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Sumatran tiger density estimates in the Leuser Ecosystem, Sumatra, Indonesia

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Density is a fundamental parameter for monitoring animal populations and determining actions for habitat management. We investigated sex-specific densities of critically endangered Sumatran tigers (*Panthera tigris sumatrae*) in provincially protected forests outside the National Park system in the Leuser Ecosystem of Indonesia. Sumatran tiger camera trap studies are characterized by imprecise density estimates derived from excessively sparse 90-day datasets, reflecting the challenges of obtaining adequate sample sizes on this rainforest carnivore. We overcame this obstacle with strategic reconnaissance, recruitment of highly skilled forest rangers, and deployment of infrequently used professional-grade camera traps. We used closed population spatial capture-recapture (SCR) models based on data from 52–64 paired camera stations to estimate densities of male and female Sumatran tigers, comparing results between 90-day and 180-day sessions. Camera trapping for 12-months (June–December 2023 and May–November 2024) accumulated 282 identifiable photographs, including 245 recaptures, of 27 adult tigers (14 females, 12 males, and 1 individual of unknown sex); average captures (recaptures) were 85 (67) and 141 (123) for the 90 and 180-day periods, respectively. Cumulatively, these results represent the most robust single-study Sumatran tiger camera trap dataset. During the 90-day sessions, sex-specific tiger densities ranged from 0.97 (\pm 0.37)–1.83 (\pm 0.59) female and 0.56 (\pm 0.22)–0.61 (\pm 0.29) male tigers. During the 180-day sessions, estimates were only negligibly more precise, ranging from 0.94 (\pm 0.33)–1.76 (\pm 0.54) female and 0.41 (\pm 0.15)–0.50 (\pm 0.22) male tigers. Across both years, densities were 1.42–2.35 tigers/100 km², about 2.5–4.1 times greater than the most recent estimates in the mountains of Gunung Leuser National Park. Our results support prioritization of spatial over temporal sampling for population monitoring of rare and elusive species as expanding the trap array resulted in greater precision of density estimates than extending the sampling period.

KEYWORDS

camera traps, density, Leuser Ecosystem, rain forest, spatial capture-recapture, Sumatran tiger

1 Introduction

Habitat loss and degradation, combined with poaching and prey depletion, continues to spur range contractions of tigers (*Panthera tigris*), already lost from ~90–95% of their historical distribution (Sanderson et al., 2023). Most tiger populations now occur in India where, bucking the trend of range-wide declines, several cases of significant tiger recoveries have followed commendable boosts in protection (Harihar et al., 2020; Karanth et al., 2020). Beyond protected areas in the productive habitats of South Asia, tiger status is mostly ominous, particularly in the rainforests of Southeast Asia (Sanderson et al., 2023). Although it contains ~33% of tiger habitats range-wide, Southeast Asia has already lost tigers entirely from the countries of Vietnam, Cambodia, and Laos (Sanderson et al., 2023). The species distribution is now restricted to 10 Asian countries.

In Sumatra, where recent work has generated more detailed distribution maps for the island's critically endangered tigers (Goodrich et al., 2022), assessments on the status and trends of their populations remain limited by the absence of reliable data on population densities. Consequently, the range of the most recent Sumatran tiger (*Panthera tigris sumatrae*) population estimate (173–883 tigers) (Goodrich et al., 2022) varies by >500% and is essentially meaningless as a basis for monitoring evaluation and conservation planning.

The Sumatran tiger is an apex predator and rainforest-adapted species that has regulating effects on prey populations and sympatric carnivores (Karanth and Sunquist, 1995; Widodo et al., 2022). It also holds significant cultural significance among people in Sumatra's forest-edge villages (Kartika, 2023). Due to their high metabolic demands, Sumatran tigers require access to expansive habitats stocked with abundant prey (Linkie et al., 2006). Monitoring of the species' population trends can therefore provide crucial indicators of ecosystem health in Sumatran tropical rain forests, among the most biodiverse biomes on the planet (IUCN, 2004; BBTNGL, 2025).

The reliability of species status assessments is dependent on the availability of accurate and precise estimates of demographic parameters, both of which have been persistently challenging to obtain for Sumatran tigers. Unbiased density estimates require adequate data, including sufficient sample sizes of distinct individuals and recaptures, both of which are rarely attainable for this rainforest carnivore. If density estimates are robust, with sufficient precision to detect significant change across study areas or through time, they can be compared with results from other surveys (Karanth and Nichols, 2017). If density estimates are constrained by biased representation of tiger habitats or lack precision, then unfounded extrapolation can result in erroneous inference (Gopalaswamy et al., 2019). Increasing sampling effort can overcome these issues, but it is beset by logistical challenges, prohibitive costs, and potential violations of key population estimation assumptions (Royle et al., 2013).

Despite 60–70% of remaining Sumatran tiger habitats occurring outside nationally-designated protected areas, all spatial capture-recapture (SCR) density estimates (n=18) focused exclusively on the species' populations inside National Parks and Wildlife Reserves

(Linkie et al., 2006; Wibisono et al., 2009; Sunarto et al., 2013; Puspardini et al., 2018). A previous attempt to estimate tiger density in Gunung Leuser National Park used single (i.e., unpaired) cameras that resulted in only ten photographs of five individual tigers (Luskin et al., 2017). Besides significant reductions in detection probabilities, use of single cameras that photograph only one flank of passing tigers inevitably reduces tiger identification datasets thereby causing greater bias in density estimates (O'Connor et al., 2017). The most recent Sumatran tiger population assessment in Gunung Leuser National Park, based on sample sizes of 4–8 individuals detected during four sampling periods, estimated densities of 0.40 (± 0.19 SD)–0.73 (± 0.42) tigers/100 km² in mountainous terrain of the park's interior (Hadi et al., 2025).

