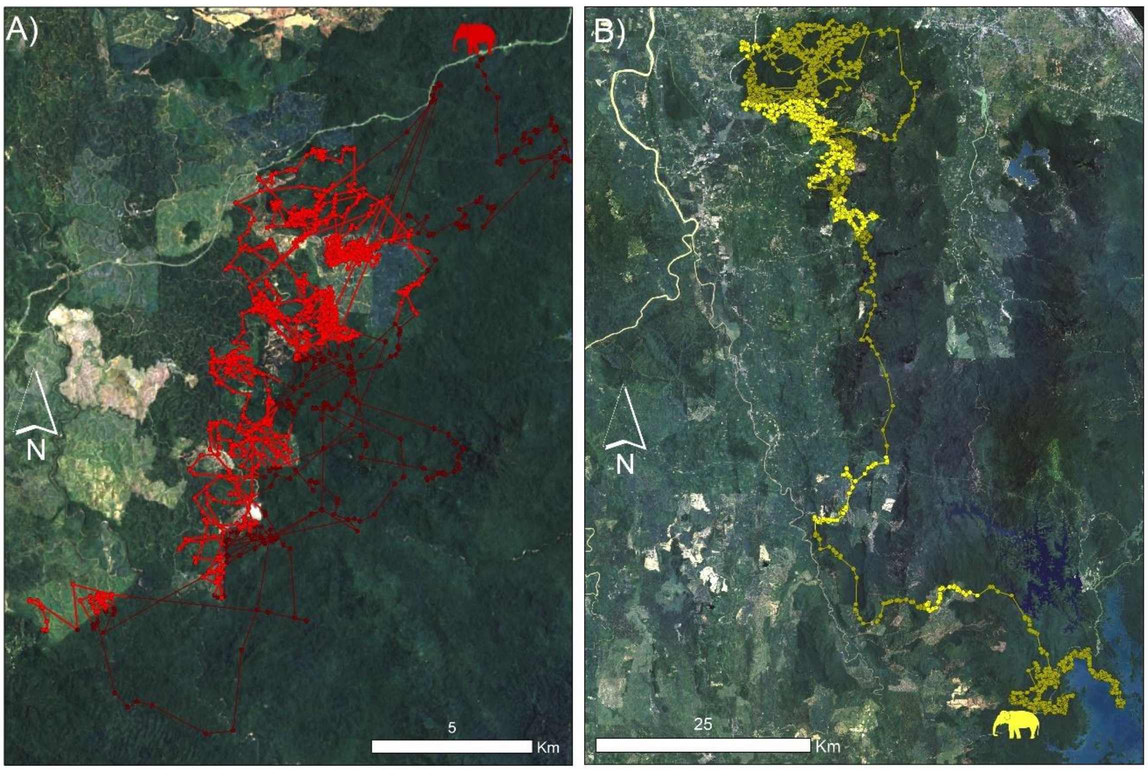


Figure 5. Movements of two elephants after the translocation process: A) Mek Dusun (female) and B) Cherang (male). The release location after the translocation is symbolized by an elephant icon", and both elephants were releases in the same site. The trajectories highlighted by a lighter colour indicate the sites of crops or human sites. Following the tracks, it is evident that both individuals enter into crop areas and sites with human activities after translocation process.



There will be conflict – agricultural landscapes are prime, rather than marginal, habitats for Asian elephants

Online supplementary information

Appendix 1.

Table S1. Asian elephant individuals tracked in this study and number of localizations per individual according to the different filters applied to the data.

No	Name	Sex	Status	Total fixes obtained	Fixes used to validate models	N fixes after data cleaning	N fixes after removing the capture effect	N fixes after resampling the fixes every 2 hour ± 10 minutes	N fixes after the filter of at least 3 sequential localizations and step length > 50 m
1	Dayang Siput	female	resident	3,951	409	3,542	3,381	3,380	2,146
2	Mama Kay	female	resident	3,923	382	3,540	3,227	1,711	1,137
3	Mek Banun	female	resident	1,183	130	1,053	894	894	589
4	Mek Dusun	female	translocated	1,167	136	1,031	1,001	1,000	317
5	Mek Fish	female	resident	4,519	447	4,072	3,913	3,913	2,456
6	Mek Gawi	female	translocated	4,458	477	3,981	3,834	3,833	2,304
7	Mek Jalong	female	translocated	7,765	750	7,015	6,856	6,854	3,809
8	Mek Kamasul	female	resident	10,796	1,070	9,726	9,628	9,628	6,647
9	Mek Kemat	female	translocated	9,498	930	8,568	8,419	8,418	5,827
10	Mek Pergau	female	resident	8,078	794	7,283	7,116	7,112	4,650
11	Mek Polis	female	translocated	4,097	396	3,701	3,638	3,638	2,214
12	Puteri Rafflesia	female	resident	10,444	1,077	9,367	9,220	9,219	4,321

