A multi-scale synthesis of mousedeer habitat associations in Southeast Asia reveals declining abundance but few extirpations in fragments and edges

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Abstract

Habitat loss and fragmentation profoundly impact Southeast Asian rainforest biodiversity and ecosystem functioning. While many larger herbivores are hunted and area-demanding apex predators are lost from degraded forests (logged forests, forest fragments and forest edges), smaller herbivore species may be comparatively resilient or even benefit from a release from competition and predation in degraded forests. Mousedeer (or chevrotains) in the *Tragulus* genus are some of the world's smallest ungulates (1.5–4.5 kg) and are widespread in Southeast Asia. We evaluated mousedeer habitat associations at three spatial scales. At the regional scale, presence-only species distribution modelling suggested mousedeer are negatively associated with aridity and elevation. At the landscape scale, variation capture rates among 186 published camera trapping studies suggested mousedeer are negatively associated with forest degradation and elevation. At the local scale (within landscapes), mousedeer abundance sampled with 1218 cameras at 10 landscapes and analysed with hierarchical abundance modelling suggested mousedeer are negatively associated with humans and elevation. Mousedeer diel activity patterns shifted towards increased nocturnality in degraded forests, possibly to avoid interactions with diurnal humans. Taken together, mousedeer prefer wet lowland forests and they persist – but decline – in degraded habitats and near humans. One exception was degraded forest fragments of Singapore where mousedeer are very abundant, likely due to the absence of hunting and predators. Our results emphasize that small herbivores persisting in fragmented rainforests decline relative to intact forests and thus are unlikely to be experiencing significant release from competition or predation. They also differ from small omnivorous generalists who experience beneficial foraging opportunities at edges. In degraded forests where larger wildlife has been lost, even low densities of small herbivores may perpetuate important ecological interactions such as herbivory, seed dispersal, or as prey for remaining predators.

KEYWORDS
abundance modelling, camera trapping, deforestation, species distribution modelling, wildlife, ungulate prey, ungulate prey

INTRODUCTION

Southeast Asian rainforest biodiversity and ecosystem functioning are threatened by forest conversion but species-specific responses remain poorly understood (Amir, Moore, et al., 2022; Wilcove et al., 2013). Deforestation in Southeast Asia has averaged 3.22 million ha per year for the last two decades (Feng et al., 2021) and >70% of forest cover remains within 1 km of a non-forest edge (Haddad et al., 2015). Forest fragments may have conservation value if they can maintain a community of resilient species and provide ecosystem services (Beca et al., 2017). Fragments are embedded in a variety of anthropogenic matrixes, such as clear-cuts, timber plantations, rice, rubber, or oil palm (Beca et al., 2017; Nijman, 2013), and different non-forest land uses can have unique influences on wildlife within remaining forests, such as if crops provide food subsidies for pest species (Luskin, Brashares, et al., 2017). Other threats like poaching disproportionately remove larger animals from fragments and edges (Harrison et al., 2016, but see Amir, Moore, et al., 2022) potentially leaving smaller species as crucial members of degraded forest food webs and thus crucial to perpetuating species interactions such as herbivory, seed dispersal, and predation (Amir, Sovie, & Luskin, 2022; Dehaudt et al., 2022; Dunn et al., 2022; Gray et al., 2018; Hendry et al., 2023; Ho et al., 2023; Honda et al., 2023; Lamperty et al., 2023). Small resilient animals in fragments and edges may also experience release from competition with larger herbivores and release from predation, leading to positive associations with habitat degradation (Moore et al., 2022). Taken together, small species may be comparatively resilient to fragmentation, edges, and other forms of forest degradation and crucial to degraded forest food webs (Luskin et al., 2021; Williams et al., 2021).

Chevrotain mousedeer (*Tragulidae* family, *Tragulus* genus) are the smallest ungulates in Asia and are distributed across the region's rainforests (Matsubayashi et al., 2003; Meijaard, 2011). The greater mousedeer (*Tragulus napu*) and the lesser mousedeer (*T. kanchil*) are the most common and widely distributed in Southeast Asia, including in Brunei, Cambodia, Indonesia, Laos, Malaysia, Myanmar, Philippines, Singapore, Thailand and Vietnam (Timmins & Duckworth, 2015a, 2015b). These two *Tragulus* species are morphologically similar with the key difference being that *T. napu* is slightly larger (adults 3.5–4.5 kg) than *T. kanchil* (adults 1.5–2.5 kg) (Meijaard, 2011). In practice, however, the difficulty of differentiating confidently of each species in the field or by photography has resulted in biodiversity surveys frequently grouping them together, especially in camera trap studies. Therefore, this paper assesses the greater mousedeer and the lesser mousedeer together and refers to this as the *Tragulus* genus or just 'mousedeer' hereafter.

Mousedeer have small home ranges (0.056 km^2) (Matsubayashi et al., 2003), short gestation periods (~5 months) (Medway et al., 1983) and broad vegetal-based diet (Farida et al., 2006), which are traits associated with resilience to habitat degradation, such as for macaques monkeys (*Macaca* genus) and common palm civets (*Paradoxurus hermaphroditus*) in Southeast Asia (Moore et al., 2022). The lesser and greater mousedeer are both listed as Least Concern in the IUCN Red List (Timmins & Duckworth, 2015a, 2015b) but are important in rainforest food webs because they are ideal-sized prey for many small and medium-sized carnivores, such as clouded leopards (*Pantheria uncia*), Asian golden cats (*Catopuma temminckii*), marbled cats (*Pardofelis marmorata*) and yellow-throated martens (*Martes flavigula*) (Amir, Moore, et al., 2022; Hendry et al., 2023; Luskin et al., 2023; Madhukumar, 2002; Ross et al., 2013). Mousedeer also disperse seeds (Chandru et al., 2020) and may have

outsized ecological roles in hunted and fragmented forests where larger ungulates are locally extinct (Brodie & Giordano, 2013; Corlett, 1998, 2007; Harrison et al., 2016). Although mousedeer can persist in degraded and fragmented forests (Chua et al., 2009; Khoo et al., 2021; Hazwan et al., 2022) and in the presence of hunting (Meijaard, 2011), the impact of humans and forest degradation on their abundance and behaviour is poorly understood.