Following the methods of pioneering tiger capture-recapture studies in India (Karanth, 1995), where the species' densities are ~5–10 times higher than those in tropical rainforests, most tiger density estimates range-wide are derived from 2–3 month sampling periods (Goodrich et al., 2022). This timeframe is required to satisfy the key assumption of demographic population closure (Otis et al., 1978; Karanth and Nichols, 2017). Compared to the productive savannahs, grasslands, and deciduous forests of the Indian subcontinent, Sumatra's extensive tracts of predominantly mountainous rainforests, lower prey biomass, and lower tiger densities create conditions that present numerous logistical challenges. Hence, there are context-dependent trade-offs between meeting population closure and obtaining sufficient sample sizes of tigers.

Sample size challenges are further magnified considering the seldom-obtained need for sex-specific population parameters. Tigers are polygamous and males do not contribute to the nursing and parental care of cubs, which makes females the most significant contributors to the species' population dynamics (Smith et al., 1987; Harihar et al., 2020). Female tigers are also more philopatric and have smaller home ranges than males (Smith, 1993; Simchareon et al., 2014). Female home range size generally varies inversely with their densities which, in turn, can be used to evaluate local carrying capacity for the species (Majumder et al., 2012; Simchareon et al., 2014). Estimation of female densities is therefore crucial for tiger population monitoring.

Despite the importance of distinguishing female and male tigers, most Sumatran tiger camera-trap studies do not report sex ratios and female-specific densities have yet to be estimated. Sex differences are challenging to obtain due to the need for adequate sample sizes of male and female tigers (Duangchantrasiri et al., 2024). Recent camera-trap studies on large felids have advocated for longer sampling sessions to increase numbers of captures and recaptures despite higher risks of violating the closure assumption (Dupont et al., 2019; Harmsen et al., 2020).

Our objectives were to 1) estimate sex-specific population densities of Sumatran tigers; 2) compare tiger density and movement estimates based on varying survey efforts in space (e.g., trap array size) and time (e.g., standard 90-day sessions and extended 180-day sessions); and 3) estimate naïve occupancy and relative abundance indices of main tiger prey, competing carnivores, and – as an index of human disturbance and

protection – humans in three categories: hunters, unarmed villagers, and rangers.

2 Materials and methods

2.1 Study area

The Leuser Ecosystem (hereafter Leuser) is part of the largest contiguous tiger habitat remaining in Sumatra. Found in the island's provinces of Aceh and North Sumatra, the ecosystem spans 2.65 million hectares (ha) of lowland (0–300 m), hill (301–800 m), submontane (801–1400), montane (1401–2000), and upper montane (2001 +) forest (BBTNGL, 2025). Significant tracts of threatened peat swamp forests flank the ecosystem's western boundary. Collectively, Leuser's habitats store an estimated 1.6 billion tons of carbon (Roberts et al., 2025). In Leuser's core lies the 8,303 km² Gunung Leuser National Park, which is part of the “Tropical Rainforest Heritage of Sumatra” UNESCO World Heritage site (IUCN, 2004). Leuser is considered a National Strategic Area for its environmental protection function (under Law No. 26/2007 juncto Law No. 26/2008).

Leuser supports populations of four ungulate species, all prey of tigers – sambar (*Rusa unicolor*), wild pig (*Sus scrofa*), southern red muntjac (*Muntiacus muntjac*) and serow (*Capricornis sumatraensis*). Tiger presence is strongly associated, in particular, with the availability of sambar; this ~130 kg cervid is a preferred prey of tigers range-wide (Karanth and Sunquist, 1995; Simchareon et al., 2018) but is largely absent from all but the most inaccessible or best protected sites in Southeast Asia (Steinmetz et al., 2021; Widodo et al., 2022). Sympatric carnivores sharing some prey preferences with tigers in Leuser include clouded leopard (*Neofelis diardi*) and dhole (*Cuon alpinus*) (Figel et al., 2024).

Leuser is critical for tiger conservation because it contains the largest expanses of unfragmented forests remaining in Sumatra. Approximately 44% of this indispensable ecosystem meets the criteria of an “intact forest landscape,” (hereafter intact forest) defined as forests that “exhibit no remotely detected signs of human activity or habitat fragmentation and are large enough to maintain all native biological diversity, including viable populations of wide-ranging species” (Potapov et al., 2013). The northern forests of Leuser also form part of key, yet tenuous, connections with the adjacent Ulu Masen Ecosystem (Figel et al., 2024). Combined, these two ecosystems comprise a contiguous 3.6 million ha expanse of tiger-occupied forests, the largest such landscape in Sumatra and the second-largest in southeast Asia (Sanderson et al., 2023).

Despite its paramount importance, Leuser is persistently threatened by habitat conversion from illegal logging, road and oil palm plantation development, and gold mining and the instability caused by the socio-ecological disasters that these activities exacerbate (Supriatna et al., 2017; Lubis et al., 2024). The region is further imperiled by chronic poaching, particularly in areas insufficiently patrolled by rangers (Figel et al., 2021, 2024).

We conducted this study in nationally unprotected forests in Leuser's northern stretches in Aceh Province, Sumatra. Mean

elevation in our study area was 693 meters above sea level (range 117–1955 meters). Landcover types include protection forest (*hutan lindung*), production forest (*hutan produksi*), and agricultural areas (*area penggunaan lain*). Whereas the ‘protection forest’ designation strictly prohibits logging or any other extractive activity, permitted logging operations are permissible in production forests. Soil type in our study area is comprised mainly of ultisols and complex entisols-inceptisols. Average annual rainfall is 1,800–2,500 mm. The major habitat type is tropical moist broadleaf forest, where rainfall occurs throughout the year. However, there is a distinct drier season from June–August; this three-month period generally receives only ~10–12% of annual rainfall. Conversely, 35–40% of annual rainfall generally falls October–December (BBTNGL, 2025).

2.2 Data collection

We conducted reconnaissance in the study area using 34 paired cameras from March–May 2023. The main objectives of this exploratory survey were to maximize probabilities of detecting tigers by locating optimal sites for camera-trap installation and to identify the most skilled local collaborators from selected forest-edge communities for subsequential hire as rangers. We were also interested to gain a better understanding of tiger sex-ratios and habitat use.