13	Rafflesia	female	resident	1,797	177	1,620	1,311	702	493
14	Yeong Chepor	female	resident	3,397	337	2,806	2,724	1,288	393
15	Yeong Jalong	female	resident	3,310	333	2,533	2,325	1,070	293
16	Yeong Jalong1	female	translocated	3,461	339	2,825	2,667	1,253	321
17	Ajit	male	translocated	3,565	379	3,186	3,033	3,186	1,913
18	Awang Badur	male	translocated	5,519	562	4,957	4,816	4,957	2,743
19	Awang Bakti	male	translocated	5,411	527	4,884	4,748	4,883	2,574
20	Awang Banun	male	resident	4,500	457	4,043	3,885	4,043	2,435
21	Awang Belitung	male	translocated	568	53	515	370	515	339
22	Awang Chepor	male	resident	4,804	477	4,312	4,045	1,010	286
23	Awang Halim	male	translocated	15,603	1,548	14,053	13,503	4,244	2,174
24	Awang Ilham	male	translocated	6,529	607	5,922	5,779	5,922	4,087
25	Awang Jenor	male	translocated	3,084	302	2,782	2,630	2,781	1,568
26	Awang Kapak	male	translocated	10,673	1,081	9,592	9,441	9,590	5,583
27	Awang Lasah	male	translocated	408	34	374	244	201	30
28	Awang Mendelum	male	resident	2,081	210	1,871	1,770	1,871	1,136
29	Awang Putih	male	translocated	2,688	266	2,422	2,279	2,422	1,547
30	Awang S Kedah	male	resident	5,424	551	4,873	4,764	4,870	2,878
31	Awang Sedili	male	translocated	3,273	312	2,648	2,562	2,128	829
32	Awang Seri Timur	male	translocated	1,579	176	1,403	1,242	1,403	908
33	Awang Sindora	male	translocated	114	12	102	0	102	67
34	Awang Sindora1	male	translocated	246	29	217	83	217	122
35	Awang Tahan	male	translocated	5,928	582	5,346	5,193	5,344	3,137
36	Awang Teladas	male	translocated	3,625	376	3,249	3,122	3,248	2,038
37	Awang Udin	male	translocated	647	68	579	437	578	342
38	Awang Waha	male	translocated	589	62	527	405	527	301
39	Baung	male	translocated	2,546	257	2,191	2,061	1,522	435
40	Castello	male	resident	1,120	107	1,012	819	683	195
41	Cherang	male	translocated	5,201	521	4,641	4,488	3,404	1,033
42	Cherang Hangus	male	translocated	1,127	116	1,011	998	944	577

43	Jerek	male	translocated	1,052	94	958	633	503	358
44	Limau Kasturi	male	translocated	610	61	548	285	295	218
45	Pak Malau	male	translocated	3,553	379	3,174	3,017	3,173	2,097
46	Sauk	male	translocated	1,591	152	1,439	1,283	1,438	828
47	Tok Giring	male	translocated	4,669	486	3,463	3,221	1,372	208
48	Yeob Bendang	male	resident	1,596	148	1,344	1,085	654	253

Appendix 2.

Table S2. The best 20 Step Selection Function models for female Asian elephants. We evaluated 80 competing models with different covariates to evaluate the main drivers that promote habitat suitability of female elephants in Peninsular Malaysia landscape.

Rank	Models	df	logLik	AICc	Delta AIC	weight
1	Dforest_3,990m + Dplant + Dwater_3,990m + Palm_750m + Slope + Regrowth_750m + MeanLight_3,990m + wetness + wetness2 + Elev + Elev2	11	-78162.84	156347.69	0.00	0.53
2	Dforest_3,990m + Dplant + Droads + Palm_750m + Slope + Regrowth_750m + MeanLight_3,990m + wetness+ wetness2 + Elev + Elev2	11	-78164.63	156351.27	3.58	0.09
3	Dforest_3,990m + Dplant + Dwater_3,990m + Droads + Palm_750m + Slope + Regrowth_750m + MeanLight_3,990m + NDVI + wetness + wetness2 + Elev + Elev2	13	-78162.70	156351.41	3.73	0.08
4	Dforest_3,990m + Dplant + Dwater_3,990m + Droads + Open_1,140m + Palm_750m + Slope + Regrowth_750m + MeanLight_3,990m + wetness + wetness2 + Elev + Elev2	13	-78162.81	156351.64	3.95	0.07
5	Dforest_3,990m + Dplant + Dwater_3,990m + Droads + Palm_750m + Slope + water_7,560m + Regrowth_750m + MeanLight_3,990m + wetness + wetness2 + Elev + Elev2	13	-78162.83	156351.66	3.97	0.07
6	Dforest_3,990m + Dplant + Droads + Palm_750m + Slope + water_7,560m + Regrowth_750m + MeanLight_3,990m + wetness + wetness2 + Elev + Elev2	12	-78164.44	156352.90	5.21	0.04