Here we quantify habitat associations of mousedeer in Southeast Asia with an emphasis on testing their responses to humans and widespread forest degradation that plagues the region. We were interested in the scale dependency of habitat associations – and in leveraging all available datasets – so we structured this paper around three hypotheses that correspond to the three spatial resolutions of three different datasets. First, since both mousedeer species have an expansive range and have been reported from a variety of different forest types, we predicted they would show weak responses to bioclimatic covariates like precipitation and elevation (Chua et al., 2009; Farida et al., 2006; Matsubayashi et al., 2003). We tested these regional (range-wide) habitat associations using a MaxEnt species distribution model (SDM) parameterized with presence-only observations and considered responses weak if the variable performance in MaxEnt Jacknife test was <0.25 (see Methods). Second, since hunting has been reported as a cause of mousedeer population declines (Chua et al., 2009; Kuznetzov & Borissenko, 2004; O'Brien et al., 2003), we predicted a negative response to humans as measured by covariates like human population and the human footprint index (Venter et al., 2016). Since humans are highly mobile around forest edges and penetrate >1 km within a short time, we predicted the effect of humans and hunting would be strongest when assessed at the landscape scale (comparing entire forest patches or national parks that are >20 km apart). We tested our second hypothesis using mousedeer counts from published camera trapping studies and analysed this with generalized linear mixed models (glmms). Third, since predators and larger hunted herbivores are often the first to decline in forest edges and fragments (Amir, Moore, et al., 2022; Decœur et al., 2023; Dehaudt et al., 2022; Dunn et al., 2022; Hendry et al., 2023; Honda et al., 2023; Moore et al., 2023; Nursamsi et al,. 2023), and because mousedeer have been reported from small forest patches, we hypothesized that release from predation and competition would produce a positive association with degraded forests (logged forest, forest edges and forest fragments). We predicted this effect would be strongest when assessed at the local scale (variation within a single forest patch or national park) and tested this using new camera trapping detection histories analysed with hierarchical abundance modelling. Last, and separate from our main questions about habitat associations, we considered the effect of humans on mousedeer diel activity. Many species perceive diurnal humans as a threat and display temporal avoidance behaviour (Gaynor et al., 2018; Mendes et al., 2020). Therefore, we hypothesized mousedeer would shift its activity to nocturnal periods in areas with higher human activity to reduce overlap with humans. We tested diel activity shifts using the timestamps of detections in our new camera trapping.

METHODS

Taxonomic considerations

Most camera trapping studies struggle to distinguish greater and lesser mousedeer species. This also reduces confidence in species-level identifications in citizen science databases. Reliable museum records for species identification were mostly collected before the year 2000, and the loss of forests in the region renders historic occurrences unsuitable for assessing contemporary habitat conditions. When live-captured, these two species can also be differentiated by the number of throat stripes and other minor external characteristics that can be observed in adult individuals only (Chua et al., 2009). To overcome these limitations, we only used post-2000 observations and performed the analysis at the genus level (*Tragulus*), acknowledging our inability to differentiate species-level results. We exclude other *Tragulus* species due to insufficient records.

Data sources

We compiled data from three sources, (i) new camera trap surveys, (ii) published wildlife camera surveys and (iii) the Global Biodiversity Information Facility database (Chamberlain, Oldoni & Waller, 2022). We define a camera trapping study as a continuous sampling effort using at least 10 cameras within a landscape. In turn, we define a landscape as a ~10 to 1000 km² area, usually a national park, a production forest, or a collection of forest patches.

We conducted 20 camera trap surveys in 10 landscapes in Thailand, Peninsular Malaysia, Singapore, Sumatra and Borneo between December 2013 and March 2019. We deployed 18–78 passive infrared camera traps across sampling areas ranging from 10 to 813 km² (Figure 1, Table S1). We standardized the deployment methods across all landscapes by placing the cameras within a pre-mapped grid and spaced at least 500 m apart in large landscapes (>50 km²) and 100–500 m apart in smaller forest patches and islands (*e.g.*, Pulau Ubin in Singapore), attached to trees 0.2–0.3 m above ground along hiking trails or natural wildlife trails, and deployed for 60–90 days. We considered captures to be independent when they occurred at least 30 min apart. New camera trapping was included in the analyses at all spatial scales.

We compiled published camera trap records by searching Web of Science with the following criteria: "camera trap* AND Asia* or Thai* or Malaysia* or Indonesia* or Singapore* or Borneo* or Cambodia* or Vietnam* or Lao* or Myanmar* or Burma* or Sumatra* or Borneo*." Studies were included when they provided (i) a list of species observed with the number of independent records (count data), (ii) number of cameras and trapping effort, and (iii) the georeferenced location of the study site. These published wildlife camera studies do not include camera-level detection nor the timestamps of each individual record, which preclude its use for local scale hierarchical abundance modelling and for analysing diel activity.