Following the 3-month reconnaissance, we covered the refined study area with 4 x 4 km grid cells and installed 1–2 paired camera stations in each cell. This grid cell size, standardized according to the best available data on Sumatran tiger movements, ensures there are no holes in the trap array where individual tigers may be undetectable during the sampling (Wibisono et al., 2009; Figel et al., 2024). We used infrared, professional-grade cameras manufactured by Reconyx (Holmen, WI, USA–HC600, PC800, HF2x, and XR6 models) and Spartan (Duluth, GA, USA–SR2-BK model). To simultaneously photograph both flanks of passing tigers, we positioned cameras at heights of 40–45 cm on trees opposite each other along forest trails. To maximize photographic detections of tigers, we placed cameras along their known travel pathways, as determined by the reconnaissance and innate ranger knowledge of the study area. To avoid damage from high humidity, we placed fresh desiccant sheets inside cameras before each session. All sampling was completed upon receiving national and regional permits.

To ensure images remain secured, we used encrypted DigiKey[®] (Thief River Falls, MN, USA) SD cards that require a user password to ‘unlock’ images before downloading. As researchers working on a highly persecuted and critically endangered species, we considered it our professional responsibility to use this measure of enhanced data security, particularly when working with rangers with whom we had not previously collaborated.

In 2023, we maintained cameras at 59 stations from June–December; 70% of the stations were in lowland and hill forests at elevations below 800 meters. With an average trap spacing of 1.64 km, the 2023 trap array spanned 308 km². Land cover in the 2023 polygon was comprised of 70% protection forest, 17% production forest, and 13% farming areas. Intact forest comprised 26% of the protection forest and 18% of the polygon overall.

In 2024, we installed cameras at 73 stations and ran them from May–November; 68% of the stations were in lowland and hill forests. For the 2024 sessions, average trap spacing was 1.51 km, and the extra 14 stations expanded the trap array to 600 km². Land cover in the 2024 polygon was comprised of 50% protection forest, 36% production forest, and 14% farming areas. Intact forest comprised 18% of the protection forest, and 9% of the polygon overall.

We completed surveys comprised of two 90-day sampling periods (hereafter sessions) and two 180-day sampling sessions. The 90-day time frame is commonly used in tiger capture-recapture studies to minimize the potential for violating the key assumption of population closure, which implies that the study population does not experience change (e.g., births, deaths, immigration, and emigration) during the study period. Given the 10–15 year lifespan of wild tigers, sampling over short durations of the standard 90-day sessions increases the likelihood of demographic closure (Sunquist, 1981; Karanth and Nichols, 2017). However, studies of more sparsely distributed populations (such as tigers in Sumatran rainforests) may require extended sampling to obtain adequate captures and recaptures (Dupont et al., 2019; Harmsen et al., 2020). Thus, we used the 180-day sessions to provide a clear basis for comparison.

2.3 Data analysis

A single observer, with 20 years of experience identifying individuals of marked animals from camera-trap images, identified tigers based on visual analysis of their unique stripe patterns (Figure 1). To test reliability of the identification, a second observer analyzed a random subset of 40% of the tiger images. We focused on side flanks and hind legs because these positions enabled more reliable identification. We assigned sex to tigers based on the presence of visible genitalia.

We compiled encounter histories for all tigers photo-captured at camera-trap locations using 1-day sampling occasions over two sampling sessions of 180 days, subsampling into two 90-day sessions.

In R v4.5.0, we used the spatially-explicit capture-recapture (SECR) package to obtain estimates of tiger density (D) based on spatial encounter data of individuals. The density estimates are based on the number of individuals photo-captured, the frequency at which they are photo-captured, and distances they move within the trap array during the sampling session (Royle et al., 2013). The SECR package, which follows a maximum-likelihood framework, also integrates detections of individuals across multiple cameras to estimate an “activity center” for each animal. Detection is modeled as a decreasing function of distance between an animal’s activity center and a given trap (Efford, 2024). The first input file for SECR included information (UTM coordinates) on trap locations and a matrix indicating the functional status of the trap: active (1) or inactive (0) on each occasion. The second file contained information on individual tigers photo-captured including the occasion (1–90 and 1–180 for the standard and extended sessions) and camera (detector) of captures.

These captures (observations) are assumed to be Bernoulli (binary) outcomes:

$$y_{ij,k} \sim \text{Bernoulli}(p_{ij,k})$$

where $p_{ij,k}$ is the probability of encountering individual i in trap j and occasion k , which is dependent on the distance between the trap location (x_j) and the activity center (s_i) of the individual, as follows:

$$p_{ij,k} = p_0 \times e^{-(1/2\sigma^2)d(x_j,s_i)^2}$$

Besides densities, SECR estimates detection probability (g_0) and sigma (σ), a spatial scale parameter that indexes animal movements and is related to the radius of an individual’s home range size (Efford, 2024). Accurate estimation of σ , which is based on captures of individuals at different locations across the camera-trap array, is dependent on adequate spatial recaptures that sufficiently sample the animals’ movement (Royle et al., 2013). If the number of sampled individuals remains constant between sessions but they exhibit greater movements, densities generally decrease. If, on the other hand, there are more individuals photo-captured between sessions, but their movements remain similar, densities would be expected to increase. This inverse relationship between densities and σ is consistent among camera-trap studies and validated by telemetry data (Sharma et al., 2010; Sunarto et al., 2013; Hadi et al., 2025).

We began the model selection process by using Akaike’s Information Criterion corrected for small sample size (AIC_c) to compare two detection functions (HN=half-normal and EX=negative exponential) that best fit the observed data. We did not consider the hazard rate (HR) detection function because it requires an extra parameter and is recommended only for study areas fully surrounded by natural or artificial boundaries (Efford, 2025), conditions inapplicable to ours. Generally, density estimates are insensitive to the specific detection function (Efford et al., 2009). However, estimates of σ – which serves as a metric of home range size (Royle et al., 2013) – will vary significantly depending on use of the HN or EX functions.