7	Dforest_3,990m + Dplant + Droads + Palm_750m + Slope + Regrowth_750m + MeanLight_3,990m + NDVI + wetness + wetness2 + Elev + Elev2	12	-78164.50	156353.01	5.32	0.04
8	Dforest_3,990m + Dplant + Dwater_3,990m + Droads + Open_1,140m + Palm_750m + Slope + Regrowth_750m + MeanLight_3,990m + NDVI + wetness + wetness2 + Elev + Elev2	14	-78162.69	156353.39	5.70	0.03
9	Dforest_3,990m + Dplant + Dwater_3,990m + Droads + Open_1,140m + Palm_750m + Slope + water_7,560m + Regrowth_750m + MeanLight_3,990m + wetness + wetness2 + Elev + Elev2	14	-78162.81	156353.64	5.95	0.03
10	Dforest_3,990m + Dplant + Dwater_3,990m + Droads + Open_1,140m + Palm_750m + Slope + water_7,560m + Regrowth_750m + MeanLight_3,990m + NDVI + wetness + wetness2 + Elev + Elev2	15	-78162.69	156355.39	7.70	0.01
11	Dforest_3,990m + Dplant + Dwater_3,990m + Droads+Forest_750m + Open_1,140m + Palm_750m + Slope + MeanLight_3,990m + wetness + wetness2 + Elev + Elev2	13	-78169.90	156365.81	18.13	0.00
12	Dforest_3,990m + Dplant + Dwater_3,990m + Forest_750m + Open_1,140m + Palm_750m + Slope + water_7,560m + MeanLight_3,990m + wetness + wetness2 + Elev + Elev2	13	-78169.90	156365.81	18.13	0.00
13	Dforest_3,990m + Dplant + Dwater_3,990m + Droads + Forest_750m + Open_1,140m + Palm_750m + Slope + MeanLight_3,990m + NDVI + wetness + wetness2 + Elev + Elev2	14	-78169.82	156367.65	19.96	0.00

14	Dforest_3,990m + Dplant + Dwater_3,990m + Droads + Forest_750m + Open_1,140m + Palm_750m + Slope + water_7,560m + MeanLight_3,990m + NDVI + wetness + wetness2 + Elev + Elev2	15	-78169.82	156369.65	21.96	0.00
15	Dforest_3,990m + Dplant + Dwater_3,990m + Droads + Forest_750m + Palm_750m + Slope + MeanLight_3,990m + wetness + wetness2 + Elev + Elev2	12	-78173.10	156370.20	22.52	0.00
16	Dforest_3,990m + Dplant + Dwater_3,990m + Droads + Forest_750m + Palm_750m + Slope + MeanLight_3,990m + NDVI + wetness + wetness2 + Elev + Elev2	13	-78173.05	156372.10	24.42	0.00
17	Dforest_3,990m + Dplant + Droads + Forest_750m + Palm_750m + Slope + MeanLight_3,990m + wetness + wetness2 + Elev + Elev2	11	-78175.62	156373.25	25.56	0.00
18	Dforest_3,990m + Dplant + Droads + Forest_750m + Palm_750m + Slope + MeanLight_3,990m + NDVI + wetness + wetness2 + Elev + Elev2	12	-78175.57	156375.14	27.45	0.00
19	Dforest_3,990m + Dplant + Dwater_3,990m + Palm_750m + Slope + Regrowth_750m + MeanLight_3,990m + wetness + wetness2 + Elev	10	-78179.76	156379.53	31.85	0.00
20	Dforest_3,990m + Dplant + Dwater_3,990m + Palm_750m + Slope + Regrowth_750m + MeanLight_3,990m + NDVI + wetness + wetness2 + Elev	11	-78179.40	156380.81	33.12	0.00

Table S3. The best 20 Step Selection Function models for male Asian elephants. We evaluated 90 competing models with different covariates to evaluate the main drivers that promote habitat suitability of male elephants in Peninsular Malaysia landscape.