Finally, to further expand the spatial coverage of occurrence records, we collated mousedeer presence records from Global Biodiversity Information Facility database (GBIF, 2021). Global Biodiversity Information Facility is an online repository for biodiversity data, including records from museum collections and citizen science records. These are presence-only records (*i.e.*, the presence of the species is reported, but absences are not reported), and therefore, can only be used for the large-scale MaxEnt SDM approach, which does not require records of the species' absence.
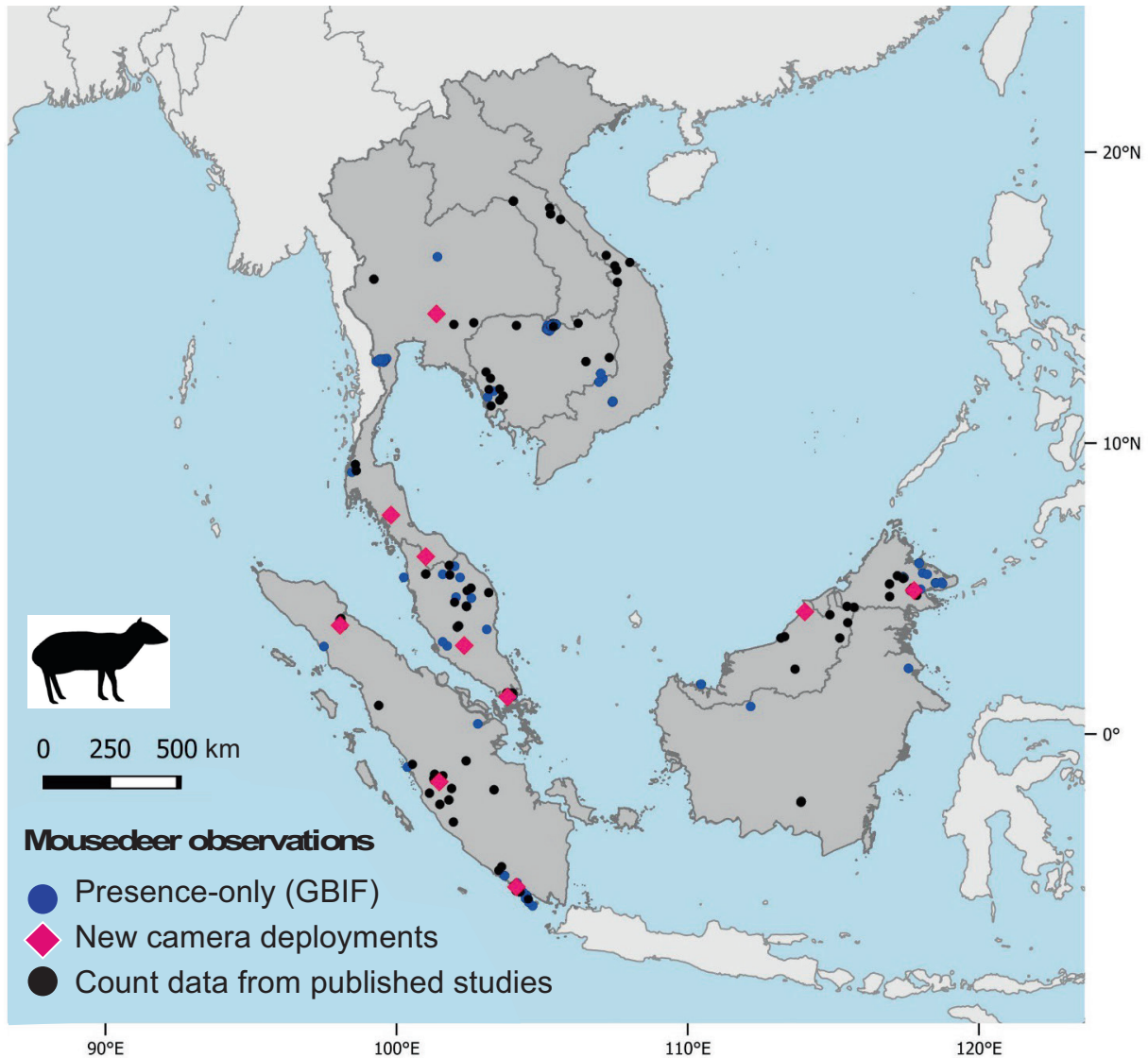
FIGURE 1 Map of the study area (grey) and sampling locations for the three types of data. The regional presence-only MaxEnt SDMs used all points reporting mousedeer presences, the landscape-scale glmms used published (blue) and new capture rates from camera studies (pink), and local-scale hierarchical abundance modelling used full detection histories from new camera trapping (pink).

Analysis – Regional MaxEnt SDMs and remaining habitat

We included eight environmental covariates: elevation, precipitation, forest cover, human population, night lights, oil palm, land cover type, and the forest landscape integrity index (hereafter 'forest integrity') (for more details, see Table S2). All eight covariates were resampled to a 1 km pixel size for spatial analyses. MaxEnt model performance was evaluated using a Receiver Operating Characteristic (ROC) analysis (Peterson et al., 2011) with cross-validation with 10 repetitions (Phillips, 2017). A jackknife test was used for estimating the relative contribution of each covariate on the mousedeer habitat suitability. For visualization, we used the Cloglog output to map the mousedeer habitat suitability, removing the areas outside the mousedeer's remaining potential habitat (Ke & Luskin., 2017; Dehaudt et al., 2022; Dunn et al., 2022; Hendry et al., 2023). We performed the calculations using the software MaxEnt (Phillips et al., 2023), QGIS and the statistical software R (Team, 2022) with the 'sf' package (Pebesma, 2018).

Analysis – Landscape-scale: Variation in detection rates in camera trap surveys

Detection rates in camera trap surveys are mechanistically related to abundance (Rowcliffe et al., 2011) and, under some circumstances, can be used as an index of animal abundance (Palmer et al., 2018; Parsons et al., 2017). However, since the detection rate does not account for variation in detectability, it is more appropriate to view it as an index of animal activity (Sollmann, 2018). Here, we take the more conservative approach and use detection rates as an index of mousedeer activity.