We fitted a null model ($D \sim 1$, $g_0 \sim 1$, $\sigma \sim 1$) with two separate detection functions: HN and EX. The null model assumes uniform distribution of activity centers throughout the region of interest, known as the state space (S) (Royle et al., 2013):

$$s_i \sim \text{Uniform}(S).$$

In total, our candidate set of models included the null model ($D \sim 1$, $g_0 \sim 1$, $\sigma \sim 1$) and a local trap response model that considered an individual’s previous detection at a specific site ($D \sim 1$, $g_0 \sim bk$, $\sigma \sim 1$). The bk predictor assumes that the animal responds differently at site-specific traps after first capture (Efford, 2024). We did not use white-flash cameras nor did we use attractants at camera stations. Therefore, we did not expect any direct behavioral response to placement of our cameras per se. Trap-specific behavioral responses are generally associated with baits or lures used to attract animals (Royle et al., 2011). However, it is plausible that cameras may have been unknowingly placed near

microhabitat features favored by individual tigers (e.g., a den for sheltering cubs or a favored hunting spot near a saltlick), thereby affecting influence of the *bk* predictor.

Estimates of tiger home range size and ranging behavior vary considerably between males and females (Smith, 1993; Simchareon et al., 2014); these differences affect capture probabilities and therefore warrant sex-specific analyses. To account for these important differences between sexes and reduce potential for biased estimates, we ran separate analyses for female and male densities.

To define the state space for our study area we used the function “suggest.buffer,” which resulted in recommended buffer widths of 8.1–9.9 km for females and 15–16 km for males in the 2023 sampling session. For the 2024 sampling sessions, when we expanded the trap array to 600 km², the recommended buffer widths were 8.8–9 km for females and 14.7–17 km for males. The resulting state space contained sampling areas of 1,560 km² in 2023 and 2,676 km² in 2024; these areas represent 6% and 10.3% of the entire Leuser Ecosystem. The state space must be sufficiently large to include the activity centers of all tigers exposed to detection on the camera-traps (Royle et al., 2013).

For sympatric carnivores, prey, and humans, we estimated naïve occupancy based on the proportion of cameras where a species or person was detected. We also calculated a relative abundance index (RAI) for each as the number of independent detections per 100 camera trap-nights. For estimating species-habitat relationships, RAI can be an informative state variable to guide management (Karanth and Nichols, 2017). Detections were considered independent if photographs taken at the same camera-trap location were separated by ≥ 60 minutes. Humans carrying firearms were categorized as “hunters” and unarmed humans were classified as “villagers.” Rangers were distinguished based on their uniforms and use of 65–80-L hiking backpacks, both of which are not worn by hunters and villagers.

3 Results

Our study accumulated 15,746 trap nights (TN) and amassed 318 Sumatran tiger photographs, of which 282 (88.7%) were deemed sufficiently clear by both observers to enable individual identification. Based on this sample, our analysis of unique stripe patterns identified 27 adult tigers—14 females, 12 males, and 1 individual of unknown sex (Table 1). During the 2023 90-day sampling session, we documented three distinct sets of cubs (Figure 2). One pair of male cubs dispersed and both individuals were photographed as adults in 2024.

Tigers were detected by 34 of the 53 (64%) cameras in 2023 and by 38 of the 64 (59%) cameras in 2024. Six of the females (43%) and three of the males (25%) were photographed during the first and last months of our surveys, exhibiting tenures of ≥ 18 months throughout the study. In contrast, four of the females (29%) and five of the males (42%) were photo-captured \leq three times throughout the sampling.

Comparing the sexes, female detection probabilities (g_0) were ~ 2 times higher than males in the 2023 90-day sampling sessions but detection probabilities were nearly identical between the sexes

during the 180-day sampling sessions. Detection probabilities declined by 50% for both sexes in 2024 as the polygon doubled in size, encompassing 2.1 times greater proportion of production forest: g_0 of female tigers were 0.046 (0.016) in 2023 and 0.024 (0.009) in 2024. Comparing the sampling sessions, female g_0 were 54–63% lower in the 180-day sessions while male g_0 were similar during both sessions.

Between sexes, estimates of female densities were consistently higher among sampling sessions, ranging from 0.92 (SE 0.34) in the 2024 180-day session to 1.80 (0.59) tigers/100 km² in the 2023 90-day session (Tables 2, 3). Estimates of male densities were more precise, ranging from 0.33 (SE 0.16) in the 2024 90-day sampling to 0.61 (0.29) tigers/100 km² in the 2023 90-day session (Figure 3).

3.1 Estimates of female densities and movements

For the 90-day sessions, detection rates of individual female tigers ranged from 1–12 (mean = 5.2) and from 1–9 (mean = 2.3) during the 2023 and 2024 sessions, respectively. Four of the females were detected only once during both years. For the 180-day sessions, detection rates of individual female tigers ranged from 1–15 (mean = 7.9) and from 1–13 (mean = 6) during the 2023 and 2024 sessions, respectively. Two of the females were detected only once during the longer session in 2023 and, in 2024, one female was detected only once.

Based on AICc, the null models with the EX detection function were the highest ranked for the female tiger data from both 90-day sessions (Table 2). However, for the 2023 180-day session, the best fit model allowed g_0 to vary by behavioral response (*bk*). For the 2024 180-day session, the best fit model was the HN detection function that allowed g_0 to vary by behavioral response (*bk*). However, we also report estimates of σ from the model containing the HN detection function because it was within 2 Δ AIC of the top-ranked model.