Rank	Models	df	logLik	AICc	Delta AIC	weight
1	Dforest + Dplant + Droads + Dwater_210m + Open_210m + Palm_210m + Regrowth_210m + Water_210m + MeanLight_1,140m + NDVI + wetness + wetness2 + slope + Elev + Elev2	15	-76422.4	152874.8	0	0.22
2	Dforest + Dplant + Droads + Dwater_210m + Open_210m + Palm_210m + Regrowth_750m + Water_210m + MeanLight_1,140m + EVI + NDVI + wetness + wetness2 + slope + Elev + Elev2	16	-76421.6	152875.2	0.41	0.18
3	Dforest + Dplant + Droads + Dwater_210m + Open_210m + Palm_210m + Regrowth_750m + Water_210m + MeanLight_1,140m + wetness + wetness2 + slope + Elev + Elev2	14	-76423.9	152875.8	1.03	0.13
4	Dforest + Dplant + Droads + Dwater_210m +Open_210m + Palm_210m + Regrowth_750m + Water_210m + MeanLight_1,167m + EVI + wetness + wetness2 + slope + Elev + Elev2	15	-76422.9	152875.9	1.08	0.13
5	Dforest + Dplant + Dwater_210m + Open_210m + Palm_210m + Regrowth_750m + Water_210m + MeanLight_1,140m + NDVI + wetness + wetness2 + slope + Elev + Elev2	14	-76424.4	152876.9	2.04	0.08
6	Dforest + Dplant + Dwater_210m + Open_210m + Palm_210m + Regrowth_750m + Water_210m + MeanLight_1,140m + wetness + wetness2 + slope + Elev + Elev2	13	-76425.9	152877.8	2.98	0.05

7	Dforest + Dplant + Dwater_210m + Open_210m + Palm_210m + Regrowth_750m + Water_210m + MeanLight_1,140m + wetness + wetness2 + slope + Elev + Elev2	13	-76425.9	152877.8	2.98	0.05
8	Dforest + Dplant + Dwater_210m + Palm_210m + Regrowth_750m + Water_210m + MeanLight_1,140m + NDVI + wetness + wetness2 + slope + Elev + Elev2	13	-76426.1	152878.3	3.44	0.04
9	Dforest + Dplant + Dwater_210m + Palm_210m + Regrowth_750m + Water_210m + MeanLight_1,140m + wetness + wetness2 + slope + Elev + Elev2	12	-76427.4	152878.9	4.06	0.03
10	Dforest + Dplant + Dwater_210m + Palm_210m + Regrowth_750m + MeanLight_1,140m + NDVI + wetness + wetness2 + slope + Elev + Elev2	12	-76428.4	152880.9	6.05	0.01
11	Dforest + Dplant + Dwater_210m + Palm_210m + Regrowth_750m + MeanLight_1,140m + wetness + wetness2 + slope + Elev + Elev2	11	-76429.4	152880.9	6.06	0.01
12	Dforest + Dwater_210m + Palm_210m + Regrowth_750m + MeanLight_1,140m + wetness + wetness2 + slope + Elev + Elev2	10	-76432.6	152885.2	10.4	0.00
13	Dforest + Dwater_210m + Palm_210m + Regrowth_750m + MeanLight_1,140m + wetness + wetness2 + slope + Elev + Elev2	10	-76432.6	152885.2	10.4	0.00
14	Dforest + Dwater_210m + Palm_210m + Regrowth_750m + MeanLight_1,140m + NDVI + wetness + wetness2 + slope + Elev + Elev2	11	-76431.6	152885.3	10.5	0.00

15	Dforest + Dplant + Dwater_210m + Forest_750m + Palm_210m + MeanLight_1,140m + NDVI + wetness + wetness2 + slope + Elev + Elev2	12	-76437	152898	23.2	0.00
16	Dforest + Dplant + Dwater_210m + Forest_750m + Palm_210m + MeanLight_1,140m + wetness + wetness2 + slope + Elev + Elev2	11	-76438.8	152899.7	24.9	0.00
17	Dforest + Dplant + Droads + Dwater_210m + Forest_750m + Open_210m + Palm_210m + Water_210m + MeanLight_1,140m + NDVI + wetness + wetness2 + slope + Elev + Elev2	15	-76435	152900	25.1	0.00
18	Dforest + Dplant + Dwater_210m + Forest_762m + Palm_210m + Water_210m + MeanLight_1,140m + NDVI + wetness + wetness2 + slope + Elev + Elev2	13	-76437	152900	25.1	0.00
19	Dforest + Dplant + Droads + Dwater_210m + Forest_750m + Open_210m + Palm_210m + Water_210m + MeanLight_1,140m + EVI+NDVI + wetness + wetness2 + slope + Elev + Elev2	16	-76434.2	152900.4	25.6	0.00
20	Dforest + Dwater_210m + Forest_750m + Palm_210m + MeanLight_1,140m + NDVI + wetness + wetness2 + slope + Elev + Elev2	11	-76439.4	152900.8	26	0.00

Appendix 3.