We used GLMMs to model the mousedeer detection rate on camera traps. Mousedeer capture counts for each survey were modelled using a negative binomial distribution, with the survey effort measured in trap nights as an offset term. The use of effort as an offset term causes the regression to model the capture rate (i.e., detections/effort) rather than the detection counts. Since this approach requires counts, the presence-only data obtained from GBIF was not included. It was not possible to identify exact survey boundaries, so covariates were summarized for the area within a 10 km buffer around the centroid, and this width was chosen to account for most study designs placing cameras over relatively large areas (10–100 km^2). Studies in which the 10 km buffer overlapped (i.e., centroids <20 km) were considered as belonging of the same spatial cluster (hereafter a 'landscape'), and the clusters were used as a random variable to account for the spatial autocorrelation. We ran both univariate and multivariate models, with up to two covariates per model. Covariates with correlation >0.4 or testing the same hypothesis (e.g., forest cover and forest integrity) were not added to the same model. The final set of 17 models was compared using Akaike Information Criterion corrected for small sample sizes (AIC$_c$). Models with a ΔAIC$_c$ <2 were considered equally plausible (Burnham & Anderson, 2002). We conducted the analysis using the R packages 'glmmTMB' (Brooks et al., 2017) and 'MuMIn' (Bartoń, 2022).

Analysis – Local-scale hierarchical abundance modelling

Using the full detection histories of the new camera trap surveys, we measured local (within a landscape) mousedeer habitat associations using Royle-Nichols (RN) hierarchical abundance models (Royle & Nichols, 2003). RN models account for variation in animal detectability between cameras and thus provide a reliable index of true abundance. In addition to previously described covariates, now calculated within a 1 km buffer around each of the camera locations, we included the distance to the nearest river and the distance to the nearest forest edge, (for more details, see Table S2). The 1 km radius width was chosen because our local scale approach focuses on the effect of covariates within the forest patch and its immediate surroundings. To account for spatial pseudo-replication of nearby cameras, we collapsed the camera trap data into a grid of hexagons (here called 'sampling units'), measuring 1 km in the short diagonal (0.866 km^2), and the number of cameras per sampling unity was added as a detectability covariate, while the site was added as an occupancy covariate (Rayan & Linkie, 2020). In most cases, each sampling unit contained only one camera associated with a unique value for each habitat covariate, but we averaged covariate values when multiple cameras fell within the same sampling unit. The detection history matrices were based on a sampling occasion of 3 days and contained presence/absence data (species not detected = 0; species detected = 1; inactive sampling unit or occasion = NA). Covariates with correlation >0.4 were excluded from the same model and we compared the final set of 16

models using AIC_c in the R packages 'unmarked' (Fiske & Chandler, 2011) and 'MuMIn' (Bartoń, 2022).

Diel activity patterns

We used the time-stamped detections from our camera trap studies to test for possible avoidance behaviour of mousedeer in response to humans. Since the effects of fear on animal behaviour are usually influenced by environmental clues, such as canopy density and light intensity, rather than direct encounters with the threat (Orrock et al., 2004; Verdolin, 2006), we used forest integrity index and human footprint index as covariates to describe human activity. The covariates were calculated in a 1 km buffer around the camera. The time-stamped detections were split in two groups, according to the covariate being tested, such as the Landscape Forest Integrity Index (Grantham et al., 2020). This way, 50% of the records are from areas with covariate values below the median (*i.e.*, low covariate group), while the other 50% are located in areas with covariate values above the median (*i.e.*, high covariate group). We compared the diel distributions between the two groups by bootstrapping 1000 diel distributions from each group, fitting a kernel density to the simulated distributions and comparing the estimates of the kernels using a Wald test. We also calculated the coefficient of overlap between mousedeer and their primary predators.

We also repeated the same analysis using the Euclidean distance from the camera trap to the nearest forest edge as a covariate. Cameras located >1 km from the nearest edge were considered to be in 'interior forest' while cameras <1 km away from an non-forested area were considered to be in 'edge forests' (Table S2). The analysis was performed using the R packages 'activity' (Rowcliffe, 2022) and 'overlap' (Ridout & Linkie, 2009). Finally, since mousedeer are assumed to be an important prey species for predators on fragmented landscapes, we computed the von Mises kernel density for mousedeer and its main potential predators. We also report the overlap coefficient between the kernel density estimates.

RESULTS

Regional MaxEnt SDMs

The presence-only dataset used in MaxEnt SDM included 1138 records (Figure 1, Table S3). The MaxEnt ROC area under the curve indicated an acceptable fit (ROC = 0.872, SD = 0.037) (Peterson et al., 2011). The environmental covariates with the greatest influence on mousedeer habitat suitability were annual precipitation and elevation (negative effect), with a contribution of 50% and 46.8%, respectively (Figure 2, Figures S1 and S2, Table S4). Precipitation had a hump-shaped with peak suitability between 800 and 2000 mm of rainfall per year.