Estimated female densities for the 90-day sessions were 1.80 individuals/100 km² (95% confidence interval 0.96–3.36) in 2023 and 0.96 individuals/100 km² (95% confidence interval 0.47–1.98) in 2024. For the 180-day sessions, estimated female densities were 1.74 individuals/100 km² (95% confidence interval 0.97–3.14) in 2023 and 0.92 individuals/100 km² (95% confidence interval 0.46–1.85) in 2024.

The σ parameter in the SCR EX model indicated the movements of female tigers ranged from 1.44 ± 0.20 to 2.06 ± 0.41 km in the 90-day sessions and 1.62 ± 0.20 km in the 2023 180-day session. For the 2024 180-day session, the HN model indicated movements of 2.4 ± 0.24 km.

3.2 Estimates of male densities and movements

Detection rates of individual male tigers ranged from 2–10 (mean = 5.7) and from 1–15 (mean = 4.8) during both 90-day sessions. All males were detected at least twice during the 2023



FIGURE 1

Determining identification of individual tigers based on stripe patterns on the flank and hind leg. This male tiger was photographed during both sampling years in the Leuser Ecosystem.

sampling while four of the males were detected only once in 2024. During the 180-day sessions, these values ranged from 2–17 (mean=10.2) and from 1–22 (mean =7.9). All males were detected at least twice in 2023 but three of the males were detected only once during the longer sampling in 2024.

For male tigers in both sessions of 2023, the null models with the EX function were the highest ranked. For male tigers in both 2024 sessions, learned behavioral response influenced capture probability, with the local trap response model (*bk*) ranking highest.

Estimated male densities during the 90-day sessions were 0.61 individuals/100 km² (95% confidence interval 0.25–1.48) in 2023 and 0.56 individuals/100 km² (95% confidence interval 0.27–1.16) in 2024. For the 180-day sessions, male densities were 0.50 individuals/100 km² (95% confidence interval 0.22–1.16) in 2023 and 0.41 individuals/100 km² (95% confidence interval 0.20–0.84).

The σ parameter in the SCR EX model indicated the movements of male tigers ranged from 2.68 km \pm 0.57 km to 4 km \pm 0.87 km in the 90-day sessions and 2.62 km \pm 0.38 to 4.23 \pm 0.70 km in the 180-day sessions.

TABLE 1 Details of Sumatran tiger camera-trap surveys in the Leuser Ecosystem, 2023–2024.

Sampling period	No. sampling days	Sampling mid-point	Final no. paired CT locations	Effort (TN)	Trap array (km ²)	Female indiv.	Female photo-captures (recaptures)	Male indiv.	Male photo-captures (recaptures)	Cumulative no. of tigers photo-captured
2023 (90-day)	90	5-Sep-23	53	4,055	308	11	57 (46)	6	34 (28)	17
2023 extended*	180	20-Sep-23	53	7,386	308	12	95 (83)	6	61 (55)	18
2024 (90-day)	90	7-Jul-24	64	4,853	600	9	34 (25)	9	43 (34)	26
2024 extended**	180	23-Aug-24	64	8,360	600	9	54 (45)	9	71 (62)	27

*Cameras from six stations lost: Stolen (n=5 stations) and malfunctioned (n=1). Camera sampling further interrupted after damage by elephants (n=3), damage by sun bear (n=1), and tree branch interference (n=1).
**Cameras from nine stations lost: Stolen (n=5 stations), malfunctioned (n=3), and destruction by elephants (n=1). Camera sampling further interrupted after damage by elephants (n=2), damage by sun bear (n=1), tampering by macaques (n=1), and tree branch interference (n=1).

3.3 Naïve occupancy and relative abundance of prey and sympatric carnivores

During the 90-day sampling sessions¹, we recorded at least one of the four ungulate prey species at 94% and 100% of the camera stations in 2023 and 2024. Cumulatively, sambar, wild pig, serow, and muntjac were detected at 24, 38, 4, and 50 camera stations, resulting in naïve occupancies of 0.45, 0.72, 0.08, and 0.94, respectively (Table 4). The highest RAI was recorded for muntjac (16.46 captures/100 TN) and the lowest for serow (0.08/100 TN). RAI for sambar and wild pig was 1.61 and 3.88 captures/100 TN.

Two competing carnivores that have overlapping prey preferences with tigers, the Sunda clouded leopard and dhole, were detected 20 and 9 times during the 90-day sessions. Naïve occupancies for clouded leopard (0.07) and dhole (0.09) were >five times lower than those for Sumatran tiger.

3.4 Human detection rates on cameras

Hunters and villagers were detected more frequently than rangers during all sessions. Across stations, we recorded rangers at 13% while hunters and villagers were detected at 21% and 43%. Overall, the RAI for rangers was 0.54 detections/100 TN. The RAI for hunters and villagers was 0.63 and 2.62 detections/100 TN.

4 Discussion

We estimated densities of Sumatran tigers based on the most robust dataset of the species collected to date, comprised of 282 photographs of 27 individuals collected over two 3-month and two 6-month subsampled sessions between July 2023–November 2024. Our results, nearly triple the average number of records obtained during previous 90-day Sumatran tiger surveys, are testament to a combination of factors including, foremost, successful efforts of the Aceh government to maintain critical tiger habitats in the form of extensive forest cover. Amidst intense pressures from agricultural and extractive industries, Aceh remains nearly 60% forested and prey populations are among the healthiest in Sumatra (Global Forest Watch, 2021; Figel et al., 2024). Our results further highlight the importance of conducting strategic reconnaissance surveys and use of durable professional-grade camera-traps installed in collaboration with highly skilled forest guides.

To place our dataset in greater context, the average results from published Sumatran tiger 90-day SCR surveys (n=18) are 27.67 photo-captures and 6.83 individuals. Recaptures are generally unreported in the Sumatran tiger camera-trap literature. Only three studies (17%), all in Bukit Barisan Selatan National Park, documented ≥ 10 tigers in any single survey (Luskin et al.,

1 Results for the 180-day sampling sessions are presented in Supplementary Table 1.



FIGURE 2
A resident female Sumatran tiger grooming one of her two large male cubs in the Leuser Ecosystem in October 2023. The cub dispersed and was recorded in June 2024 at a straight-line distance of 6.2 km from the site of this photograph.