Table S4. Univariate results indicating scales of selection of female and male elephants in Peninsular Malaysia. Scales (in meters) and the response of the variable (+ or -) to the Step Selection Function.

		Female		Male	
Type	**Variable**	**Scale**	**Response**	**Scale**	**Response**
Natural	Proportion of primary forest	750	-	210	-
	Proportion of regrowth/plantation	750	+	750	+
	Proportion of open areas	1,140	-	210	+
	Proportion of mosaic areas	210	-	750	+
	Proportion of water bodies	7,560	+	210	+
	Proportion of large-scale palm oil plantations	750	-	210	-
	Distance to water sources	3,990	+	210	-
	Elevation	30	-	30	-
	Slope	30	-	30	-
	Enhanced Vegetation Index	30	+	30	+
	Normalized Difference Vegetation Index	30	+	30	+
	Normalized Difference Water Index	30	-	30	-
	Wetness	30	+	30	+
Anthropogenic	Distance to forest edge	3,990	-	30	-
	Distance to mono-cultures edge	30	-	210	-
	Mean of nightlight	3,990	-	1,140	-
	Distance to motorway and primary roads	30	-	210	+

Appendix 4.

Figure S1. Marginal plots with the relationship between the predicted relative probability of selection and the covariates that best explained the habitat suitability of female elephants.

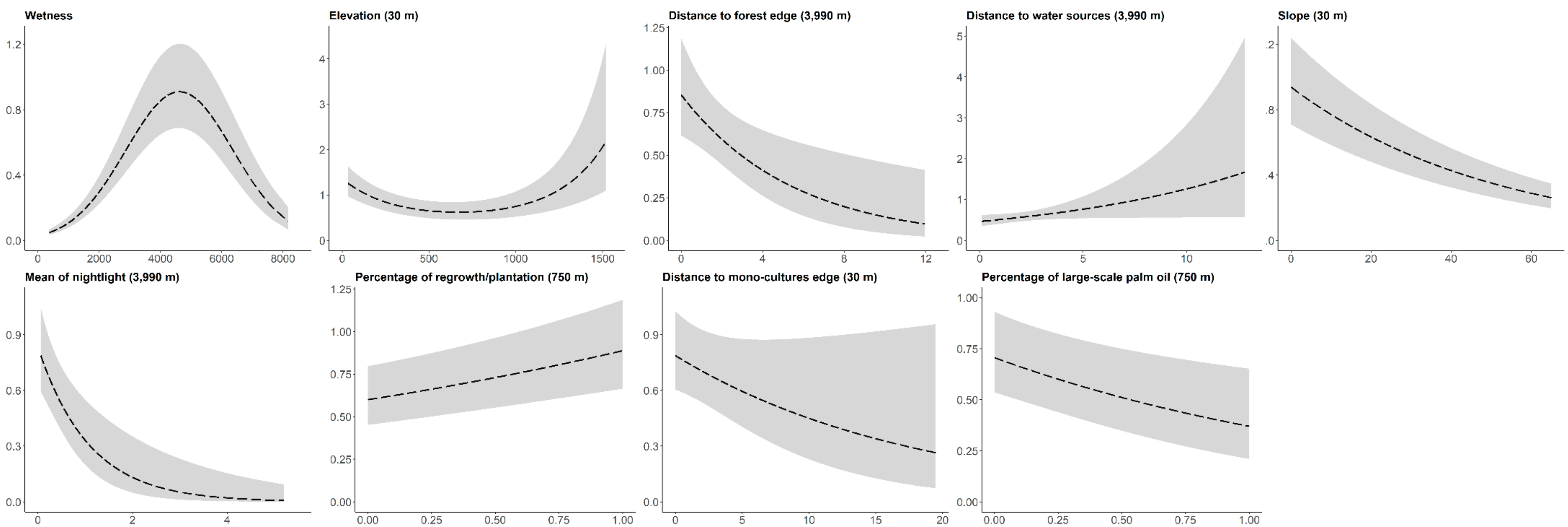


Figure S2. Marginal plots with the relationship between the predicted relative probability of selection and the covariates that best explained the habitat suitability of male elephants.