Landscape-scale variation in detection rates

Mousedeer were detected in 80% of the 186 studies compiled from the literature (including the 20 new surveys reported here), with a combined total effort of 592 099 trap/nights (Table 1, Table S5). The top glmm was included a negative effect of elevation ($\beta = -0.578$, SE = 0.18, $z = -3.18$) and human population ($\beta = -2.07$, SE = 0.57, $z = -3.65$). The top model obtained an AIC weight = 0.53 with no other models within two AIC_c points. It is
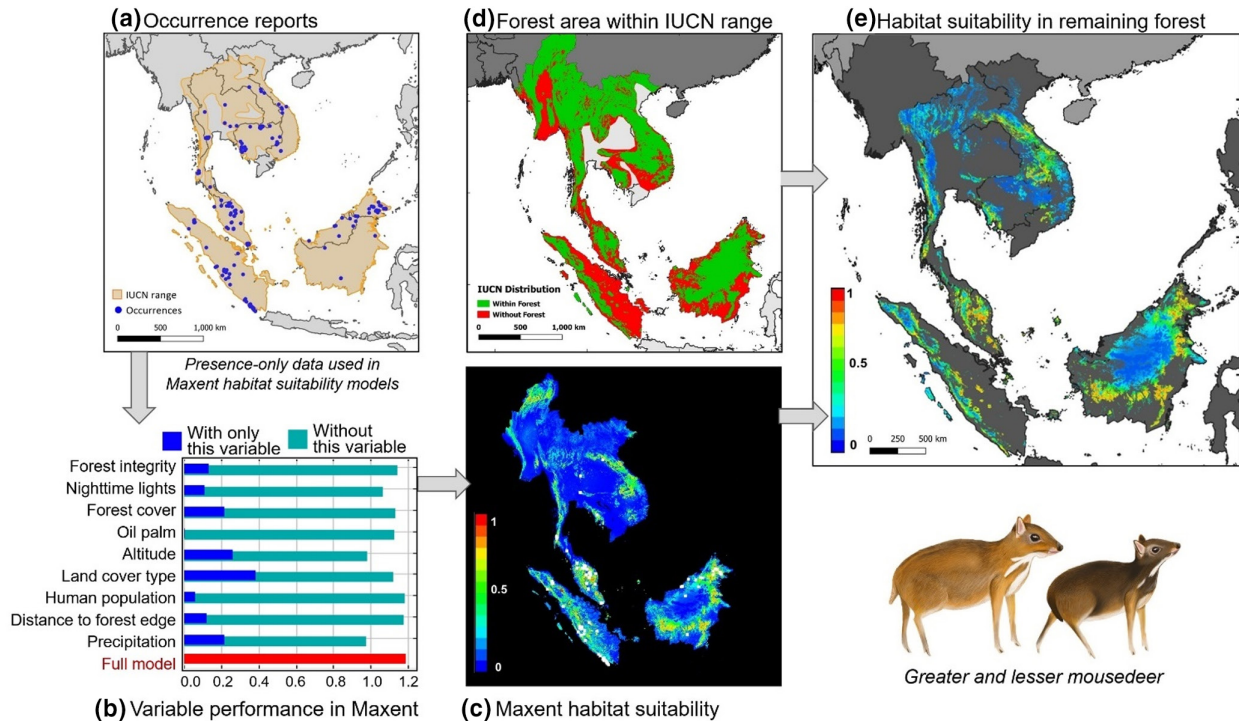
FIGURE 2 Mousedeer regional species distribution modelling (SDMs). Panel (a) shows the presence-only data that was obtained from GBIF and complemented by presence-only records extracted from camera trap studies. Panel (b) shows the MaxEnt jackknife variable performance test. The top variable was landcover, a categorical variable and showed mousedeer are strongly associated with forest versus non-forest classifications (all covariate layers are described in Table S2). Panel (c) shows SDM results mapped across the entire study area. Panel (d) shows the remaining forest within the study area. Panel (e) shows SDM results after removing non-forested areas where mousedeer are unlikely to occur.

TABLE 1 Camera trapping in Southeast Asia and mousedeer detections.

Region	Studies	Camera stations	Effort (trap nights)	Independent detections	Capture rate
Cambodia	10	690	52859	2006	3.790
Indonesia	47	1131	106565	1774	1.665
Laos	21	1140	60991	1289	2.113
Malaysia	52	2809	166657	4439	2.663
Singapore	36	1372	133269	2447	1.836
Thailand	17	485	53973	2001	3.707
Vietnam	3	334	17785	204	1.147
Total	186	7961	592099	14160	2.391

Note: We were unable to locate suitable studies for Brunei and Myanmar and Indonesia only includes Sumatra and Borneo for our study. Capture rate was calculated as the number of independent detections per 100 trap nights.

noteworthy that the second-best ranked model was the 'human population' univariate model with a $\Delta AIC_c = 2.05$ and an AIC weight$=0.19$. These two models, which share the 'human population' covariate, have a cumulative $\Delta AIC_c = 0.72$ (Figure 3a, Table 2).

Local-scale hierarchical abundance modelling

Our 20 camera trap studies included 1218 camera deployments with an accumulated effort of 58608 trap/nights and 1867 independent mousedeer captures. Mousedeer were recorded at 33% of all cameras. The top
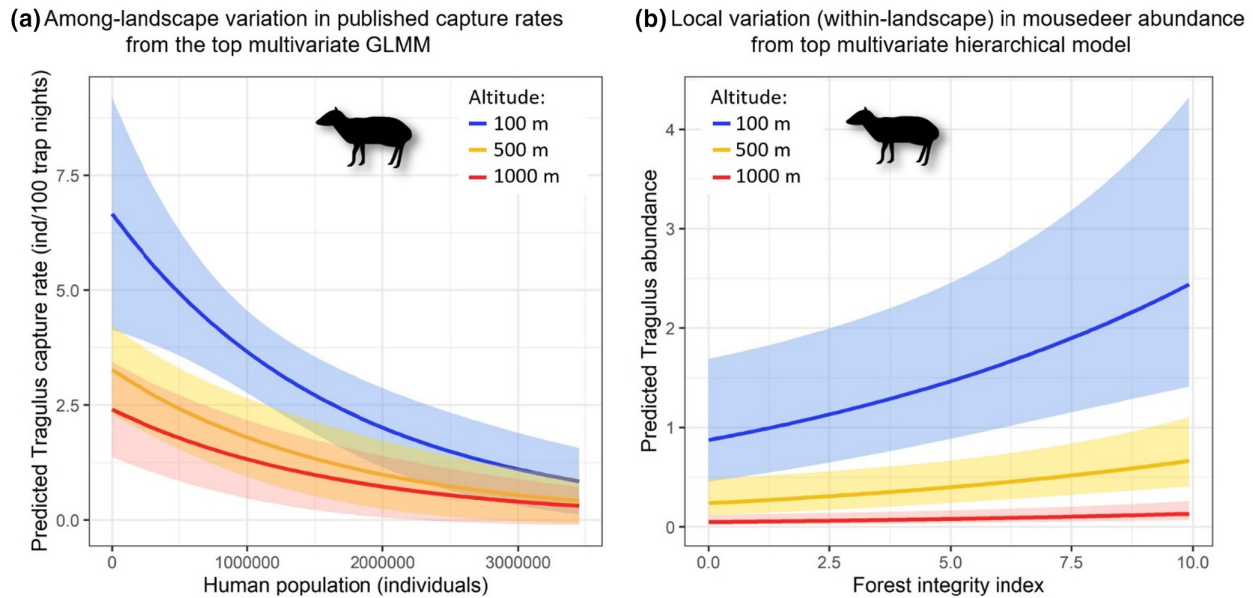
(a) Among-landscape variation in published capture rates from the top multivariate GLMM