TABLE 2 Parameter estimates from two detection functions for male and female Sumatran tiger density estimates in the Leuser Ecosystem, 90-day, 2023–2024.

Sex	Parameter	Half normal	Negative exponential
Male_2023	Density (SE)	0.59 (0.29)	0.61 (0.29)
	95% CIs of density	0.24-1.48	0.25-1.48
	g ₀ (SE)	0.008 (0.003)	0.022 (0.009)
	σ (SE)	4,558 m (867)	2,683 m (574)
Male_2024	Density (SE)	0.58 (0.23)	0.56 (0.22)
	95% CIs of density	0.27-1.22	0.27-1.16
	g ₀ (SE)	0.005 (0.002)	0.011 (0.005)
	σ (SE)	5,957 m (1,057)	3,998 m (869)
Female_2023	Density (SE)	1.90 (0.62)	1.80 (0.59)
	95% CIs of density	1.02 - 3.54	0.96-3.36
	g ₀ (SE)	0.011 (0.004)	0.046 (0.016)
	σ (SE)	2,526 m (232)	1,438 m (203)
Female_2024	Density (SE)	1.03 (0.39)	0.96 (0.37)
	95% CIs of density	0.50-2.12	0.47 - 1.98
	g ₀ (SE)	0.009 (0.003)	0.024 (0.009)
	σ (SE)	3,157m (539)	2,062 m (409)

Values for the highest-ranked detection function are marked in bold.

TABLE 3 Parameter estimates from two detection functions for male and female Sumatran tiger density estimates during the 180-day sessions in the Leuser Ecosystem, 2023–2024.

Sex	Parameter	Half normal	Negative exponential
Male_2023	Density (SE)	0.52 (0.24)	0.50 (0.22)
	95% CIs of density	0.22-1.22	0.22-1.16
	g ₀ (SE)	0.010 (0.002)	0.026 (0.007)
	σ(SE)	4,351 m (561)	2,617 m (382)
Male 2024	Density (SE)	0.42 (0.16)	0.41 (0.15)
	95% CIs of density	0.20-0.86	0.20-0.84
	g ₀ (SE)	0.005 (0.001)	0.011 (0.004)
	σ (SE)	6,601 m (947)	4,227 m (697)
Female 2023	Density (SE)	1.77 (0.53)	1.74 (0.53)
	95% CIs of density	0.99 - 3.15	0.97-3.14
	g ₀ (SE)	0.009 (0.002)	0.025 (0.008)
	σ (SE)	2,657 m (222)	1,623 m (196)
Female 2024	Density (SE)	0.94 (0.33)	0.92 (0.34)
	95% CIs of density	0.48-1.84	0.46-1.85
	g ₀ (SE)	0.014 (0.003)	0.015 (0.006)
	σ (SE)	2,421 m (237)	1,929 m (337)

Values for the highest-ranked detection function are marked in bold.

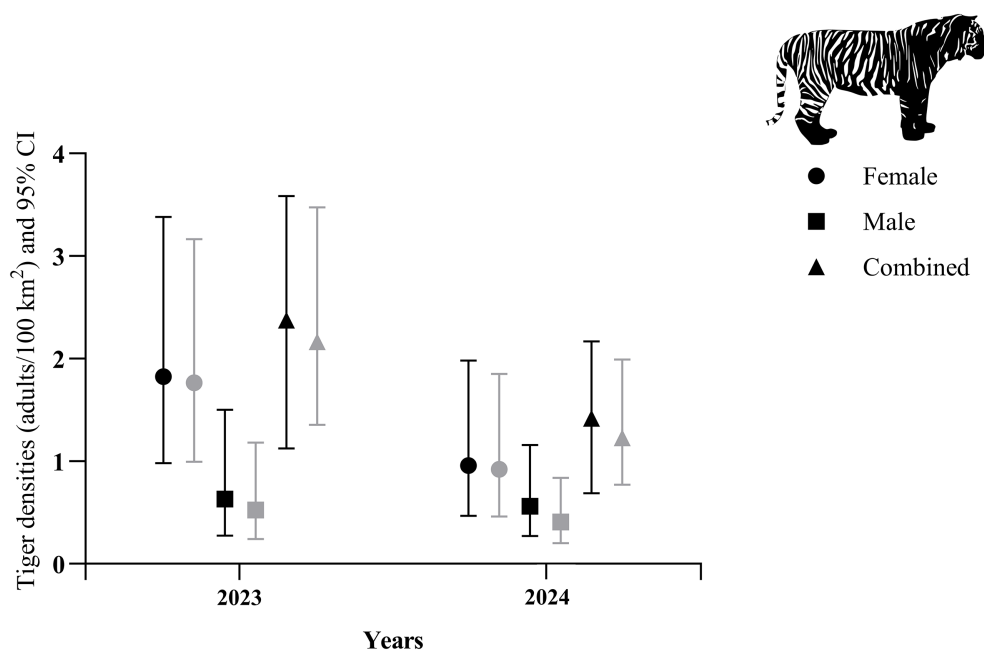


FIGURE 3

Densities of male and female Sumatran tigers in the Leuser Ecosystem, 2023–2024. Data are separated by 90-day (black symbols) and 180-day (gray symbols) sampling sessions. The vector graphic is from phylopic.org.

2017; Pusparini et al., 2018) and five of the studies (28%) documented ≤ 5 individuals (Sunarto et al., 2013; Hadi et al., 2025). Sparse datasets comprised of captures from fewer than 5 individuals regularly produce imprecise and unreliable estimates unsuitable for monitoring tiger population trends (Karanth and Nichols, 2017).