(b) Local variation (within-landscape) in mousedeer abundance from top multivariate hierarchical model

FIGURE 3 Mousedeer habitat associations assessed among landscapes (a) and locally, within landscapes (b). Plots show the top models based on AIC_c explaining variation in mousedeer from camera trap sampling. (a) Mousedeer capture rate (per 100 trap nights) from 186 published camera trap studies, as predicted from the top GLMM that included multiple covariates and random effects to control for spatial replication. The landscape-scale covariates were measured in a 10 km radius around the centroid of the study. (b) Abundance estimated by a Royle-Nichols hierarchical model with data from 1218 cameras in 20 surveys at 10 landscapes and covariates measured in a 1 km radius around each camera.

TABLE 2 Model selection for the landscape-level factors influencing mousedeer capture rates in Southeast Asian camera trap studies.

Model	Degrees of freedom	AIC_c	ΔAIC_c	AIC weight	R^2
Elevation + Human population	5	1725.79	0	0.62	0.15
Human population	4	1727.84	2.05	0.22	0.29
Precipitation + Human population	5	1729.92	4.13	0.08	0.30
Elevation + Human footprint	5	1732.63	6.85	0.02	0.12
Elevation + Forest integrity	5	1732.82	7.04	0.02	0.05
Null model	3	1734.46	8.67	0.01	0.00
Elevation	4	1734.84	9.05	0.01	0.03
Precipitation	4	1736.10	10.31	0.00	0.01
Human footprint	4	1736.12	10.33	0.00	0.13
Forest integrity	4	1736.21	10.42	0.00	0.00
Human footprint + Forest cover	5	1736.26	10.47	0.00	0.10
Forest cover	4	1736.33	10.54	0.00	0.00
Elevation + Precipitation	5	1736.44	10.65	0.00	0.03
Precipitation + Forest cover	5	1737.77	11.98	0.00	0.01
Precipitation + Human footprint	5	1737.90	12.11	0.00	0.13
Precipitation + Forest integrity	5	1738.02	12.24	0.00	0.00
Human footprint + Forest integrity	5	1738.23	12.44	0.00	0.09

Note: The covariates were calculated within a 10 km radius surrounding the study centroid. The glmms are further described in Table S2.

Royle-Nichols model describing detection-corrected mousedeer abundance included a negative influence of elevation ($\beta = -0.59$, SE $= 0.08$, $z = -7.32$) and a positive influence of forest integrity ($\beta = 0.29$, SE $= 0.1$, $z = 2.96$). No other model obtained $\Delta AIC_c < 2$ and the second-best model

had $\Delta AIC_c = 6.48$ and included elevation and human footprint (Figure 3b, Table 3). We did not observe an association with riverine areas, which has been reported in the literature (Cao et al., 2010) with the hypothesis that mousedeer use water bodies to escape from predators (Meijaard, 2011; Meijaard et al., 2010).

Diel activity

In intact forests, mousedeer diel activity was crepuscular with two clear activity peaks occurring around dawn and dusk (Figure 4). Their diel activity is significantly more nocturnal in areas with lower forest integrity ($w = 5.12$, $p = 0.023$; Figure 4a) and closer to edges ($w = 5.86$, $p = 0.015$; Figure 4b). There was a significant shift showing crepuscular activity peaks were muted where human footprint was higher compared where it was lower ($w = 9.62$, $p = 0.002$; Figure 4c). Finally, there was significant dial activity overlap with several predators, including 0.85 with Asian golden cats, 0.65 with marbled cats, 0.62 with clouded leopards, and 0.61 with yellow-throated martens (Figure 4e–h).

DISCUSSION

Contrary to our predictions that widespread Southeast Asian mousedeer (*T. napu* and *T. kanchil*) are habitat generalists and thus only have weak associations with bioclimatic variables, they were significantly associated with lower elevations at all spatial scales and wetter sites at regional scales. There was support for our second prediction that hunting would negatively impact mousedeer, with lower landscape capture rates and lower local abundance in degraded forest and nearby humans. Hunting's negative influence was also supported by high detection rates and abundance in

TABLE 3 Royle-Nichols hierarchical abundance model selection that assesses variation in local mousedeer abundance (within-landscape).

Model	K	AIC$_c$	ΔAIC_c	AIC weight	Cumltv. AIC weight	R^2
Elevation + Forest integrity	24	7458.57	0.00	0.87	0.88	0.07
Elevation + Human footprint	24	7465.06	6.48	0.03	0.91	0.06
Elevation + Forest cover	24	7465.18	6.60	0.03	0.94	0.06
Elevation + Distance to forest edge	24	7465.68	7.11	0.02	0.97	0.06
Elevation	23	7465.82	7.25	0.02	0.99	0.06
Elevation + Distance to river	24	7467.54	8.97	0.01	1.00	0.06
Distance to river + Distance to forest edge	24	7503.84	45.27	0.00	1.00	0.03
Distance to forest edge	23	7511.74	53.17	0.00	1.00	0.01
Distance to river + Forest cover	24	7518.56	59.99	0.00	1.00	0.01
Distance to river	23	7518.70	60.13	0.00	1.00	0.01
Distance to river + Human footprint	24	7519.73	61.15	0.00	1.00	0.01
Distance to river + Forest integrity	24	7520.68	62.10	0.00	1.00	0.01
Null model	22	7526.82	68.24	0.00	1.00	0.00
Forest cover	23	7527.49	68.91	0.00	1.00	0.00
Human footprint	23	7528.46	69.89	0.00	1.00	0.00
Forest integrity	23	7528.80	70.23	0.00	1.00	0.00

Note: Columns show the number of parameters (*K*) and Akaike Information Criterion (AIC). Models performing worse than the null_reduced are not shown (including forest cover, human footprint, oil palm, and forest integrity).

small forest fragments in Singapore where there is a complete ban on hunting. Mousedeer diel activity behaviour supported their perception of humans as a threat (likely as a result of hunting), evidenced by their increased nocturnality near humans and edges. Finally, the results contradicted our third prediction that small mousedeer would be resilient to degradation, with no evidence that they increase in edges and fragments due to release from predation or competition with larger herbivores. Taken together, these results indicate hunting and forest quality – and not forest size – play a dominant role in explaining mousedeer in contemporary forests.

Despite the negative associations with forest degradation and humans, mousedeer were detected in nearly every study, demonstrating that declining abundance rarely leads to extirpations for these species. The dearth of extirpations provides support for the IUCN Red List threat assessment of 'Least Concern' for both species at present (Meijaard, 2011; Timmins & Duckworth, 2015a, 2015b). Mousedeer's relatively high persistence compared to larger herbivores (Amir, Moore, et al., 2022; Amir, Sovie, & Luskin, 2022; Carr et al., 2023) may be due to their small home range of 0.056 km^2, with reports from forest patches as small as 0.138 km^2 in oil palm-dominated landscapes in northern Sumatra (Luskin, Albert, & Tobler, 2017) and long-term persistence on the 10 km^2 island of Pulau Ubin in Singapore (Chua et al., 2009). Mousedeer persistence but declines in small patches and edges differentiates them from some small omnivorous or frugivorous monkeys and civets whose abundance has increased in the same degraded forests (Dehaudt et al., 2022; Honda et al., 2023; Moore et al., 2023). Such omnivores are often reported to benefit from foraging opportunities in agriculture, which has not been reported for mousedeer.

Our results contradict a recent paper by Hazwan et al. (2022) that reported a positive association with forest degradation for mousedeer in central-west Peninsular Malaysia. Specifically, Hazwan et al. found forest patches had four times greater detection of *T. kanchil* than continuous forests and logged forests had three times higher detections than intact forests. However, there are several issues in Hazwan et al. (2022) that warrant consideration. First, they confuse three species of *Tragulus* reported in prior papers by the same authors. Specifically, they used data from Jamhuri et al. (2018) that reported the mousedeer species as *Tragulus javanicus*. Hazwan et al. also included 51 records of *T. kanchil* from Sasidhran et al. (2016), but the original paper reports 21 records of *T. napu* and 30 records of *T. kanchil*. Second, of the two sites Hazwan et al. (2022) reported as unlogged, 98.5% of the Sungai Menyala Forest Reserve has been logged (Manokaran & Kochummen, 1987; Razak et al., 2019) and at the Pasoh Research Forest, their sampling predominantly occurred in logged areas (Luskin et al., 2023; Okuda et al., 2013). Third, they define fragmented forests as those <10000 ha (*i.e.*, <100 km^2), which is large relative to the small mousedeer home range of 0.056 km^2 and raises issues about the utility of their findings. These errors about logging at their sites and the spatial scale of fragmentation matters may flip Hazwan et al.'s conclusions related to the purported benefits of forest degradation for mousedeer. Nonetheless, their results may still be valid within the limited areas sampled. For example, we recovered similar associations with elevation as Hazwan et al. other prior work (Cao et al., 2010; Farida et al., 2006; Meijaard, 2011). In fact, we found mousedeer preference for lowlands was consistent at all three spatial scales we examined. The causal pathways by which elevation affects mousedeer are not clear but could be related to temperature given their small size which makes thermoregulation costly.