Our results build on the importance of estimating female demographic parameters, which hold crucial importance for tiger population vitality (Harihar et al., 2020). Survival and fecundity of breeding females are among the most important factors determining the species' population growth (Smith, 1993; Harihar et al., 2020). Higher female densities are reflective of healthy tiger social system dynamics and higher quality habitats (Sunquist, 1981; Smith, 1993; Bisht et al., 2019). In landscapes with ample prey, female tigers can raise 3 or 4 litters – about 6–10 cubs – during territorial tenures lasting, on average, 8–10 years (Sunquist, 1981; Harihar et al., 2020). These ecological traits have shaped global tiger conservation strategies through, for example, the identification of source sites, whereby breeding females produce a surplus of tigers that disperse from sufficiently protected natal territories (Harihar et al., 2018).

Despite their importance for revealing key demographic parameters such as survival, recruitment, tenure and population growth rate, long-term studies – informed by continuous *yearly* sampling (Duangchantrasiri et al., 2024) – are lacking on Sumatran tigers. These data can only be obtained with durable professional camera-traps capable of withstanding yearly sampling in humid tropical rainforests. Many Sumatran tiger camera-trap surveys appear to favor the use of Bushnell Trophy cams (e.g., Luskin et al., 2017; Saputra et al., 2025), a recreational-grade camera-trap prone to malfunctioning and breakdown (Newey et al., 2015). The frequency

of grainy and overexposed images produced by these cameras (e.g., Figure 2 in Saputra et al., 2025) may enable *species* identification for presence-absence surveys but *individual* identification is frequently hampered by the camera's infrared flash which does not adequately “freeze” the animal in motion (McHenry et al., 2025). The result is a poorer dataset comprised of excessive proportions of blurry or overexposed images that inhibit identification of individual tigers. As further evidence of the low durability and various limitations of recreational-grade cameras, tiger researchers in Thailand structurally modified the Bushnell models (Simasathien et al., 2015).

The relatively high number of male and female, including breeding female, tigers we recorded are suggestive of an adequate prey base in Leuser. Lower elevations generally support greater populations of prey, which is one of the main predictors of tiger abundance (Karanth et al., 2004; Simchareon et al., 2014). Two recent studies of Sumatran tigers and their prey in Aceh independently documented negative correlations between sambar habitat use and elevation (Figel et al., 2024; Hadi et al., 2025). Wild pig and sambar occupied only 10% of the sampled area in Gunung Leuser National Park (Hadi et al., 2025), a mountainous protected area where ~88% of the landmass is comprised of habitats exceeding 600 meters in elevation (Supriatna and Margules, 2022). In stark contrast, we documented naïve occupancy rates at least four times greater for sambar and seven times greater for pig in our lower elevation study area. Maintaining these prey populations, which are vulnerable to diseases such as African Swine Fever (Luskin et al., 2023), will be critical for tiger conservation in Leuser.

Among all Sumatran tiger SCR density estimates to date, only in an “Intensive Protection Zone” patrolled by 12 ranger teams in a protected area of south Sumatra, did tiger density (2.80 individuals/100 km², 95%

TABLE 4 Camera-trap derived (90-day sessions) naïve occupancy and relative abundance indices (RAI) for Sumatran tigers and competing carnivores, main prey species, and humans in the Leuser Ecosystem, Sumatra, Indonesia, 2023 and 2024.

Target species/ human categories	Combined			2024			2023		
	Captures	Naïve	RAI	Captures	Naïve	RAI	Captures	Naïve	RAI
Tiger	192	0.53	2.11	86	0.59	1.57	106	0.64	2.50
Dhole	9	0.09	0.10	7	0.11	0.14	2	0.04	0.05
Clouded leopard	20	0.07	0.22	3	0.05	0.06	17	0.08	0.40
Sambar	146	0.45	1.61	73	0.34	1.50	73	0.40	1.72
Wild pig	353	0.72	3.88	180	0.78	3.71	173	0.66	4.09
Muntjac	1,496	0.94	16.46	883	0.97	17.16	613	0.94	14.47
Serow	7	0.08	0.08	4	0.06	0.08	3	0.06	0.07
Humans									
Rangers	49	0.13	0.54	35	0.13	0.72	14	0.12	0.33
Hunters	57	0.21	0.63	39	0.22	0.80	18	0.17	0.43
Villagers	238	0.43	2.62	133	0.44	2.74	105	0.38	2.48

Total sampling effort was 4,235 and 4,853 trap nights in 2023 and 2024.

CI 1.7–4.4) (Pusparini et al., 2018) exceed our highest estimate (2.35 individuals/100 km², 95% CI 1.10–3.56). The persistence of tigers and their prey in Leuser will depend on consistent patrolling by trained rangers. Effective ranger patrols deter poaching and logging, both of which are generally more intense in lowland areas due to their greater accessibility and susceptibility to human disturbances (Supriatna et al., 2017; Lubis et al., 2023). Agricultural conversion in lowland areas has also triggered disproportionate rates of human-tiger conflict, one of the main threats to Sumatran tigers (Figel et al., 2023a).

At present, our study area is patrolled by rangers from two organizations: Forum Konservasi Leuser and Hutan Harimau. Combined density of these patrollers in our study area is approximately 2.5 rangers/100 km² which, although better than most areas of Sumatra, is still ~four times lower than required target numbers to maintain tiger populations in rainforests (Figel et al., 2024; Gray et al., 2024). Besides patrols, the rangers are imperative for executing camera trap surveys (Brackzkowski et al., 2024).

To increase alignment with the species' ecology, our data on tiger movements from Leuser could inform adjustments of standardized Sumatran tiger survey protocols. Following advancements in optimal camera survey designs for estimating density, which recommend trap spacings of 1.5–2.5 times σ (Royle et al., 2017), the size of sampling polygons for Sumatran tigers could be doubled by separating camera stations at distances of 4–6 km, rather than the 2–3 km spacing used currently.