Our conservative genus-level and multi-scale approach has strengths and weaknesses. First, due to misidentifications in Southeast Asian mousedeer in camera trap images, we group the two sympatric *Tragulus* species,
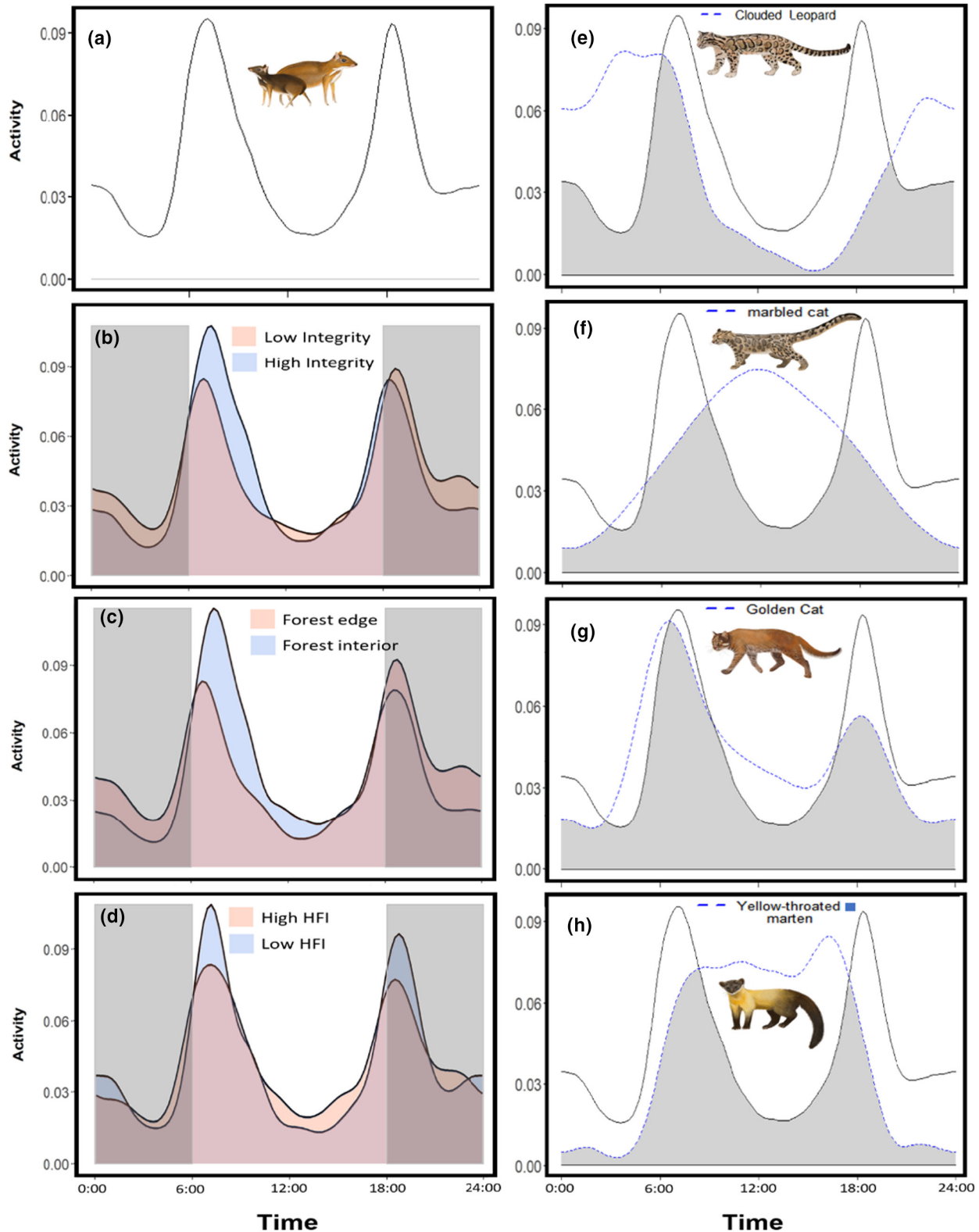
FIGURE 4 Diel activity patterns of greater and lesser mousedeer (a) and differences in response to forest degradation and human variables (b–d) and overlap with key predators (e–h). The threshold between the high and low forest integrity and human footprint index (HFI) is defined by the median of those variables. Edges were defined as forest cover <1 km from a non-forested border. In panels b–d, the nocturnal hours are shaded. In panels e–h, mousedeer activity patterns are shown by solid lines, predators with dashed lines, and their overlap is shown by the shaded region.

and this inhibits inferences on specific species. Genus-level trends could be driven by one or another of the two sympatric *Tragulus* species. We considered the conservative but accurate genus-level approach preferable to Hazwan et al.'s species-specific approach with known misidentifications. Another weakness of our conservative and accurate multi-scale analysis is that it requires more investment from readers to fully understand the complexity. We consider this preferable to including inappropriate covariates or spatial scales, such as Hazwan et al.'s inaccurate binary categorization of logging across entire landscapes. An important limitation of our approach is that mousedeer may show inconsistent trends across their range, and our approach included range-wide occurrence data from GBIF, 186 landscape-level camera surveys across Cambodia, Sumatra, Indonesia, Laos, Peninsular Malaysia, Malaysian Borneo, Singapore, Thailand, and Vietnam and 20 new camera surveys. Our analysis was also unable to isolate trends in mousedeer populations within truly intact forests that are >1 km from forest edges, which represents <25% of remaining habitat in Southeast Asia and is predominantly relegated to high elevations where mousedeer are less abundant (Figures 2 and 3).

Our results emphasize that even small resilient wildlife persisting in fragmented rainforests decline relative to intact forests, which may have repercussions for species interactions, food web ecology and ecosystem functioning. Future studies should focus on key gaps in mousedeer ecology including (i) species interactions with predators, (ii) diet and seed dispersal in degraded forests, (iii) genetic isolation and inbreeding depression in mousedeer populations persisting in small island and forest fragments, such as in Singapore.

AUTHOR CONTRIBUTIONS

Calebe P. Mendes: Conceptualization (equal); data curation (equal); formal analysis (equal); visualization (equal); writing – original draft (equal); writing – review and editing (equal). **Xiaohan Liu:** Formal analysis (equal); investigation (equal); writing – original draft (equal). **Zachary Amir:** Conceptualization (equal); data curation (equal); formal analysis (equal); writing – review and editing (equal). **Jonathan H. Moore:** Conceptualization (equal); data curation (equal). **Matthew Scott Luskin:** Conceptualization (equal); data curation (equal); formal analysis (equal); funding acquisition (equal); methodology (equal); project administration (lead); resources (lead); supervision (lead); writing - original draft (equal); writing – review and editing (equal).

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DATA AVAILABILITY STATEMENT
The data is partially available upon request. A subset of the data is not available as it belongs to a third party.

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