In SCR survey designs, there is a compromise between obtaining sufficient recaptures and robust sample sizes of individuals (Royle et al., 2013). Our results are consistent with recommendations to prioritize increasing the latter. In a review of 137 studies that combined camera-trapping with SCR-based density estimation, the number of individuals in the sample was the single most important variable for producing precise density estimates (Palmero et al.,

2023). Thus, achieving higher precision for Sumatran tiger density estimates will inevitably require increasing the spatial extent of sampling particularly since male home ranges are almost exclusively nonoverlapping and female home ranges exhibit limited overlap (Simchareon et al., 2014). This aspect of tiger ecology may also explain how temporal extension of sampling yields diminishing returns in precision, as tiger territoriality dictates their movements in the sampling polygon (Smith et al., 1987; Chanchani et al., 2018).

The 180-day sessions also increase the likelihood of including transients in the analysis, which inflates density estimates, lowers detection probability, and severely biases estimation of σ (Pradel et al., 1997; Larrucea et al., 2007; Palmero et al., 2023). These transients, i.e., non-resident animals without established home ranges, can comprise at least 18% of tiger populations (Karanth et al., 2006). Including these transients also increases potential for violation of closure, further decreasing precision of estimates (Kendall, 1999). We recognize the limitations of identifying transients from camera-trap data but the single detections for 17% of the females and 22% of the males suggests that the population was not closed to immigration.

The dilemma of transients provides further justification for increasing the size of the trap array and sampling over shorter periods. If there are resource restrictions such as insufficient cameras, the study area can be subdivided into 2–4 blocks of trapping stations with cameras in each block run for 2–4 weeks (Royle et al., 2009). Then cameras are moved to the next block for another 2–4 weeks and the process repeated until all blocks are sampled. The number of blocks and sampling duration will depend on availability of resources, terrain of the study area, densities of the tiger population, among other factors. In SCR analyses, capture data from a “block” trap design can be used without issue because the data matrix specifies trap status (e.g., active or inactive) during each sample (Karanth and Nichols, 2017; Efford, 2024).

Interestingly, after our polygon doubled in size in 2024, we detected 18% fewer females and their recaptures declined by 46% while the number of males detected increased by 33% and their recaptures increased by 18%. We believe there are at least two plausible explanations for this discrepancy. First, females in Leuser appear more reliant on intact forests, consistent with breeding female dependence on inviolate forests at tiger recovery sites in India (Harihar et al., 2020). As the polygon encompassed 2.1 times greater proportion of disturbed production forest when it expanded to 600 km² in 2024, the proportion of intact protected forest decreased from 18% to 9% of the overall polygon. Secondly, male large carnivores generally exhibit greater tolerance for fragmented areas as they commonly increase their movements and home range sizes in disturbed landscapes where essential resources are more scarcely distributed (Smith, 1993; Morato et al., 2016; Snider et al., 2021). Movements of males were ~1.5 greater in 2024 while those of females were 1.25–1.43 greater.

Although still widespread in Leuser, Sumatran tigers are intensely persecuted in the ecosystem (Figel et al., 2023b). From 2010–2019, law enforcement staff in Leuser responded to 26 cases of tiger trafficking and patrol teams removed 780 snares, which entangled at least nine tigers (Hadi et al., 2025). We observed signs of incursions, including armed hunters captured on our cameras, throughout our study area. Besides illegal logging activity, some people enter the protected forests to fish, collect honey and, of concern for tiger conservation, to hunt sambar and muntjac. Sumatran tigers may be especially vulnerable to human-induced prey depletion because, even in the best conditions, their rainforest habitats do not support the prodigious ungulate biomass found in the savannahs, grasslands, and deciduous forests of mainland Asia (Karanth et al., 2004; Steinmetz et al., 2021).

5 Conclusions

The number of our records and the balanced sex ratio are indicative of an important breeding population of Sumatran tigers in Leuser. With maintained protection, the population could serve as a key source for adjacent forests where tiger status is more precarious (Figel et al., 2024). Our study further reveals the disparity in tiger densities between Gunung Leuser National Park and our study area that lies outside the National Park system. We provide evidence that supports the need for increasing spatial extent of Sumatran tiger surveys, maintaining shorter sampling durations, and for sampling of intact hill and lowland forests outside National Parks. Additional surveys, which deploy durable camera equipment and use skilled rangers guided by reconnaissance, are likely to reveal critical habitats for Sumatran tigers in these areas.

Data availability statement

The datasets presented in this article are not readily available because: data sharing for this critically endangered species will take place selectively on a case-by-case basis following agreement with

partner data owners from DLHK. Requests to access the datasets should be directed to joe.figel@fulbrightmail.org.

Ethics statement

The animal study was approved by Ethical Clearance # 182/KE.02/SK/09/2023 from Badan Riset dan Inovasi Nasional (BRIN), Indonesia. The study was conducted in accordance with the local legislation and institutional requirements.

Author contributions

JF: Writing – original draft, Supervision, Formal Analysis, Writing – review & editing, Data curation, Software, Methodology, Conceptualization, Resources, Project administration, Visualization, Validation, Funding acquisition, Investigation. MA: Funding acquisition, Writing – review & editing, Supervision, Resources, Visualization, Project administration. KK: Writing – review & editing, Supervision, Investigation, Project administration. D: Supervision, Project administration, Investigation, Writing – review & editing. Suh: Investigation, Writing – review & editing. Sup: Investigation, Writing – review & editing. ZA: Investigation, Writing – review & editing. MA: Investigation, Writing – review & editing. KA: Project administration, Investigation, Writing – review & editing. MP: Supervision, Conceptualization, Project administration, Investigation, Writing – review & editing. Re: Visualization, Investigation, Writing – review & editing. Rh: Investigation, Writing – review & editing. IH: Investigation, Writing – review & editing. Ri: Investigation, Writing – review & editing. I: Investigation, Writing – review & editing. H: Investigation, Writing – review & editing. IY: Supervision, Writing – review & editing. EH: Supervision, Writing – review & editing.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fcsc.2025.1691233/full#supplementary-material>

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